

Introduction of the American grey squirrel (*Sciurus carolinensis*) in Europe: a case study in biological invasion

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The introduction of the eastern grey squirrel (native to America) in Europe is causing a dramatic decline in the range of the native European red squirrel, due to competition. Grey squirrels compete with the native species mainly for food; furthermore, they can maintain and spread a poxvirus, which causes a lethal disease in red squirrels in Britain. According to some modelling scenarios, grey squirrels will spread from Italy to France and Switzerland in the next 20–30 years, and to a large part of Eurasia in the long term. This would represent a serious threat for the survival of the red squirrel throughout its range. This case study of biological invasion suggests that the risks posed by the introduced species may be minimized with a reduction in animal trade between countries and using a procedure of risk-assessment for every imported species.

Keywords: Alien species, competition, damage, grey squirrel.

Introduction

THE introduction of species in new areas is considered one of the most important threats to biodiversity¹. Introduced species may interact with native ones through different ecological processes that include competition, predation, parasitism, disease vectoring and hybridization^{1,2}. A well-documented case of competition by an invasive alien species is the replacement of the native Eurasian red squirrel (*Sciurus vulgaris*) by the introduced eastern grey squirrel (*Sciurus carolinensis*) on the British Isles and in parts of northern Italy^{3,4}. However, the grey squirrel is only one of the many squirrel species introduced worldwide. Long⁵ reported more than 20 introduced species of Sciuridae, with hundreds of translocations across the world, most of them successful. The impacts recorded include damage to vegetation, competition as well as other effects on the native species.

The aim of this article is to review the history and results of grey squirrel introductions in Europe, the impact that the species has on biodiversity and human activities, describe how it is managed and report future risks for the red squirrel. This will be presented as a case study on

biological invasions to discuss some elements of a general policy toward invasive alien species.

The species

The eastern grey squirrel is a North American species that is naturally distributed from the Gulf of Mexico to the southern part of Quebec and Ontario. It is a medium-sized tree squirrel (body length 380–525 mm, adult weight 300–710 g)⁶ that feeds mostly on large seeds, flowers, buds, fruits, fungi, some insects and occasionally bird eggs. Grey squirrels are more common in mature continuous woodlands, with higher densities in areas with tree species that provide winter-storable foods. Density in the native range is usually < 3 individuals ha⁻¹, but could increase to 16 ha⁻¹ in small woodlots and 21 ha⁻¹ in urban areas⁶. In Europe, in an oak wood in England, the mean density was 8.5 ha⁻¹ (range 3–18 ha⁻¹)⁷; a peak of 18 ha⁻¹ was also recorded in an urban park in Italy⁸.

The Eurasian red squirrel is widely distributed over the northern Palearctic, from the Iberian Peninsula to the eastern coast of Russia and the island of Hokkaido in Japan⁹. In Europe, it is the only native tree squirrel. The adult dimensions are: body mass 280–380 g, body length 180–210 mm. The red squirrel occurs in broadleaf, conifer and mixed forests, woodland fragments and suburban parks, from sea-level to the upper tree-line in the mountains. Density is usually <1 individual ha⁻¹, with peaks up to 1.6 ha⁻¹ in mixed broadleaf woodlands⁹.

The history of introductions

Grey squirrels have been introduced in Australia, South Africa, Great Britain, Ireland and Italy⁵. In Europe¹⁰, the grey squirrel was introduced into Great Britain from 1876 until 1929, into Ireland¹¹ in 1913, and into Italy four times between 1948 and 1994, with one failure¹². At present, the range of the grey squirrel covers most of England and Wales, the southern part of Scotland and part of Ireland^{3,11,13} (Figure 1). In Italy, the species is present in the northwestern part of the country (Figure 2). The largest population covers an area of about 900 km² in Piedmont, another one is present in an urban area along the coast in Liguria, and the last in the woodlands along the

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Ticino river in Lombardy¹⁴. In all these countries the rapid spread of the grey squirrel coincided with a dramatic decline in the range of the native red squirrel^{3,4,14}.

Population development

Propagule pressure (i.e. number of animals released) is one of the characteristics that is reported to be a limit to the establishment of many species¹⁵. The grey squirrel adapted very well to European habitats and on several occasions viable populations originated from the release of few individuals. In the British Isles, grey squirrels were released on 31 occasions and in 24 cases the population increased in size; in 11 of these cases, less than ten animals were released¹⁰. In Ireland, a single release with six pairs of squirrels was successful and now the species is widespread there¹¹. In Italy, three out of four introductions with 4–6 animals were successful¹².

The pattern of grey squirrel spread in England was described as random dispersal, with occasional major advances¹⁶. The recorded mean rate of spread was

7.7 km yr⁻¹, while the two-dimensional diffusion coefficient¹⁷ was 17.9 km² yr⁻¹. In Ireland, these values were 1.94 km yr⁻¹ and 1.15 km² yr⁻¹ respectively¹¹. Comparable data are not available for Italy, but estimations from range size and years of presence gave a range increase¹⁴ of 17.2 km² yr⁻¹.

Interspecific competition

Grey squirrels use the same food resources as red squirrels, and have similar space use and activity patterns, while there is no evidence of interference competition in the form of overt aggression^{18,19}. However, grey squirrels are able to digest acorns more efficiently than can red squirrels and feed on these seeds more intensively than do the native species^{19,20}. Furthermore, grey squirrels pilfer many seeds scatter-hoarded by the congener, which are more important for successful overwintering²¹. The competition for food results in reduced body growth, lower juvenile recruitment and reproductive success, which cause a decline in population densities in red squirrels and local extinctions¹⁹.

In Great Britain, competitive exclusion between these two species is also mediated by a squirrel poxvirus (SQPV): grey squirrels act as a vector of the virus, which causes a lethal disease in red squirrels²². Replacement of the red squirrel by the grey squirrel could be 17–25 times faster in the presence of the disease²³. Seroprevalence of SQPV in the grey squirrel is high in England and Wales, and some infected grey squirrels have been recently discovered on the border with Scotland²⁴. In Ireland, there are some grey squirrels seropositive for SQPV, but there are no confirmed cases of disease in red squirrels, while in Italy the SQPV has not been recorded at all²⁵.

Other impacts

The grey squirrel frequently causes damage to woodlands and plantations by stripping bark from trees²⁶. Bark-stripping activity degrades timber quality and can facilitate the penetration of insects and fungi. In Italy, damage to poplars, hornbeams and cereal crops has been recorded¹². Damage is most likely to start in areas with high densities of young squirrels, possibly triggered by agonistic behaviour or exploratory feeding behaviour²⁷. There is also evidence that grey squirrels eat sap and damage trees with high phloem volume, suggesting nutritional benefits from such behaviour. In woodlands in the UK, the grey squirrel was estimated to reduce the value of tree crops by around 25% or 10 million GBP, while estimated current annual control cost for timber protection is 3 million GBP²⁸. Bark-stripping of selective tree species could also change the composition of forests or hinder the establishment of new woodlands²⁹. Grey squirrels are also suspected of having negative impacts on woodland birds through nest predation³⁰.

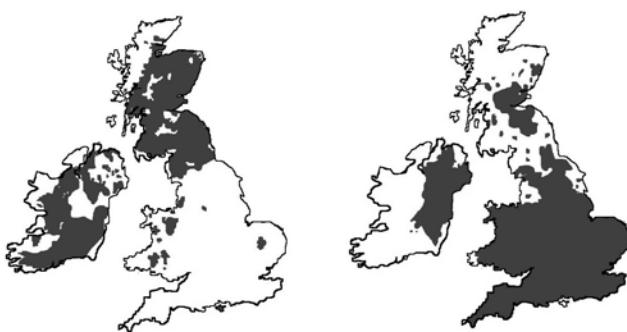


Figure 1. Distribution of red squirrels (left) and grey squirrels (right) in Great Britain and Ireland. Drawn from Forestry Commission (maps 1998, source <http://www.forestry.gov.uk/fr/INFD-69EKTZ>), O'Teagana et al.¹¹ and O'Neill and Montgomery¹³.

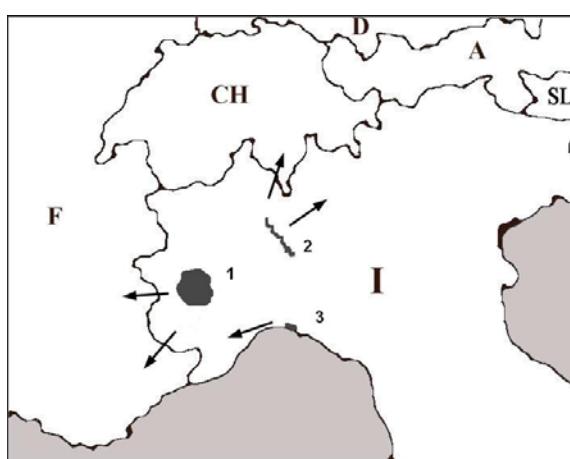


Figure 2. Colonies of grey squirrels in Italy and possible routes of expansion (arrows) to neighbouring countries. 1, Piedmont; 2, Ticino river; 3, Ligurian colonies; I, Italy; F, France; CH, Switzerland; D, Germany; A, Austria and SL, Slovenia.

Modelling future expansion

Computer modelling and simulation have proved to be a valuable tool in predicting the future spread and projected impact of grey squirrels³¹. Spatially explicit population dynamic models (SEPMs) combine a population dynamic model (which considers a species' life-history traits) with a Geographic Information System (GIS) that takes into account the movements of the animals in real habitats. SEPM models have been used to predict future distribution and population size of the grey squirrel, effects of competition between grey and red squirrels, possibility of controlling grey squirrels, and disease spread between the two squirrel species^{25,31–33}.

In Italy, SEPMs have been used to illustrate the potential expansion of the populations in Piedmont³² and along the Ticino river³³. A recent study evaluated the future expansion of the grey squirrel from Italy into neighbouring countries (Bertolino *et al.*, unpublished). In this simulation, two scenarios were investigated considering a period of 100 years since 1996. According to the worse scenario, grey squirrels will reach France and Switzerland within 20–30 years.

Management activities

Introduction of new grey squirrels into Great Britain was banned in 1937 with the 'Grey squirrel prohibition of importation and keeping order'³⁴. A bounty scheme to control the species, operated by the British government in the 1950s, made no significant impact on grey squirrel populations and was considered ineffective³⁴. Grey squirrels are now controlled in the country mainly to reduce damage to trees by cage or kill trapping, shooting or warfarin poisoning³⁵. Small numbers of grey squirrels are also trapped to protect designated red squirrel areas³⁵.

In 1996, a trial eradication of a small population in Italy, implemented to evaluate the efficiency of the removal techniques and to assess the feasibility of a complete eradication, was stopped by a court after the opposition by some radical animal rights groups^{14,36}. After a distribution survey in 1999, the eradication of the Piedmontese population was considered impracticable for logistical, political and social reasons. In 2006, an action plan for the eradication of the grey squirrel population along the Ticino river was proposed to eliminate the risk for Switzerland, but is still under consideration.

A possible new approach that has been proposed as a non-lethal grey squirrel population control measure is reproductive inhibition through immuno-contraception. This technique was investigated in the past³⁷ and is still under discussion for new projects; however, at the moment, this is purely an area of potential research.

Conclusions

The grey squirrel adapted very well to European habitats, invading the areas wherever introduced. In Italy, grey

squirrels have reached the foothills of the Alps in Piedmont and are present in the woodlands along the Ticino river. In a few decades they will manage to cross the borders, entering France and Switzerland. Colonization of large areas in Eurasia will then be only a matter of time and this would represent a serious threat for the survival of the native red squirrel throughout its range. Considering differences in population density and weight of the two species, the replacement of the native species by the American species may change energy flow in woodland ecosystems, with consequences that cannot be yet completely evaluated.

Political concern about the lack of action in Italy has been expressed by the Permanent Commission of the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats), which has produced two recommendations (n. 78 of 1999 and n. 114 of 2005) underlining the necessity to eradicate grey squirrels in Italy in order to stop their further expansion into Europe, and save the native red squirrel from wide-scale extinction.

In a more general context, squirrel species have been introduced worldwide many times, and have often proven to be invasive^{5,12}. In Europe, apart from the grey squirrel, three other introduced species are already established with many populations: *Callosciurus erythraeus*, *Callosciurus finlaysonii* and *Eutamias sibiricus*, all from Asia³⁸; *Atlantoxerus getulus* has been introduced from Morocco into the Canary archipelago that administratively belongs to Spain. In Italy, for example, there are eight populations of three introduced species¹², while in France there are ten populations of *E. sibiricus*³⁹ together with a population of *C. erythraeus*³⁸. These and other populations come from deliberate releases of animals or from escapes from pet shops and private owners.

It is now accepted that the best strategy for preventing the negative consequences caused by biological invasions is based on a hierarchical approach that comprises: (1) prevention of new introductions; (2) in case prevention fails, prompt eradication of the introduced species; (3) when eradication is not feasible, spatial containment and/or a population control². Eradication remains a controversial issue, though many introduced species have been eradicated worldwide⁴⁰. Eradication campaigns of squirrel species are not easy to achieve, mainly due to the dispersal ability of the animals and the necessity to act when populations are still small, but also due to the opposition by a part of the society that is concerned with the costs and the undesired effects of removal techniques. The wide dissemination of more information regarding the value of native species and the threat posed by alien species is thus necessary.

For the future, considering the difficulty in removing established populations, it is important to adopt a preventive strategy. The invasion process can be divided into arrival, establishment and spread. In Europe, squirrels released into the wild established new populations with ease. Thus,

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it is important to reduce the arrival rate of new animals and species. This could be done by working toward a trade restriction between countries where the squirrels are already established, and also by evaluating the threats that new species could pose to European biodiversity. According to a precautionary principle, all species imported in Europe as pets or for other reasons have to be evaluated through a risk-assessment procedure, banning those that may adapt to natural habitats. A similar strategy could apply also to other groups of species that are widely imported.

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