PREDICTION OF THE GREY SQUIRREL SPREAD FROM ITALY INTO ADJACENT COUNTRIES

February, 2006

Bertolino S.[1], Lurz P.W.W.[2], Rushton S.P.[2]

[1] *DIVAPRA Entomology & Zoology, Via L. da Vinci 44, 10095 Grugliasco (TO), Italy*

[2] *IRES, School of Biology, Devonshire Building, University of Newcastle, Newcastle upon Tyne, NE1 7RU, UK*

1. INTRODUCTION

The grey squirrel (*Sciurus carolinensis*) was introduced many times into the United Kingdom and Ireland in the second half of the XIXth century and the first three decades of the XXth century (Gurnell & Pepper, 1993). This species was also released in Italy where now it is present with three populations in Piedmont, Lombardy (along the Ticino), and Liguria (at Genoa Nervi) (Genovesi and Bertolino, 2001; Tattoni *et al.*, in press). In Piedmont the squirrel has been spreading faster in the last decades and the colonisation of the Alps could occur in the near future (Lurz *et al.*, 2001; Bertolino & Genovesi, 2003). The population in Lombardy seems still to have a low density, but the risk of a colonisation of the Ticino valley and of Switzerland is very high (Tattoni *et al.*, in press).
The grey squirrel has negative impacts on the ecosystem and on human activities. In Great Britain, Ireland, and Italy this species is causing the progressive disappearance of the native red squirrel through competition (Gurnell & Pepper, 1993; Wauters *et al*., 1997a; Gurnell *et al*., 2004). A role of a squirrel poxvirus (formerly known as parapox virus) in the replacement has also been suggested (Sainsbury *et al*., 2000). In addition the possibility has been highlighted that grey squirrels may have a negative impact on forest birds, especially on species nesting in cavities (Hewson & Fuller, 2003) but this has not been quantified. In Great Britain the grey squirrel causes heavy damage to forests and tree commercial plantations because of bark-stripping (Dagnall *et al*., 1998). Bark-stripping activity inflicts wounds that degrade timber quality severely and can facilitate the penetration of insects and fungi (Dagnall *et al*., 1998). In Italy, damage to poplars, hornbeams and cereal crops has been recorded (Currado *et al*., 1987).
The replacement of red by grey squirrels that is taking place in northern Italy, will have serious implications for red squirrel conservation in all Europe (Genovesi & Bertolino, 2001; Lurz *et al.*, 2001). Political concern about the lack of action in Italy has been expressed by the Permanent Commission of the Bern Convention, which has produced a specific recommendations (n. 78 of 1999) underlining the necessity to eradicate grey squirrels in Italy in order to stop their further expansion in Europe, and save the native red squirrel from wide-scale extinction (Genovesi & Bertolino, 2001). A new recommendation was approved by the Standing Committee of the Bern Convention in 2005 "Draft Recommendation on the control of the Grey squirrel (*Sciurus carolinensis*) and other alien squirrels in Europe" This recommendation [*urge the authorities of the Ticino valley, in particular the Ticino park, to start without delay an eradication programme on the Grey squirrel, following the guidelines developed by the Istituto Nazionale per la Fauna Selvatica (INFS) and the Italian Ministry of Environment, so as to prevent its expansion to Switzerland and other neighbouring states*].

A spatially explicit population dynamics model (SEPM) has been tested on grey squirrels in Britain (Rushton *et al*., 1997), and used in Italy to evaluate the spread of this species in Piedmont and along the Ticino river (Lurz *et al*., 2001; Tattoni *et al*., 2005). ESI (European Squirrel Initiave) sponsored the present project with the aim to extend the simulation to other European countries. We will use SEPM to illustrate the potential expansion of the grey squirrel from Piedmont to other parts of Italy and to neighbouring territories, particularly France and Switzerland. We will also evaluate the effects of the removal of some populations of the grey squirrel on the spatial spread of this species.

2. METHODS

2.1. Modelling Methodology and Approach

The model for simulating the distribution of grey squirrels in the landscape has two main components. The first is a geographical information system which stores habitat and animal population information. GRASS (Westervelt *et al*., 1990) was the geographical information system (GIS) used to store and retrieve habitat information and the model output. This system undertakes data manipulation and abstraction and provides input for the second component. This consists of programs simulating the population dynamics of grey squirrels and their interactions and dispersal within the GIS-held landscape The population dynamics programs were written in the programming language 'C' and integrated with the GIS component in a UNIX-shell environment. A detailed description of the original model is given in Rushton *et al.* (1997) and a brief outline of model structure and extensions are given below. The model was applied and tested in Piedmont and details are given in Lurz *et al.* (2001).

2.2. Squirrel habitat suitability

In order to predict grey squirrel range expansion, we obtained land cover data for all Europe (CORINE project). This project did not include Switzerland and few other countries. We thus requested to the Section Géoinformation of the Office fédéral de la statistique de la Swisse (the service for spatial data in the Swiss Federal Administration), the land cover produced as an integration of CORINE (projet intégration de la statistique de la superficie dans CORINE Land Cover). In this land cover, forests are not separated in deciduous, coniferous and mixed forests, as in CORINE. This separation was obtained acquiring also, from the same office, the land cover called "Mixité des forets". Swisse land covers were then imported in GRASS and homogenized with CORINE (Fig. 2.1).
We than extracted data from CORINE and Swisse land cover for the areas where the grey squirrel is expected to spread in a near future (Fig. 2.2). Habitat types were classified using CORINE-biotopes. The digitised map resolution was 250 m, thus each 250 m^2 cell was characterised by a single habitat type (predominant landcover type, Tab. 2.1). The major areas utilised by grey squirrels are broadleaf and to some extend conifer woodlands and parks, although they will feed on maize in fields and on fruit in orchards (Currado *et al*., 1987; Gurnell, 1987; Wauters *et al*., 1997a,b). As a result of the resolution scale of the landcover data, some small woodlands suitable for grey squirrels may not have been recognised as squirrel habitat. This would result in making model predictions of grey squirrel spread more conservative as it reduces the total available habitat and features such as corridors, linear features or small groups of trees important as stepping stones for dispersal The map data were edited and imported into the GIS system.

2.3. Carrying capacity and life history processes

The population dynamics model is individual-based and predicts the distribution of squirrels by simulating the life history processes of births, deaths, home range formation and dispersal in yearly time steps. Landcover data (e.g. habitat type, location, area) were classified either as areas of habitat used by the squirrel or areas of non-habitat through which animals could move when dispersing. Suitable habitats were defined according to landcover type (Tab. 2.1) and the size, composition and distribution of habitat blocks was used to identify blocks in which the squirrels could be found. The carrying capacity of each type of habitat for grey squirrels for the area considered (Tab. 2.1) was calculated on the basis of an estimated squirrel density. For forested habitats and general landcover categories we relied on published estimates for similar habitats, where no information on squirrel density was available, they were estimated by authors.

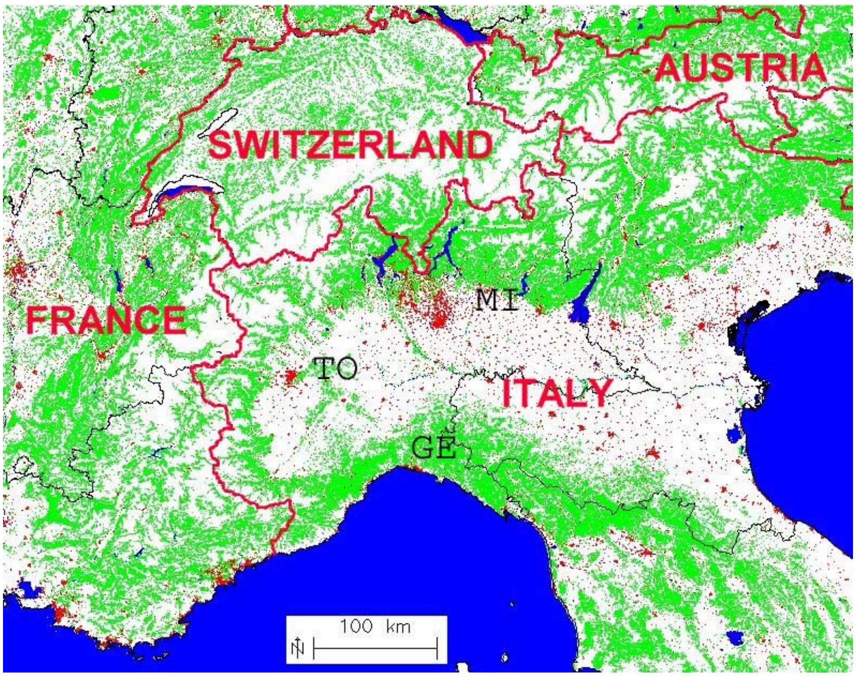


Figure 2.1 Land cover data from the CORINE project integrated with data from Switzerland land cover. TO = Turin; MI = Milan; GE = Genoa

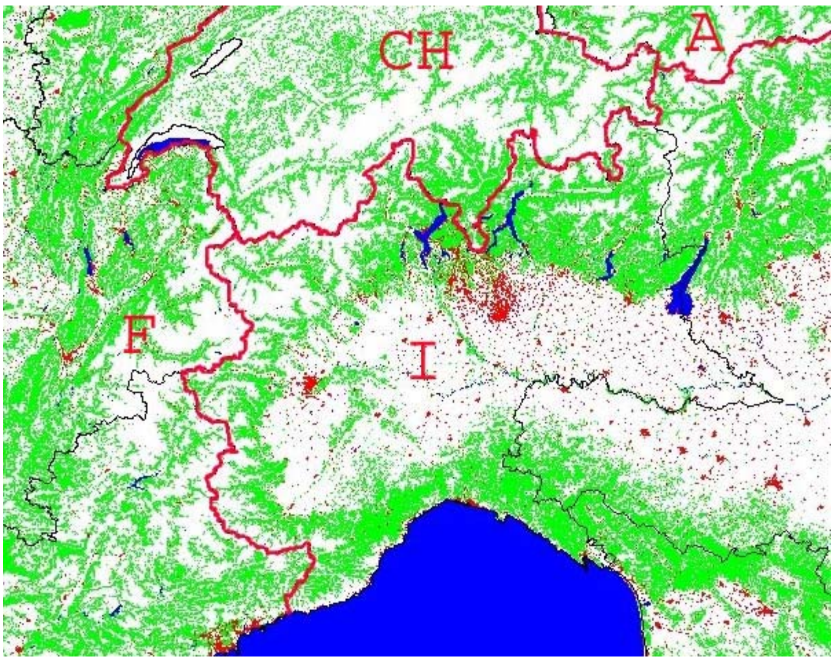


Figure 2.2. A zoomed view of the area between Italy, France, and Switzerland which were the focus of the simulations. F = France; I = Italy; CH = Switzerland; A = Austria

Table 2.1. Habitat description, grey squirrel maximum densities (D_{max} = squirrels/ha) based on field work and published literature for suitable landover types (at 250m resolution). Unsuitable habitats indicated by '-' had a value of zero in the model.

Landcover type	D_{max}	References
Non-classified	-	-
Other artificial surfaces	-	authors estimate; Koprowski, 1994
Green urban areas	0.013	authors estimate; Koprowski, 1994
Sport and leisure facilities	0.013	authors estimate; Koprowski, 1994
Non-irrigated arable land	0.013	authors estimate
Permanently irrigated land	0.013	Smith, 1999; Wauters *et al.*, 2000
Rice	0	authors estimate
Vineyards	1	authors estimate
Fruit trees and berry plantations	1	authors estimate
Olive groves	1	authors estimate
Pastures	-	-
Annual crops associated with permanent crops	0.013	authors estimate
Complex cultivation patterns	0.013	authors estimate
Land principally occupied by agriculture- with significant areas of natural vegetation	0.013	authors estimate
Agro-forestry areas	0.013	authors estimate
Broad-leaved forest	4	authors estimate; Gurnell, 1991; Wauters & Gurnell, 1999; Kenward *et al.*,1998
Coniferous forest	0,2	authors estimate; Smith & Gurnell, 1997
Mixed forest	1,5	Gurnell, 1991, 1996; Smith, 1999
Natural grasslands	0	authors estimate
Scrub and/or herbaceous vegetation associations	0	authors estimate
Open spaces with little or no vegetation	0	authors estimate
Wetlands	0	authors estimate
Water bodies	-	-
No data	-	-

Each block of suitable habitat within the landscape was modelled as having separate populations of squirrels. Squirrel population processes were modelled at the integer level, that is fractional squirrels were not permitted. Each population had its own dynamics which interacted through the process of dispersal with other habitat patches. For each habitat block, in each year, population size was modelled in terms of the net change due to several factors. These were (i) gains due to recruitment from breeding and immigration of adults and (ii) losses due to adult and juvenile mortality and emigration. Reproduction was assumed to occur in two waves, in early and late spring.

Mean litter size was varied in three different fecundity scenarios and modelled as a poisson deviate. Mortality was assumed to occur after breeding and was modelled at the level of the individual as a stochastic process and different values were applied to juvenile and adult life stages (Rushton *et al*., 1997; Rushton *et al*., 1999). Dispersal was modelled as a process occurring once a year in autumn and the mechanism was assumed to be saturation dispersal, *i.e.* occurring as a result of intraspecific competition.

Dispersal amongst grey squirrels tends to occur in autumn and spring and mainly amongst sub-adult/juveniles, normal dispersal movements are usually within the range of a few kilometres (Thompson, 1978; Koprowski, 1994). Individuals were allowed to disperse to blocks of habitat that were below the carrying capacity for grey squirrels. In addition if there were no suitable habitat blocks available for occupation within the maximum dispersal distance of 5 km, dispersers were assumed to die. As some individuals are likely to move beyond the 5 km dispersal distance parameter used (Koprowski, 1994), model predictions of grey squirrel expansion were intentionally conservative. A Flow diagram illustrating the population dynamics processes in the model is shown in Fig. 2.3.

Squirrel life history parameters such as mortality and fecundity vary with annual tree seed crop abundance. Seed crop patterns in turn depend on detailed tree species composition and age structure. The more diverse the habitat, the less likely are years with no or poor seed crops. However, these data are not available at the scale of the Corine Landcover data. We have therefore modelled two different scenarios. One in which we simulate a random seed crop pattern of poor, average and good seed crops with concomitant effects on squirrel fecundity and mortality (Tab. 2.2); and one worst case scenario in which we assume that no poor years occur.

Table 2.2. Squirrel life history parameters in relation to annual changes in tree seed crops. Data are based on Shorten, 1951; Gurnell, 1983, 1987; Koprowski, 1991; Wauters *et al.*, 2000.

Parameter	Poor year	Good year	Mast year
Fecundity	2.00	2.80	3.50
Adult survival	0.55	0.60	0.65
Juvenile survival	0.25	0.30	0.40
Proportion of breeding 1st litter	0	67	100
Proportion of breeding 2nd litter	50	25	50

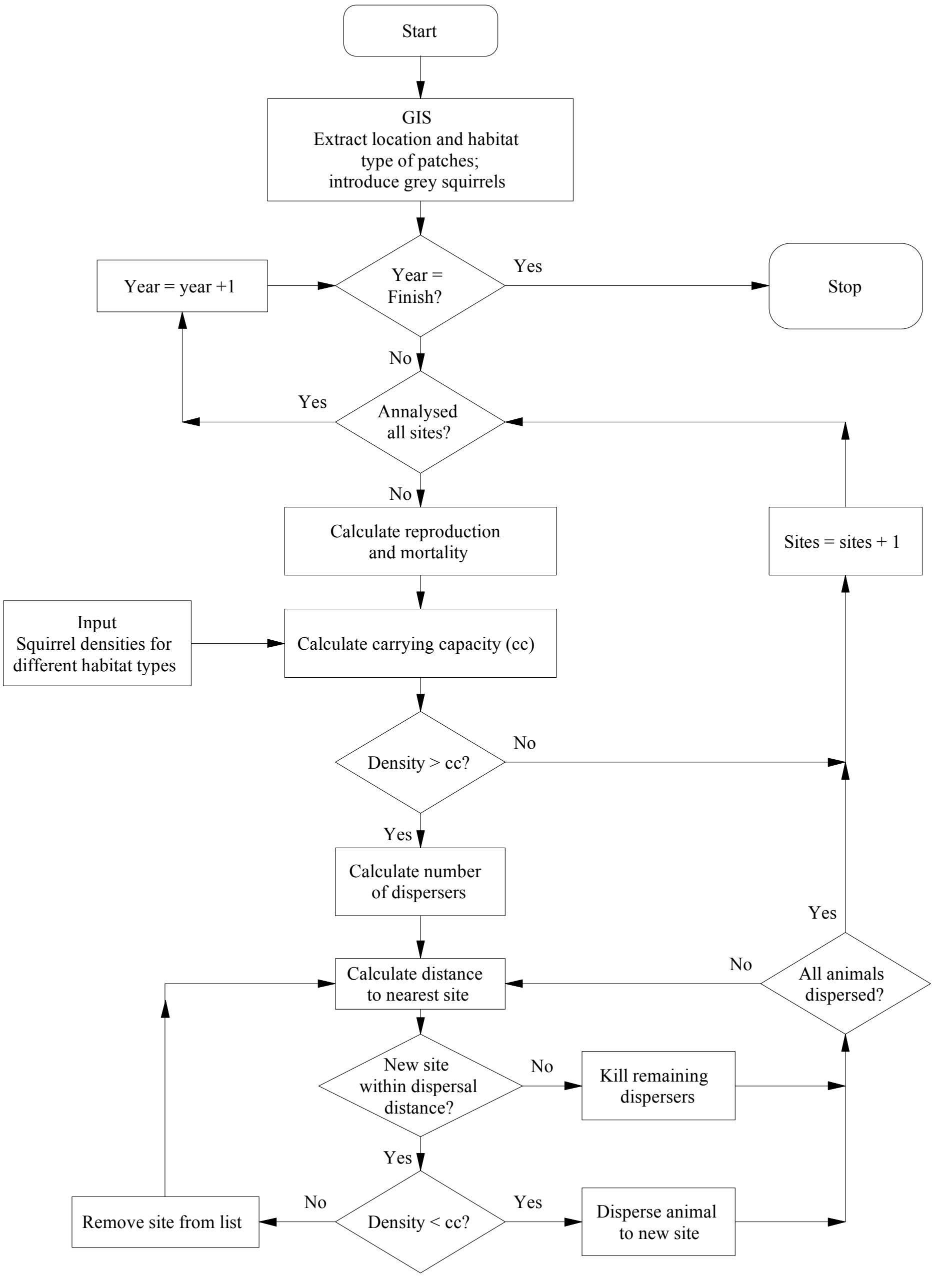


Figure 1.3. Flow diagram of population dynamics model.

3. RESULTS

3.1. The spread to France (best case scenario)

The landscape in the Alps is suitable for squirrels, and grey squirrels are likely to spread over a wide area in the next decades. Our predictions suggest that it will take 30-40 years for grey squirrels to start invading the Alps up to the coniferous forests and about 70-75 years, since 1996, to cross the border between Italy and France (see maps Figs. 3.1.3a,b). Squirrels get close to the border much sooner, but the alpine habitats (size/type of patch) make for a very slow crossing (Figs. 3.1.4a,b). The expansion will progressively cover all the valleys in the province of Turin south of the Valley of Viu, the alpine valleys in the province of Cuneo, and the north-eastern part of Liguria (Fig. 3.1.1). The grey squirrel will colonise also the hilly system of Piedmont. The colonisation of the Alps will start from the valleys of Susa, Chisone, and Pellice in the province of Turin, and then will continue progressively in the province of Cuneo in the valleys Po, Varaita, Maira, Grana, and Stura di Demonte.

The model predicts 4072 sub-populations totalling more than 1 million individuals in the year 95 (Fig. 3.1.2). The fluctuations in population size between years are small until year 65 and then increase significantly. Population growth rates are dependent on the life history parameters, the annual seed crop pattern and the availability of habitat and its carrying capacity within current distributions. There is a large leap in population size when greys start to leave the mainly agricultural plane in Piedmont and start to colonise the forest belt in the alpine areas. Population size remains under 200,000 animals in the first 50 years, then it increases drastically between the years 60-70, reaching a peak of over 1,000,000 in the year 95 with a mean size of 600,000 animals between years 90-100.

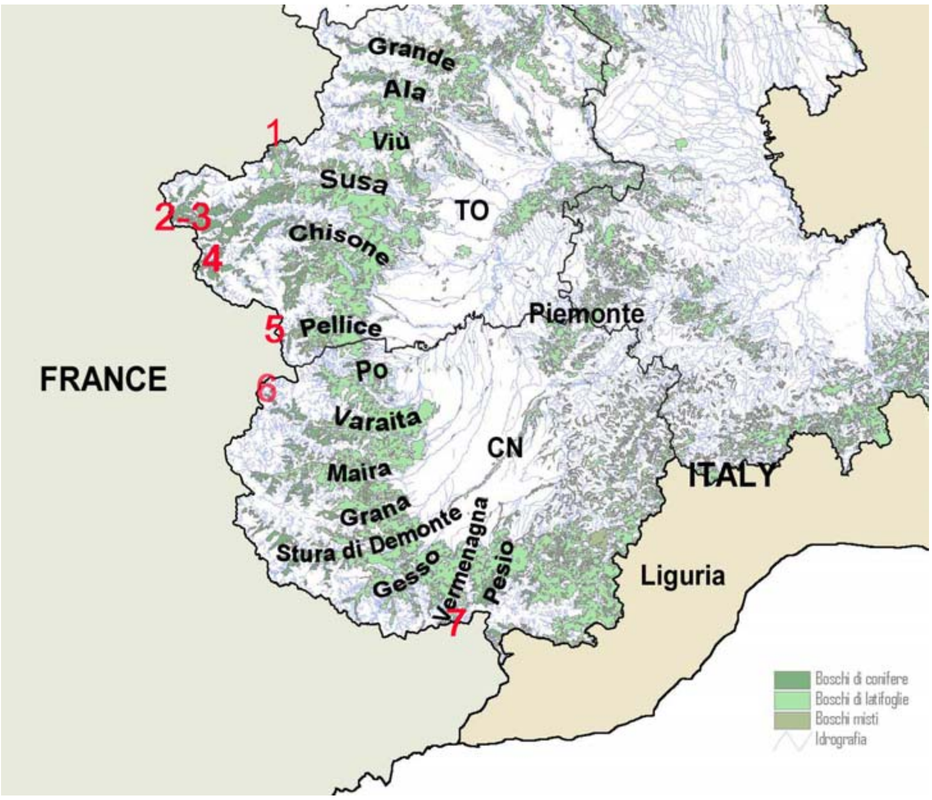


Figure 3.1.1. Italian Alpine valleys in province of Turin (TO) and Cuneo (CN).

Numbers in red are possible corridors through the Italian and French border of the Alps (see also Fig. 3.1.5):

1 Moncenisio Col in Val Cenischia, a lateral valley of the Susa valley.
2-3 Area of Bardonecchia at the end of the Susa valley (2 Valle Stretta, 3 Val de la Clarée)
4 Monginevro Col, the Col between Cesana and Claviere (Italy) and Mongenève (France).
5 Locality called Pra in the upper part of the Pellice valley.
6 Maddalena Col in the Stura di Demonte valley.
7 Tenda Col that connects the Vermenagna valley (Italy) and the Roya valley (France)

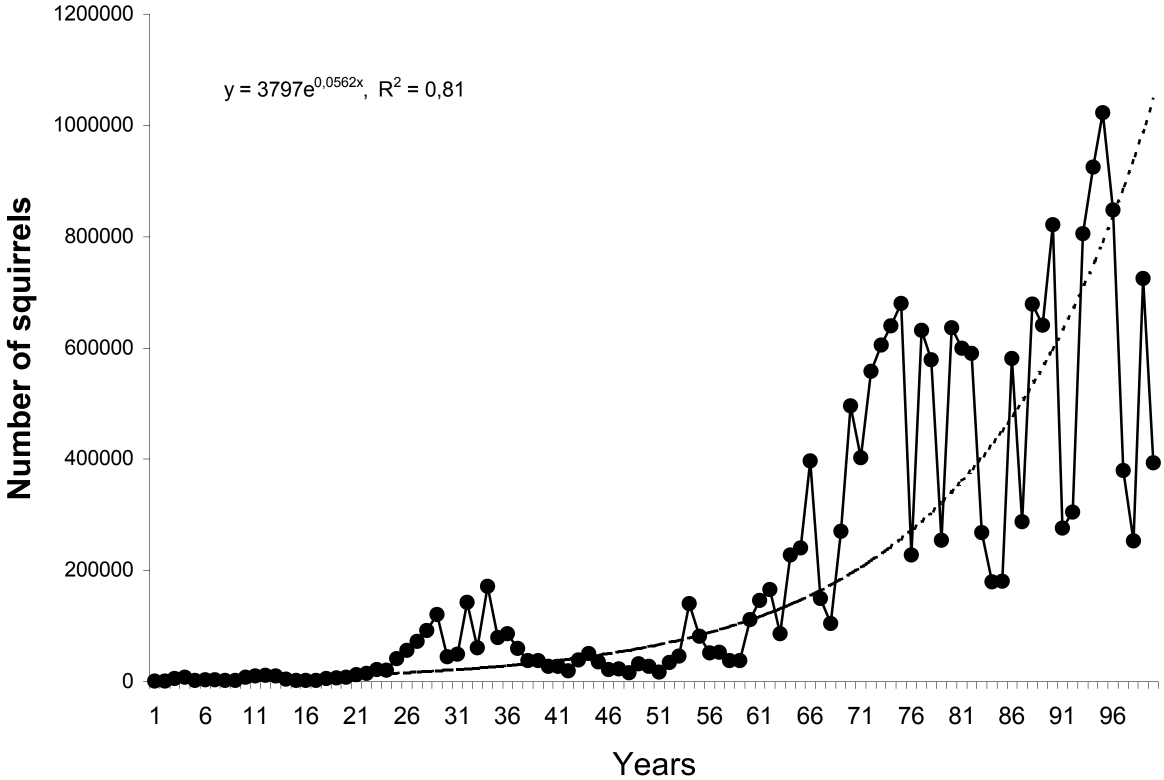


Figure 3.1.2. Average predicted grey squirrel population size in the scenario which simulated a random pattern of poor, good and mast year seed crops.

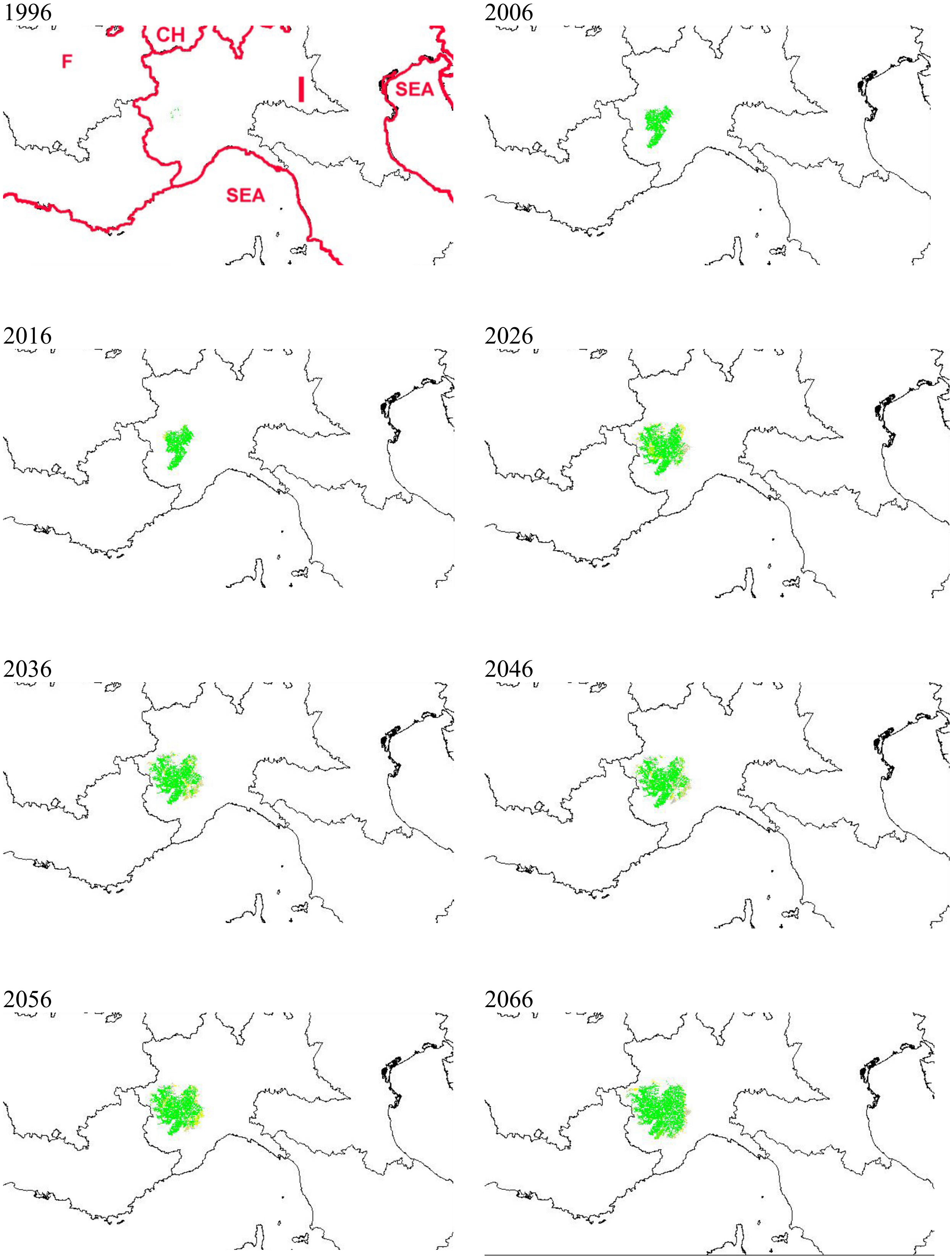


Figure 3.1.3a. Simulation results illustrating at a large scale the grey squirrel spread from Piemont during 1996-2066 in a scenario with random pattern of poor, good and mast year seed crops. Colour scheme: grey = 5% chance of greys colonising, yellow 50% probability and green 100%. F = France, Ch = Switzerland, I = Italy.

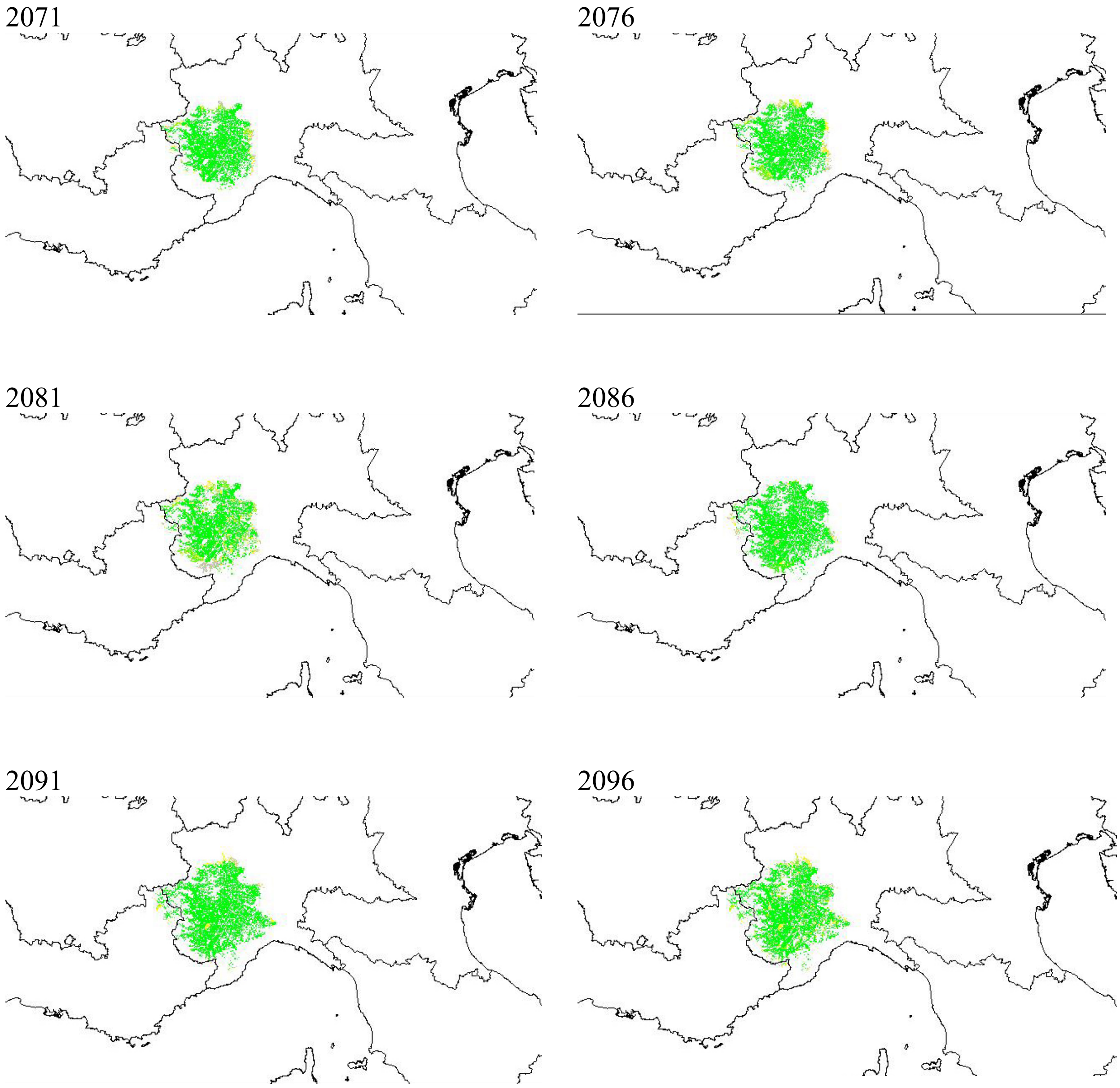


Figure 3.1.3b. Simulation results illustrating at a large scale the grey squirrel spread from Piemont during 2071-2096 in a scenario with random pattern of poor, good and mast year seed crops. Colour scheme: grey = 5% chance of greys colonising, yellow 50% probability and green 100%.

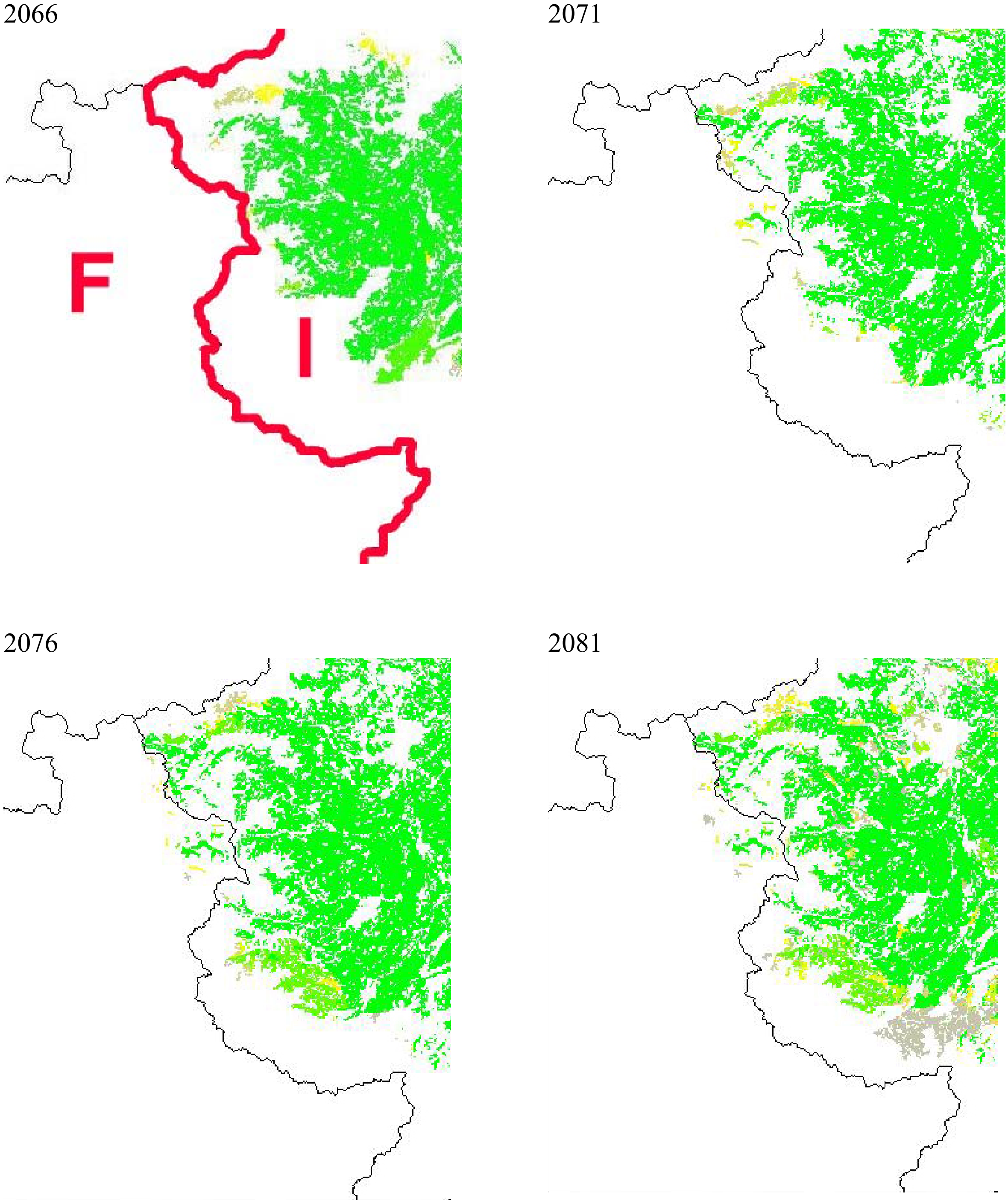
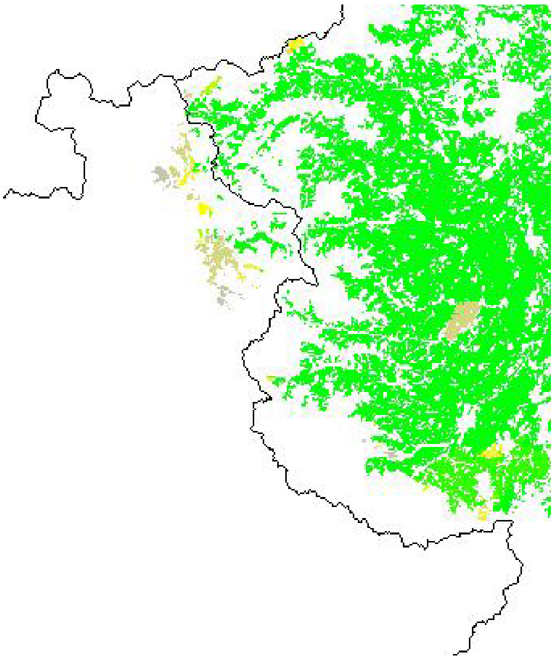
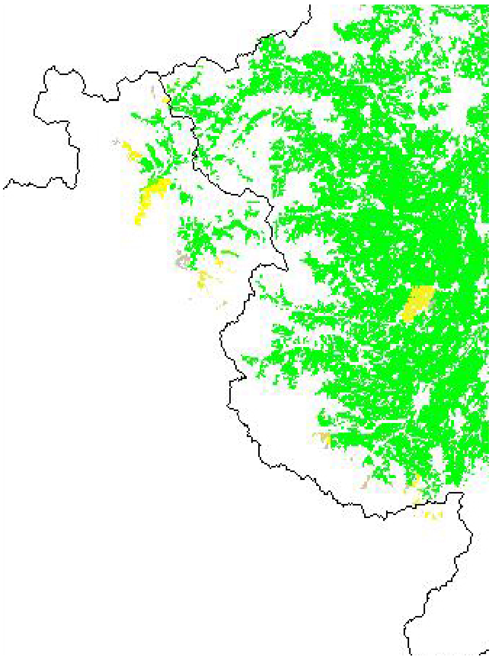


Figure 3.1.4a. Simulation results illustrating at a detailed scale the grey squirrel spread from 2066 to 2081 in a scenario with random pattern of poor, good and mast year seed crops. Colour scheme: grey = 5% chance of greys colonising, yellow 50% probability and green 100%. F = France, I = Italy.

2086



2091



2096

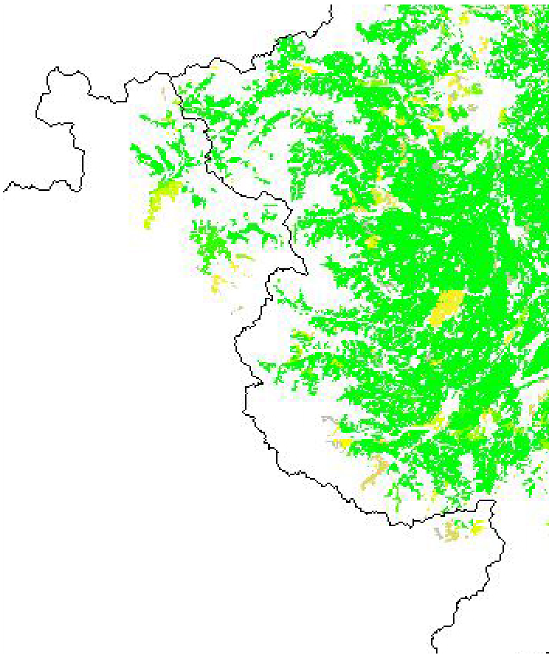


Figure 3.1.4b. Simulation results illustrating at a detailed scale the grey squirrel spread from 2086 to 2096 in a scenario with random pattern of poor, good and mast year seed crops. Colour scheme: grey = 5% probability of greys colonising, yellow 50% chance and green 100%.

3.1.1. Province of Turin

According to our simulation, the grey squirrel will reach the French border in about 70-75 years from 1996. This will happen along the valleys of Susa, Chisone, and Pellice (Figs. 3.1.1, 3.1.5). In the lower part of these valleys (Figs. 3.1.8a,b) the forests are mixed broadleaf (oak, and chestnut mixed with other species, like sycamore and ash), with beech in the slopes facing the north. In the high valleys the broad-leaves are mixed with conifers (Fig. 3.1.9) and then, at higher altitudes, there are coniferous forests composed mainly of larch, sometimes mixed with spruce. Less frequent are mixed forests with spruce and silver fir, or composed of Scots pine (Fig. 3.1.10). Despite their reduced distribution, Scots pine forests may act as a stepping stone in the colonisation of these valleys, due to the energy content and dimension of seeds that may be manipulated more easily by grey squirrels.
The maps from years 75 to 100 (Figs. 3.1.4a,b), show that the main expansion routes to France are in the area of Bardonecchia and Claviere (Monginevro Col, Fig. 3.1.5). On the other hand, the expansion of the grey squirrels in Val Cenischia (Moncenisio Col, Fig. 3.1.5) seems to stop just at the border, before reaching the Col of the Moncenisio and the Moncenisio lake in France. Another route of colonisation to France is along Val Pellice.
In order to better understand if the grey squirrel could really pass into France using these routes, we carried out field surveys in the areas highlighted by the model outputs. Considering that the border between Italy and France is usually along the crest line of the mountains, and thus at altitudes often > 3000 m a.s.l., we surveyed the areas where the border is at a lower altitude.

3.1.1.1. Moncenisio Col

Val Cenischia is a side valley of Val Susa that goes northwards to France through the Moncenisio Col. Inside the valley the forest cover is continuous on both sides. The upper part of the valley is covered by coniferous forests that reach very close to the col (Fig. 3.1.11a). However, at the Col and along the border between Italy and France, trees are nearly absent and the woody vegetation is made mainly of shrubs (Figs. 3.1.11b). On the French side, around the Moncenisio lake, the vegetation is only alpine pastures without trees (Fig. 3.1.11c). This kind of habitat is completely unsuitable for squirrels and this explains why in the simulation the grey squirrel stopped spreading just at the border, before they reach the Col of Moncenicio in France.

3.1.1.2. Area of Bardonecchia

It appears that there is a corridor that may be used by the grey squirrel to spread from the area of Bardonecchia to France. This is south-west of the village of Bardonecchia, through the area of Melezet and Pian del Colle (1441 m a.s.l.) in Italy and Valle Stretta (1784 m a.s.l.) or south-east of the Aiguille Rouge in France. The forest cover is nearly continuous on the Italian side (Fig. 3.1.12a). On the French side, in Valle Stretta there are patches of forests with larch and Scots pine (Fig. 3.1.12b). However the valley is a dead end for squirrels because it is surrounded by peaks of over 2500 m of altitude (Figs. 3.1.12c,d). Moving from the French border in a south-west direction, through Col of La Scala (1743 m a.s.l.), squirrel could arrive in Val de la Clarée, where there are large forests. However, looking at the output maps from year 80 to 100, it seems that the grey squirrels will colonise France mainly from the south (Col of Monginevro) and will then move to the north.

3.1.1.3. Monginevro Col

The area between Cesana and Clavere (Italy) and Mongenèvre (France) through the Col of Monginevro, is a main corridor for the spread of the grey squirrel in France. The slopes in the valley between Cesana and Claviere are covered with patches of conifers that, although fragmented, could assure the presence of squirrels. In some sectors the larch forest is interrupted by groups of Scots pine (Fig. 3.1.13a). There is also good forest cover on the border between Italy and France (Fig. 3.1.13b), that continues in France. Here, at Mongenèvre, the forest is fragmented due to a ski run (Fig. 3.1.13c), but beyond it becomes more continuous (Fig. 3.13d). The presence of a continuous forest cover in Italy, beyond the border, and then in France, confirms the presence of an ecological corridor in this area that could be used by grey squirrels to colonise the French side of the Alps. According to model predictions, this is likely to happen in the second half of this century (between 70 and 75 years since 1996).

3.1.1.4. Val Pellice

The Pellice valley (Fig. 3.1.1) goes west from the Po plain to France and then, in the upper part turns southwards. The ridge that faces east in the upper part of the valley constitutes the border with France. This border is usually at an altitude > 2,500 m a.s.l., but on the Col called "Colle della Croce" in locality Pra (Fig. 3.1.5) it is at 2,300 m. Here the vegetation is composed of conifers that connect the two sides of the border and could let the grey squirrel pass into France.

3.1.2 Province of Cuneo

Our predictions suggest that it will take more time for grey squirrels to start invading the alpine valleys in the province of Cuneo. The colonisation of the valleys Po, Varaita, Maira, Grana, and Stura di Demonte (Fig. 3.1.1) will happen progressively, with a faster colonisation southwards, through the low part of the valleys covered by broadleaf forests, than westwards, where higher up the valley the vegetation is composed of conifers, a suboptimal habitat for grey squirrels (Figs. 3.1.3a,b). In the valleys Po, Varaita, Maira, and Grana, the border between Italy and France is at altitudes of > 2500 m a.s.l., and the colonisation of France through these directions would be unlikely in the future.

According to the model output the colonisation of Stura di Demonte valley is nearly completed in one century. After this period, and thus outside our simulation, the spread into France through the Maddalena Col (Fig. 3.1.5) will be possible because the altitudes remain < 2000 m. Moving southward squirrels will find a good corridor to France through the Tenda Col that connects the Vermenagna valley (Italy) with the Roya valley (France) (Fig. 3.1.5).

Our simulations predict the spread of the grey squirrel in Liguria starting from 2060-2070. However, it must be remembered that in Liguria, at Genova Nervi, there is another population of grey squirrels that was not considered in this simulation because it seems still confined in a small urban area. However, around the urban area there are tree corridors to the hilly area and the Apennines. Thus, it is very possible that this population will spread in Liguria before the arrival of animals from Piedmont. Considering that the altitude of the border between Liguria and south France decreases as one moves closer to the coast, it is probable that the colonisation of France would be easier and spread rates may increase.

The effects due to the possible spread of the grey squirrel from Genoa is presented in the following chapter.

Tenda Col

The model predicts the colonisation of south France, from the Vermenagna valley (Italy) through the Tenda Col and the Roya valley (France, 3.1.5) in the last years, after 2090. The Tenda Col is at 1900 m a.s.l. and the forest cover is continuous through the Vermenagna and Roya valleys and will constitute a corridor for the grey squirrel. In Italy forests are composed of deciduous trees (Fig. 3.1.14a,b), while in France squirrels will find extensive coniferous forests, composed mainly of Scots pine (Fig. 3.1.14c,d).

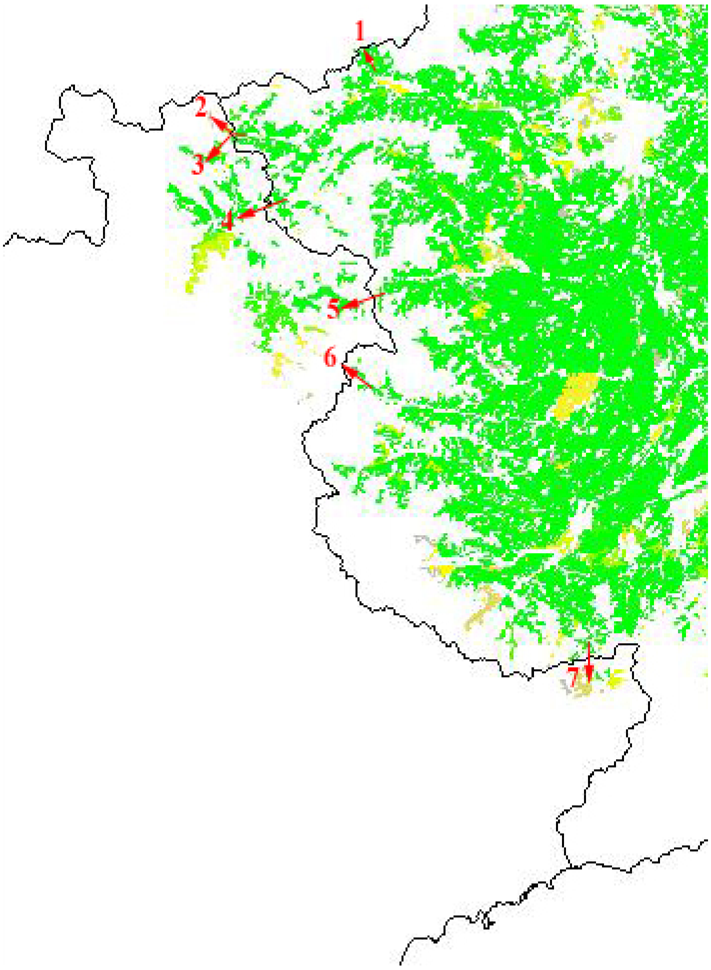


Figure 3.1.5. Illustration of possible corridors through the Italian and French border of the Alps.

1	Moncenisio Col in Val Cenischia, a lateral valley of the Susa valley.
2-3	Area of Bardonecchia at the end of the Susa valley (2 Valle Stretta, 3 Val de la Clarée)
4	Monginevro Col, the Col between Cesana and Claviere (Italy) and Mongenève (France).
5	Locality called Pra in the upper part of the Pellice valley.
6	Maddalena Col in the Stura di Demonte valley.
7	Tenda Col that connects the Vermenagna valley (Italy) and the Roya valley (France)

3.1.3. Simulation with no poor years (worst case scenario)

Previous simulations were performed with a random pattern of seed production, with poor, good and mast years, and varying the life history parameters accordingly (see Tab. 2.2). This is because squirrel life history parameters such as mortality and fecundity vary with annual tree seed crop abundance, and we know, at least for some tree species (Mencuccini *et al.*, 1995), that seed production changes from low to high between years. However, we felt that if the habitat is diverse (i.e. woodlands are composed of different tree species) grey squirrels may not experience poor years like established populations.

In mixed forests, seed production may be not synchronised between different tree species, and during years of crop failure of some species squirrels could feed on the others, thus not experiencing the effect of poor years. In fact, in mixed broadleaf woodlands grey squirrels could reach very high densities (Montgomery *et al.*, 1975; Mosby, 1969). In a previous study, Wauters *et al.* (1997) found that in the Po-plain in Piedmont woodland plots with many species of large-seed producing trees had a good understory of hazel, and that squirrel density increased with tree species diversity. In mixed coniferous forests, red squirrels responded to a cone crop failure in spruce adapting their behaviour and foraging more frequently on larch that, in a six-year period, was more stable in seed production between years (Wauters *et al.*, 2005).

At the moment we do not know if woodlands in the part of Piedmont where grey squirrels are predicted to spread are really mixed, and an adequate forest survey will be necessary in the future. However, given the lack of information, we ran a second scenario without poor years in the random pattern of seed crops in order to see the response of grey squirrels if food conditions do not limit their spread. Average life history values were used in correspondence of poor years of the previous scenario.

With no poor seed years in the simulation the spread of the grey squirrel is faster. In 20 years from 1996 the species is predicted to colonise the western Alps in the provinces of Turin and Cuneo, and in about 30 years they will reach France (Figs. 3.1.6a,b). Grey squirrels would reach Liguria around year 2046, colonising the western part of the region. The animals would then enter France through a long border that is completely forested and at an altitude that goes from 1600 m down to the sea level.

By the end of this century predictions suggest in some years more than 2 million grey squirrels (Fig. 3.1.7). The between year fluctuations in population size are low, especially compared to results obtained in the previous simulation (Figs. 3.1.2, 3.1.7). Comparing the graphs with population size increase and the output maps of the two scenarios, with poor years and without, it seems that the influence of years with low production on the grey squirrel spread is very high. Thus, how the squirrels will perform during years with low production of some tree species, and if they could find alternative resources (for example other tree species if woodlands are mixed) will be a key factor influencing the spread rate.

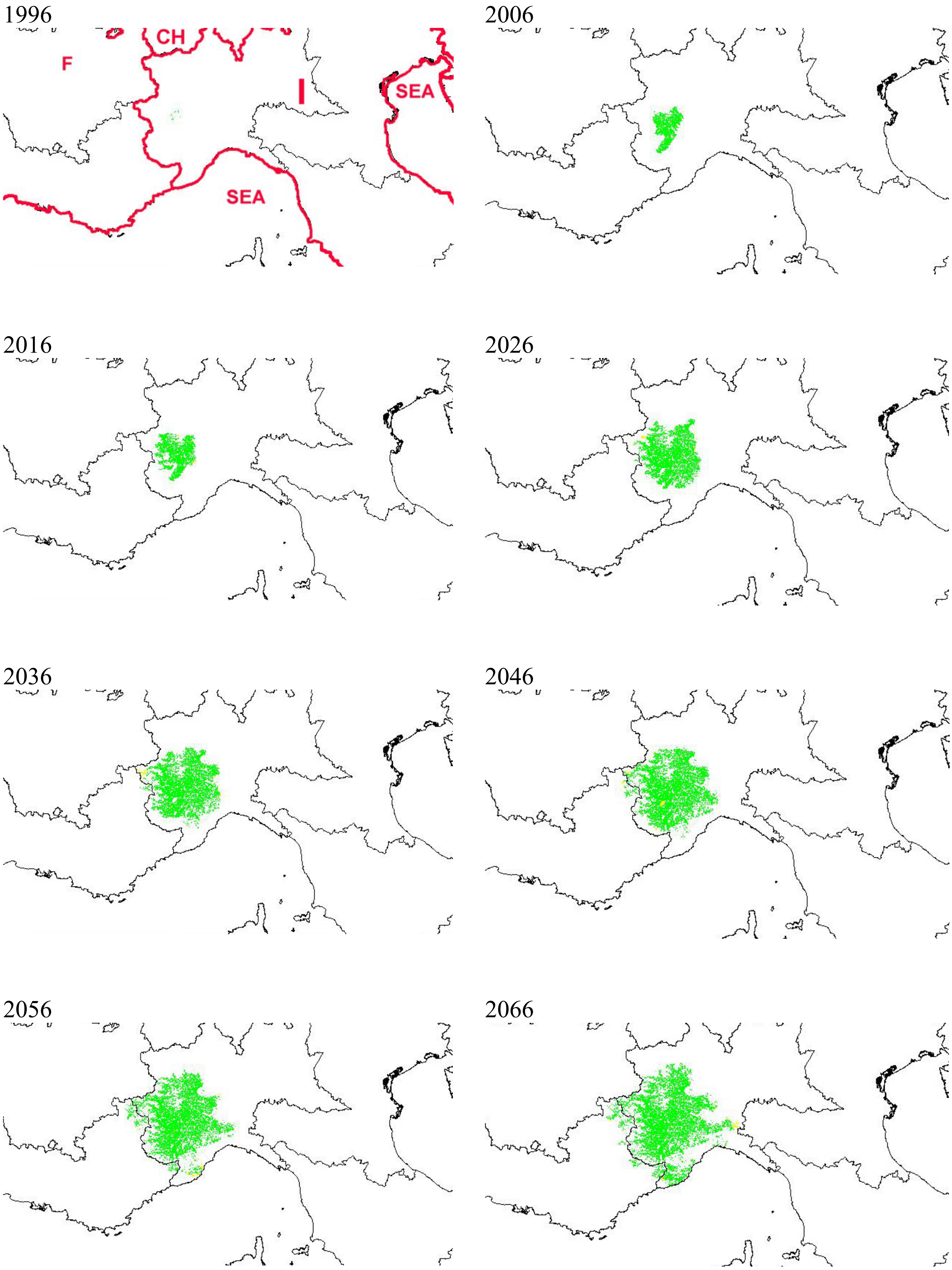


Figure 3.1.6a. Simulation results illustrating at a large scale the grey squirrel spread from 1996 to 2066 in a scenario with no poor years seed crops. Colour scheme: grey=5% probability of greys colonising, yellow 50% chance and green 100%. F = France, Ch = Switzerland, I = Italy.

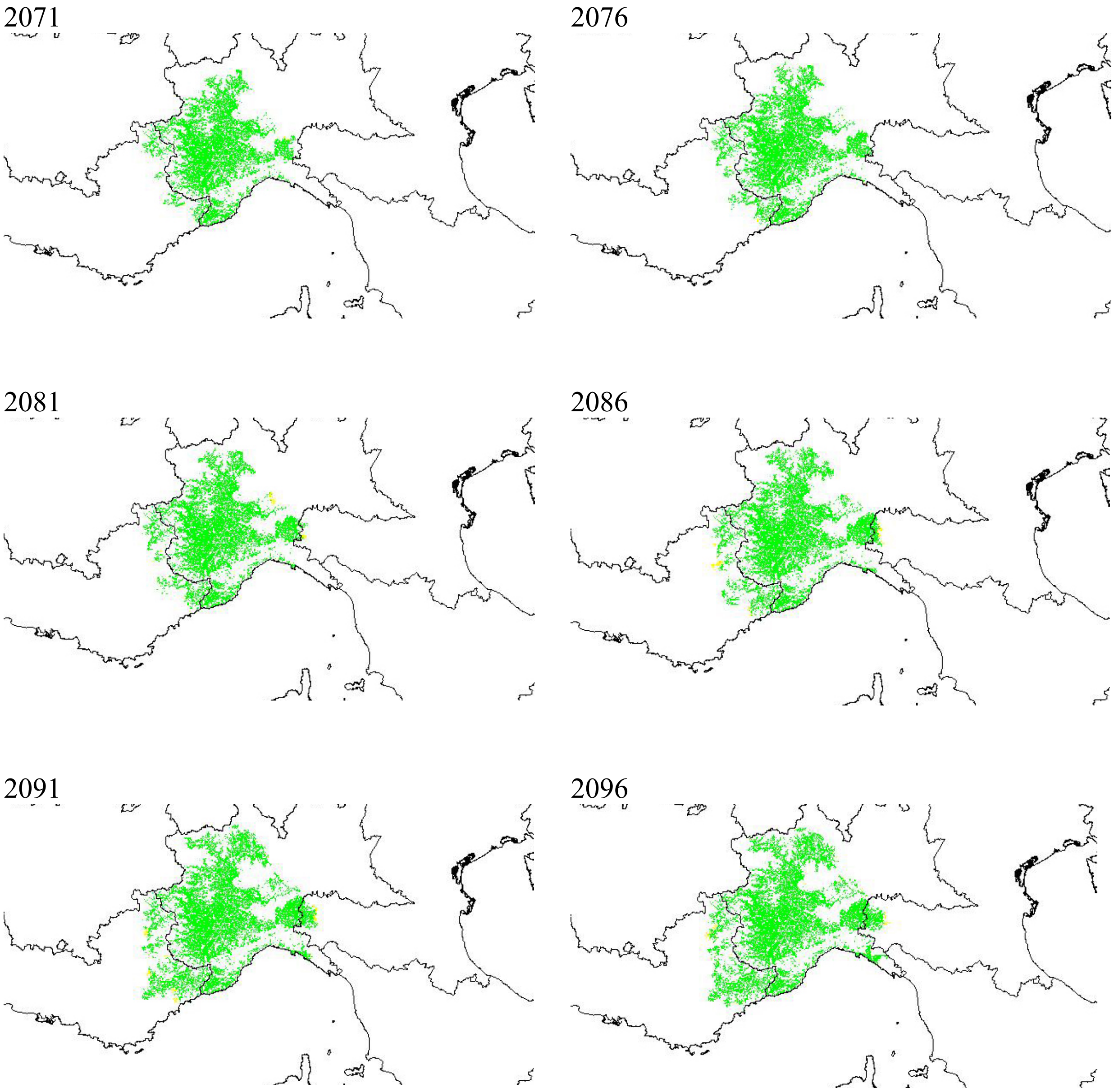


Figure 3.1.6b. Simulation results illustrating at a large scale the grey squirrel spread from 2071 to 2096 in a scenario with no poor years seed crops. Colour scheme: grey=5% probability of greys colonising, yellow 50% chance and green 100%.

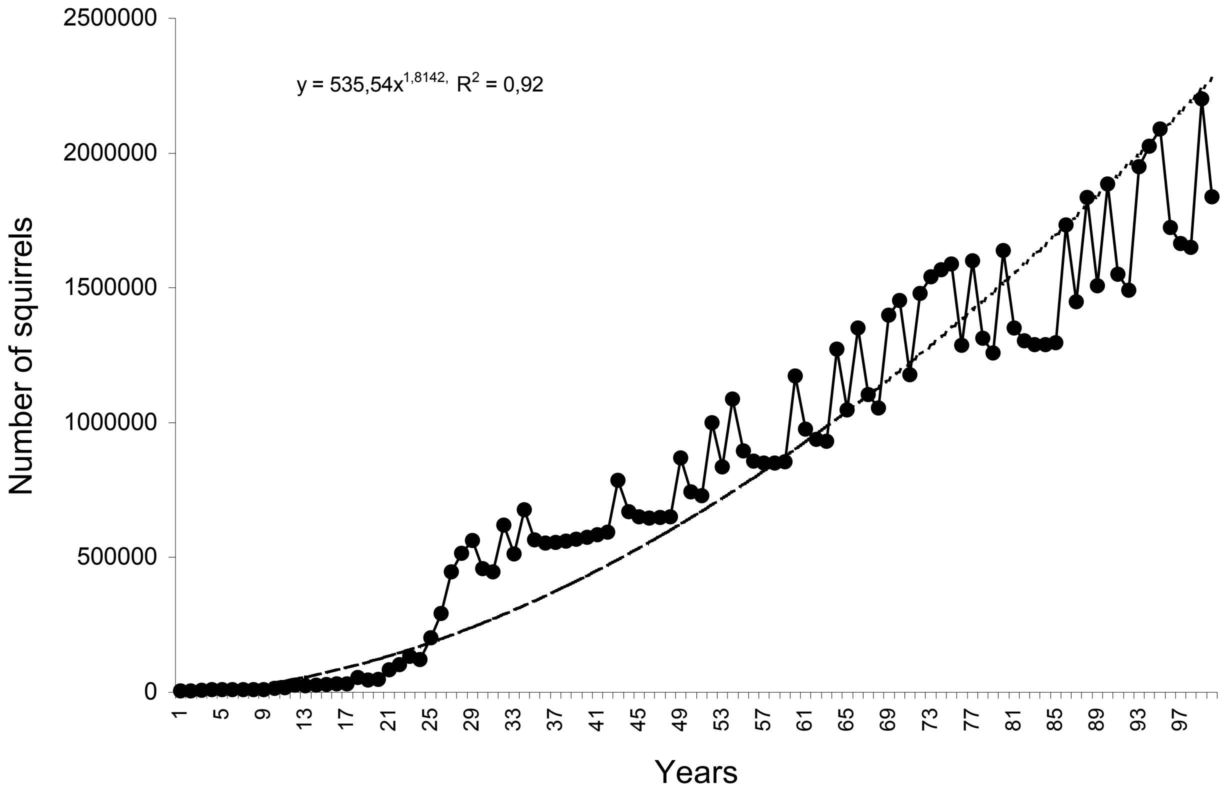


Figure 3.1.7. Average predicted grey squirrel population size in the scenario which simulated a random pattern without poor year seed crops.

Figure 3.1.8a. Susa valley - Broadleaf forest surrounding the "Sagra di S. Michele" at the entrance of the valley (for the location of the valley see map in Fig. 3.1.1).

Figure 3.1.8b. Susa valley - Extensive broadleaf forest.

Figure 3.1.9. Chisone valley - Broadleaf and coniferous patches (for the location of the valley see map in Fig. 3.1.1).

Figure 3.1.10. Chisone valley - The Scots pine woodland at Fenestrelle may become an important stepping stone for the spread of the grey squirrel in the western Alps.

Figure 3.1.11a. Moncenisio Col - The upper part of Val Cenischia (Italy) is covered by coniferous forest (for the location of the Col see map in Fig. 3.1.1).

Figure 3.1.11b. Moncenisio Col - At the col, the border between Italy and France, the woody vegetation is made only of shrubs.

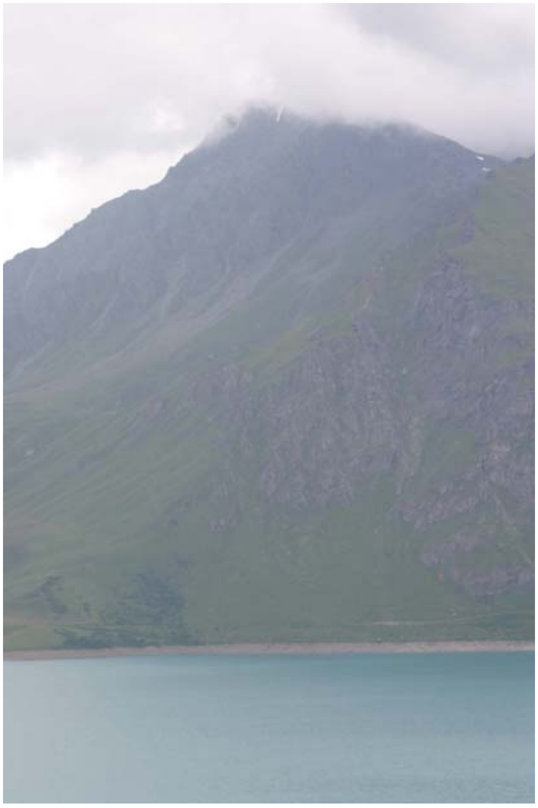


Figure 3.1.11c. Moncenisio Col - In the French side the vegetation around the lake of Moncenisio is composed of alpine pastures where trees are completely absent.

Figure 3.1.12a. Area of Bardonecchia - Large forests at Melezet near Bardonecchia (Italy) (for the location of Bardonecchia see map in Fig. 3.1.1).

Figure 3.1.12b. Area of Bardonecchia - Conifer and some broadleaf at the entrance of Valle Stretta (France).

Figure 3.1.12c. Area of Bardonecchia - The bottom of Valle Stretta (France) with high peaks.

Figure 3.1.12d. Area of Bardonecchia - Valle Stretta (France) is surrounded by high peaks that squirrels could not pass.

Figure 3.1.13a. Monginevro Col - The slopes between Cesana and Claviere near to the French border are covered with patches of larch and Scots pine (for the location of the Col see map in Fig. 3.1.1).

Figure 3.1.13b. Monginevro Col - At the border between Claviere (Italy) and Mongenèvre (France) the larch forest is continuous.

Figure 3.1.13c. Monginevro Col - The forest at Mongenèvre is crossed by the ski run.

Figure 3.1.13d. Monginevro Col - After the ski centre the forest is continuous.

Figure 3.1.14a. Tenda Col - A view from Limone Piemonte (Vermenagna valley, Italy) that shows the continuous deciduous woodland (for the location of the Col see map in Fig. 3.1.1).

Figure 3.1.14b. Tenda Col - At the entrance of the tunnel that connects Italy to France the vegetation is still composed of deciduous trees.

Figure 3.1.14c Tenda Col - On the French side the woodland is composed mainly of Scots pine.

Figure 3.1.14d. Tenda Col - In France the coniferous forests are continuous.

3.2. The spread in Italy

3.2.1. The populations from Piedmont and Ticino

Simulation of the grey squirrel spread in Italy started in1996 for the population in Piedmont and in 1999 for the population along the Ticino river that was introduced recently (Tattoni *et al.*, in press). Output maps start from 1999 and are presented every 10 years until 2048 and then every 5 years till 2098 (Fig. 3.2.1.a,b).

In this first simulation we did not include the grey squirrel population at Genoa Nervi. This population remained localised since the introduction in 1966 to 2004 in a small urban area and the spread in the nearby hilly area seems to be difficult, although not impossible, due to the presence of grassland in the possible spread directions (Venturini *et al*., 2005). Thus, we considered a first scenario where the grey squirrels could not spread from Genoa Nervi, and a second where the population of Genoa was allowed to spread outside the urban area starting from 2010.

Our predictions suggest that it will take a few years for the grey squirrel to colonise the hilly areas of Monferrato and Langhe in Piedmont. In this hilly system the woodland vegetation is in some parts reduced and fragmented due to the presence of extensive vineyards, but in other parts the forest cover is quite extensive and consists of mixed deciduous woodlands (De Biaggi *et al*., 1990) that are a good habitat for the grey squirrel. The Langhe area is characterised by the presence of extensive hazelnut (*Corylus avellana*) plantations that are often grown near deciduous woodland. Thus, it is probable that squirrels would colonise the woodland and use hazelnut as an important food resource. In this case the damage could potentially be very serious. In the Ticino, dispersal tends to occur along the wooded banks of the river, and it would take about 15-30 years for the grey squirrel to colonise the park and the surrounding areas.

In sixty years grey squirrels are predicted to colonise the western Alps, the internal hilly system in Piedmont, and the area along the Ticino river from Switzerland to the confluence in the Po river. In this phase of the project does not consider the expansion in Switzerland (see Section 3.3) . Between 2060 and 2080 the two populations will join and then the expansion will continue in all Piedmont, part of Liguria and western part of Lombardy.

The model predicts a maximum of 7,513 sub-populations totalling over 2 million individuals in the year 99 (Fig. 3.2.2.). The fluctuations in population size between years are small until year 30 and then increase progressively. This is related to the annual changes in tree seed crops that were modelled. Population size remains under 1 million in the first 70 years, and then increases to 2 million in year 95, with a large fluctuation in number, and a drop to 750,000 animals in some years as a result of simulated poor seed years.

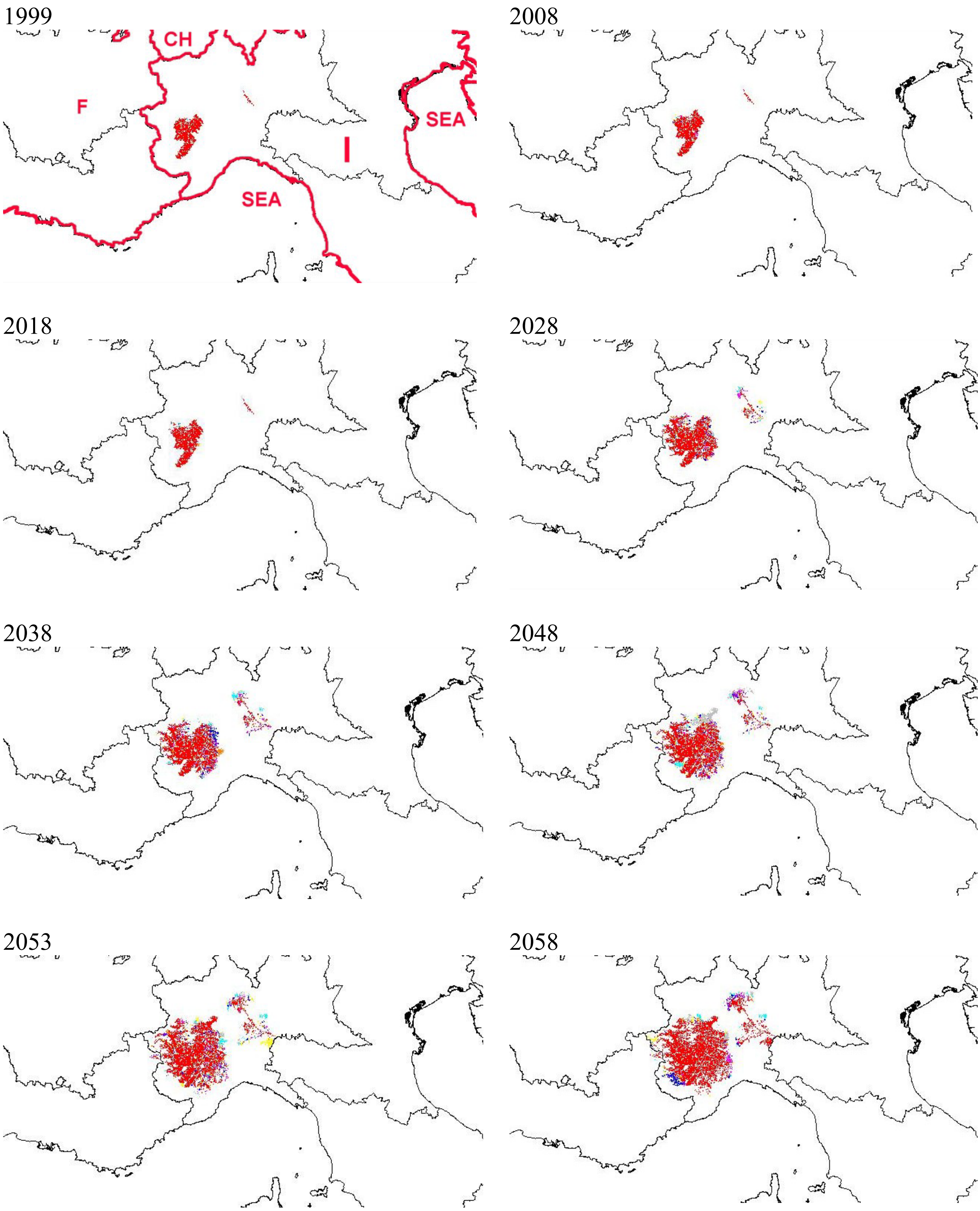


Figure 3.2.1.a. Simulation results illustrating the grey squirrel spread in Italy from 1999 to 2058 in a scenario with a random pattern of poor, good and mast year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: grey 10% probability of grey squirrels colonising, yellow 20%, cyan 30%, blue 50%, orange 60%, magenta 75%, violet 85%, red 100%.

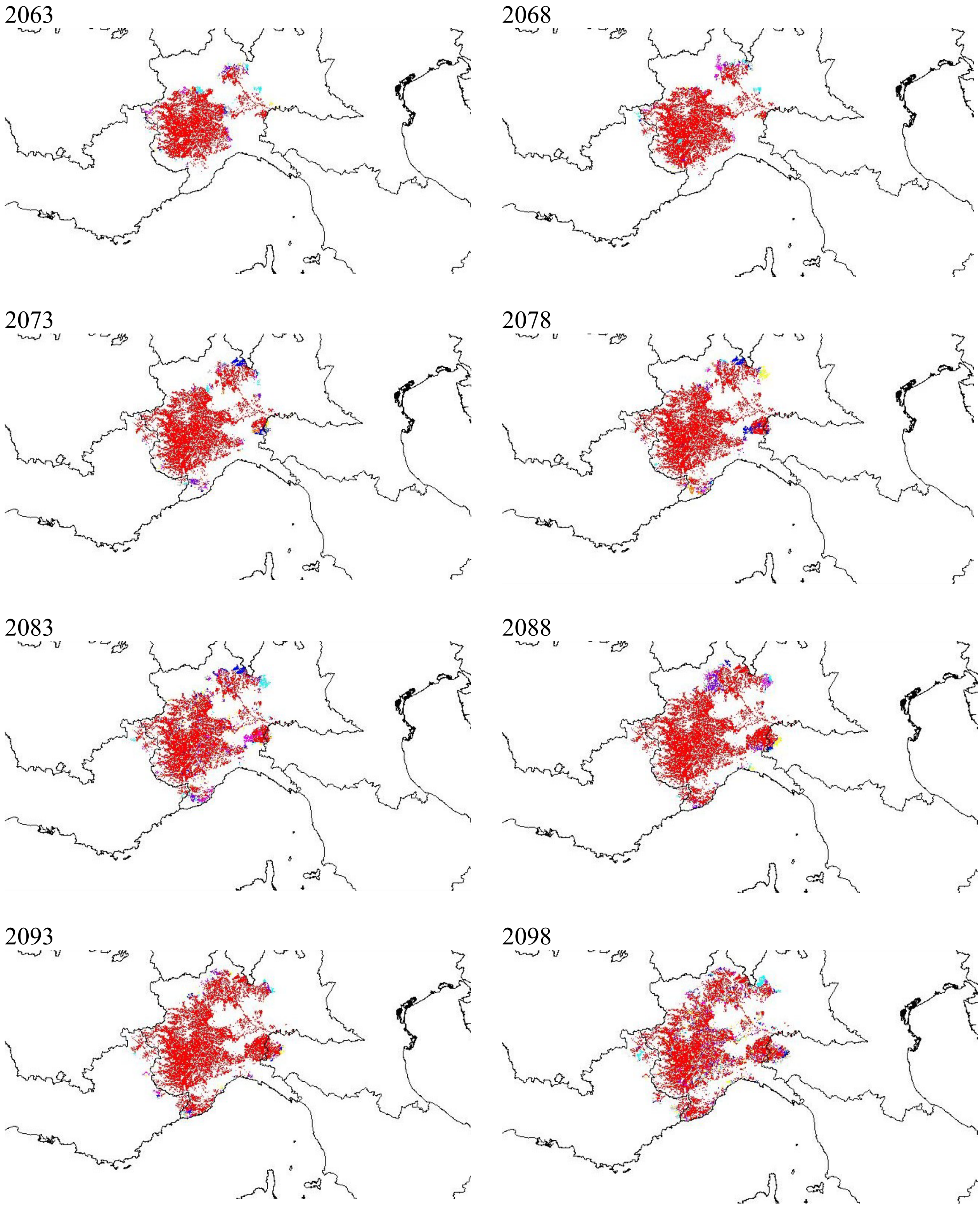


Figure 3.2.1.b. Simulation results illustrating the grey squirrel spread in Italy from 1963 to 2098 in a scenario with a random pattern of poor, good and mast year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: grey 10% probability of grey squirrels colonising, yellow 20%, cyan 30%, blue 50%, orange 60%, magenta 75%, violet 85%, red 100%.

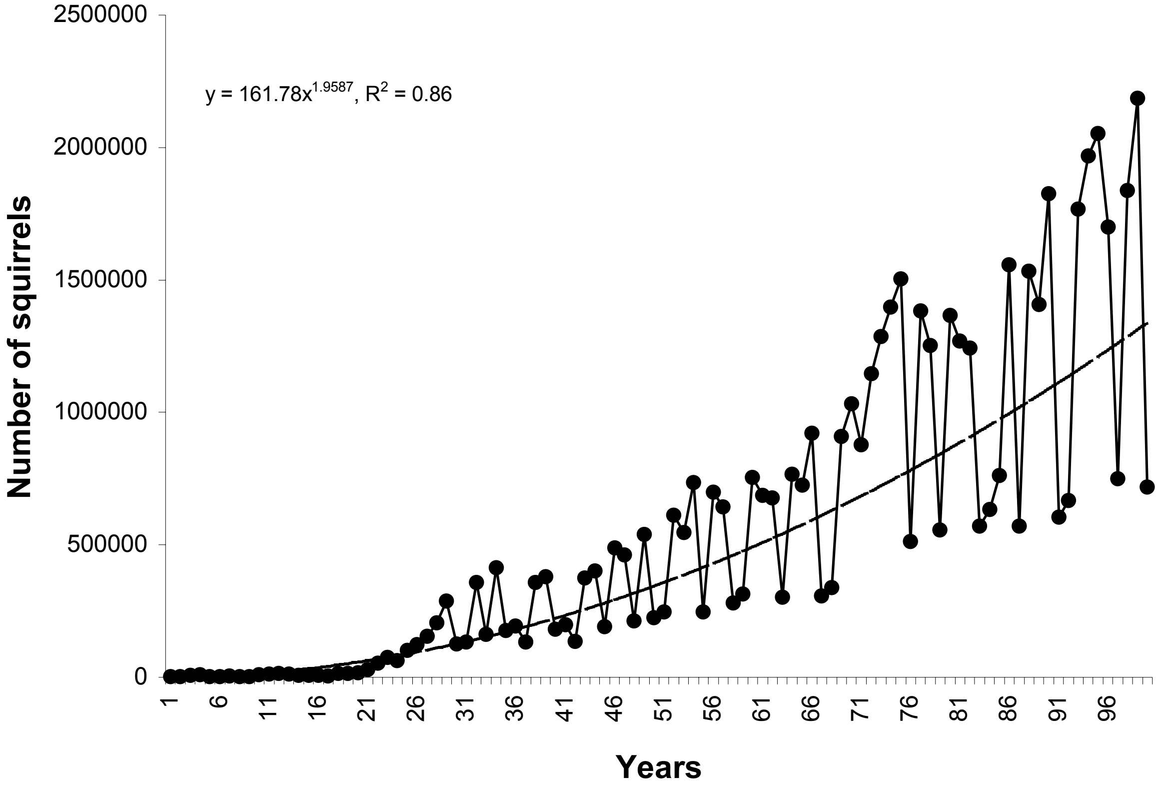


Figure 3.2.2. Average predicted grey squirrel population size in the scenario which simulated the grey squirrel spread in Italy from the source populations in Piedmont and the Ticino river. A random pattern of poor, good and mast year seed crops was used.

3.2.2. Including the population at Genoa Nervi

As reported in the previous paragraph, in this second modelling scenario the grey squirrel population present at Genoa Nervi was allowed to spread outside the urban area from 2010. It must be underlined that, in addition to the possibility of squirrels being able to spread to new habitat, there is the risk of animal translocations to other areas (Aloise & Bertolino, 2005). This phenomenon is particularly dangerous because it could create new founder populations and help the species to overcome ecological barriers increasing its rate of spread.

3.2.2.1. "Best case" scenario

In 2001 we assumed the presence of 114 squirrels in the two locations of Genoa Nervi and Bogliasco. This situation considers the results of recently published research (Venturini *et al.*, 2005). In the study, the population size of Genoa Nervi and the presence of the species in surrounding areas were investigated. In 2002 the population size was estimated at 115/286 individuals by distance sampling method, while, by direct observation, it varied from 80 individuals (2004) to 114 individuals (2003). The sampling by hair tubes in surrounding areas confirmed the presence of the grey squirrel in Bogliasco and excluded a bigger distribution of the species.

The population of Genoa was allowed to spread outside the urban area from 2010. This date is arbitrary, and was chosen to show what would happen if the grey squirrels could overcome the habitat barrier around the urban area in the near future. In this case, the species will spread in the next 20 years to a larger area, colonising the eastern part of the Ligurian region until 2070 (Fig. 3.2.3. a,b). Towards 2068-2073, the model seems to predict a sudden huge jump in distribution, from the Ligurian region toward Emilia-Romagnia and Tuscany, in a south-easterly direction. This is a slight Corine/model artefact, connected to the presence of a huge continuous suitable habitat patch. When the squirrels enter it, the maps highlight the whole habitat block as one unit.

The greys will reach the Swiss border in the north after 2060. The current scenario did not include landcover data for Switzerland and spread is only shown to the border (see Section 3.3 for details). According to the predictions of the model, there will be a mean of 8,186 sub-populations in the last 10 years (with a peak of 9,123) totalling more than 4 million individuals in the year 99 (Fig. 3.2.4.). The fluctuations in population size between years are small in the first 60-70 years, and then will increase, with a huge change in population size between years in the last period. This is an effect related to the annual changes in tree seed crops that we have simulated.

3.2.2.2. "Worst case" scenario

In the worst case scenario, where seed production was modelled with no poor years, the output maps indicate that the spread will be significantly faster. The greys will reach the Swiss border in 40-50 years (Fig. 3.2.5.a). The eastern part of Liguria will be colonised in the next 35-40 years, and in 50-60 years the colonisation of the Apennine between Emilia-Romagna and Tuscany will start (Fig. 3.2.5.a,b). At the end of the simulation, the French and Swiss territories beyond the Italian border will be colonised by the grey squirrels. In Italy, the Piedmontese region will be colonised completely, as well as Liguria, the western part of Lombardy, and the northern part of the Apennine. The colonisation of France would be deeper than in previous simulations, due to the spread of grey squirrels through the Italian border in Liguria and the southern part of Piedmont. In these areas the border between Italy and France is covered by continuos deciduous forests, that are good habitat for grey squirrels.

The total population size at the end of 100 years is enormous and could reach 6 millions of animals in the last years of the simulation, with up to 14,476 sub-populations (Fig. 3.2.6.) However, we consider this worst case scenario as quite unrealistic, as it is difficult to assume that squirrels would not experience any bad seed years at all.

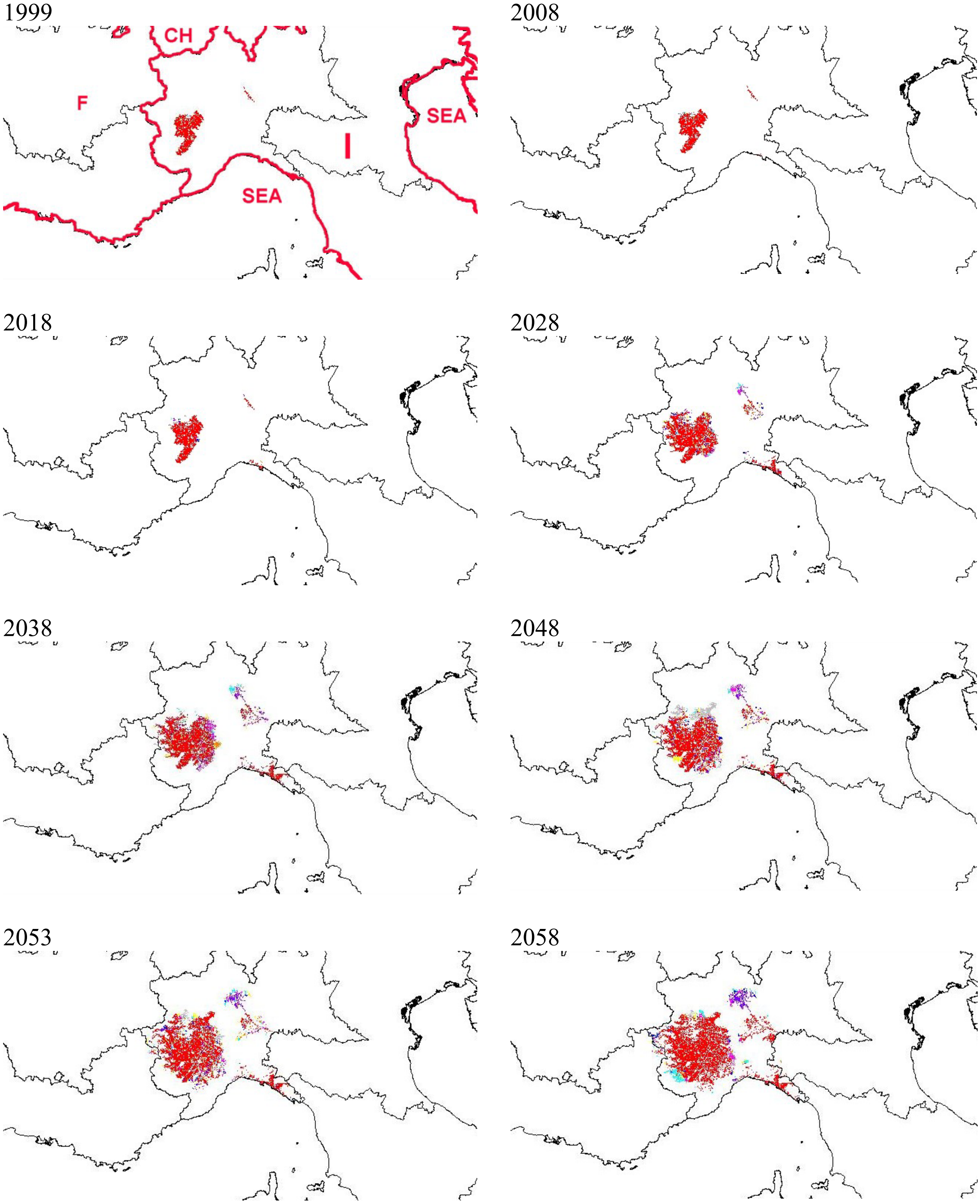


Figure 3.2.3.a. Simulation results illustrating the grey squirrel spread in Italy from 1999 to 2058 in a scenario with a random pattern of poor, good and mast year seed crops (best case scenario). The source populations were in Piedmont, along the Ticino river and at Genoa Nervi. The grey squirrels were considered to spread outside the urban area of Nervi starting from 2010. Colour scheme: grey 10% probability of grey squirrels colonising, yellow 20%, cyan 30%, blue 50%, orange 60%, magenta 75%, violet 85%, red 100%.

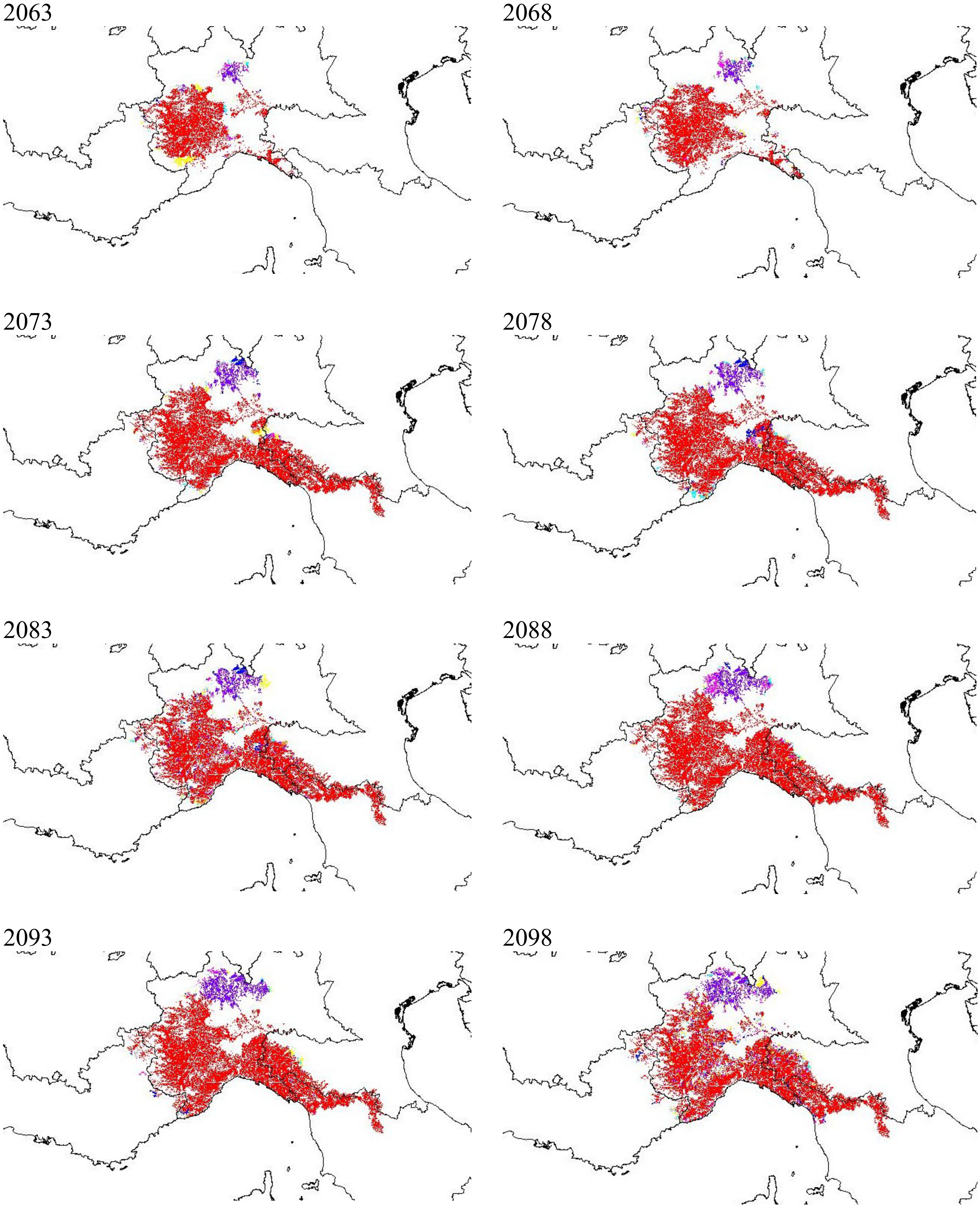


Figure 3.2.3.b. Simulation results illustrating the grey squirrel spread in Italy from 2063 to 2098 in a scenario with a random pattern of poor, good and mast year seed crops (best case scenario). The source populations were in Piedmont, along the Ticino river and at Genoa Nervi. The grey squirrels were considered to spread outside the urban area of Nervi starting from 2010. Colour scheme: grey 10% probability of grey squirrels colonising, yellow 20%, cyan 30%, blue 50%, orange 60%, magenta 75%, violet 85%, red 100%.

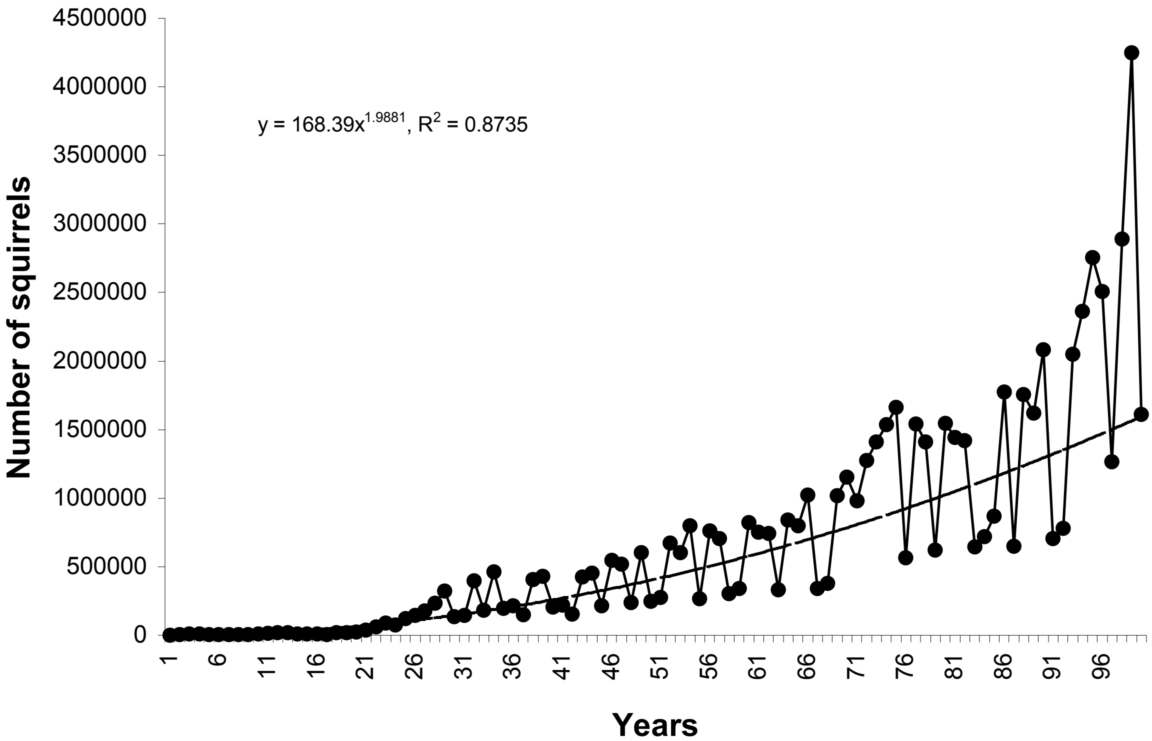


Figure 3.2.4. Average predicted grey squirrel population size in the scenario which simulated the grey squirrel spread in Italy from the source populations in Piedmont, along the Ticino river, and at Genoa Nervi. The grey squirrels were considered to spread outside the urban area of Nervi starting from 2010. A random pattern of poor, good and mast year seed crops was used.

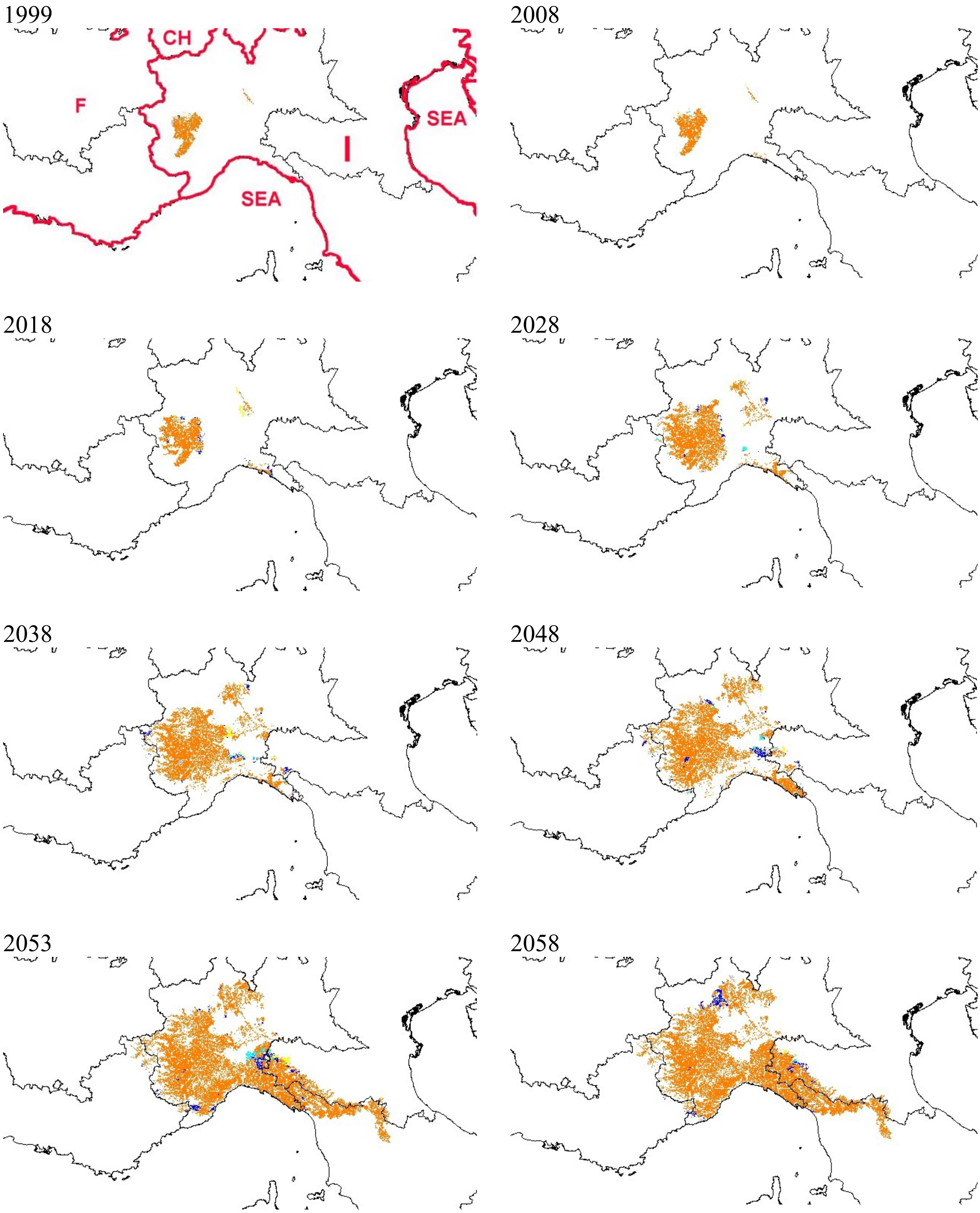


Figure 3.2.5.a. Simulation results illustrating the grey squirrel spread in Italy from 1999 to 2058 in a scenario with no poor year seed crops (worst case scenario). The source populations were in Piedmont, along the Ticino river and at Genoa Nervi. The grey squirrels were considered to be able to spread outside the urban area of Nervi starting from 2010. Colour scheme: yellow 10% probability of grey squirrels colonising, cyan 60%, blue 80%, orange 100%.

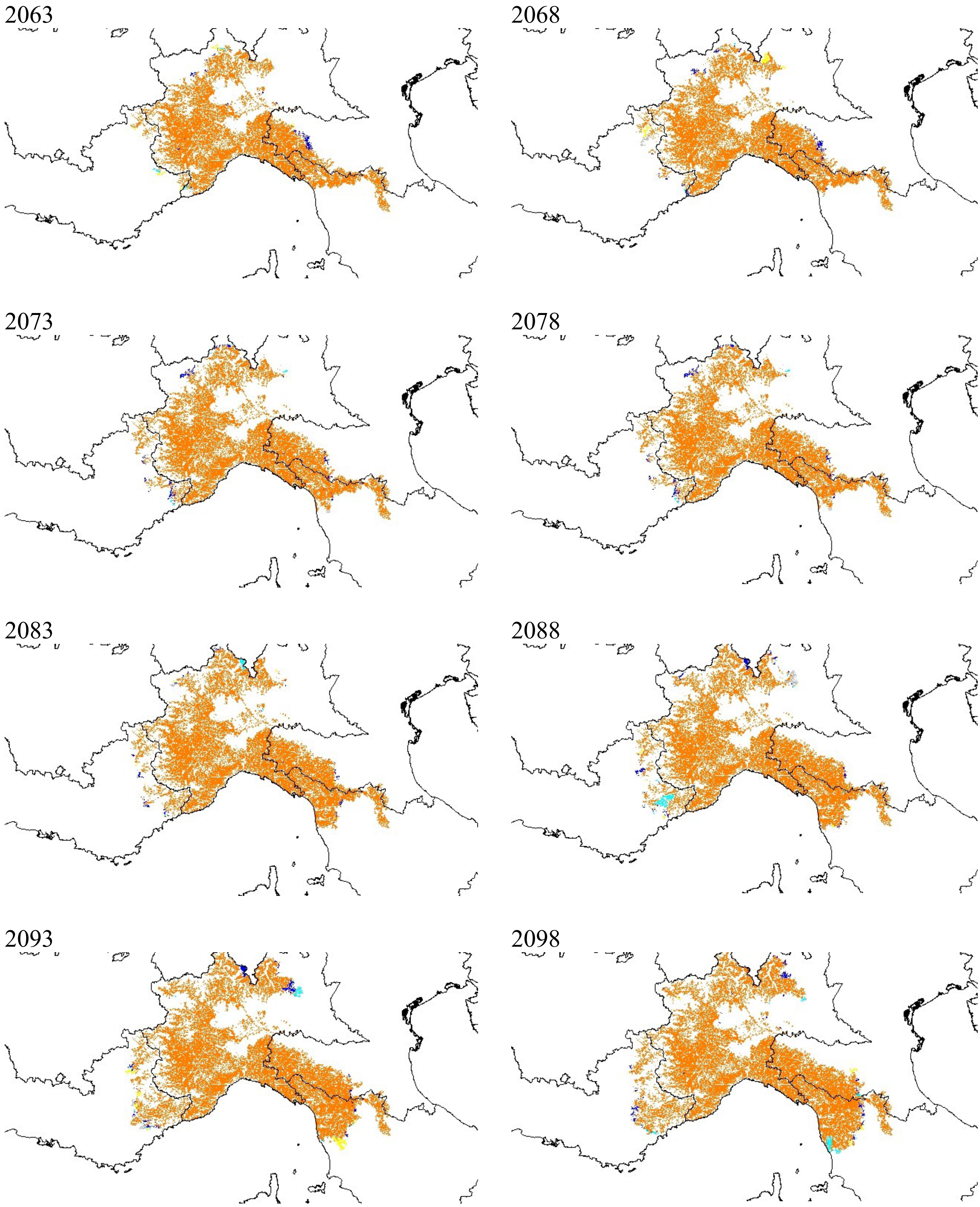


Figure 3.2.5.b. Simulation results illustrating the grey squirrel spread in Italy from 2063 to 2098 in a scenario with no poor year seed crops (worst case scenario). The source populations were in Piedmont, along the Ticino river and at Genoa Nervi. The grey squirrels were considered to be able to spread outside the urban area of Nervi starting from 2010. Colour scheme: yellow 10% probability of grey squirrels colonising, cyan 60%, blue 80%, orange 100%.

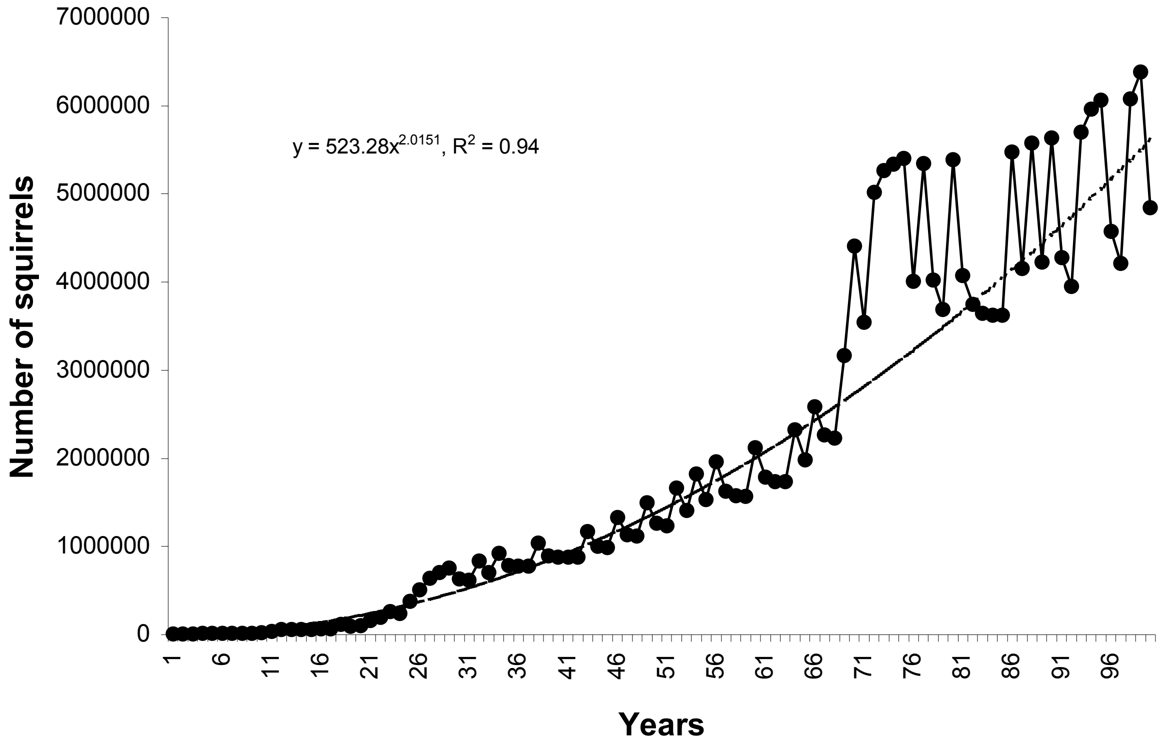


Figure 3.2.6. Average predicted grey squirrel population size in the scenario, which simulated the grey squirrel spread in Italy from the source populations in Piedmont, along the Ticino river, and at Genoa Nervi. The grey squirrels were considered to be able to spread outside the urban area of Nervi starting from 2010. A random good and mast year seed crops, without poor years, was used.

3.3. Predicted spread to Switzerland

3.3.1. "Best case" scenario

Simulation of the grey squirrel spread to Switzerland started in 1996 for the population in Piedmont and in 1999 for the population along the Ticino river. The population at Ticino had been introduced more recently (Tattoni *et al.*, in press). Output maps are presented every 10 years until 2046 and then every 5 years until 2096. In this simulation we did not include the grey squirrel population in Genoa Nervi as the focus of the predictions was the likely spread to Switzerland.

The border between Lombardy (east) and Piedmont, along the Ticino river, is covered by extensive mixed deciduous woodlands that connect with contiguous hardwood along the eastern side of Lake Maggiore and lead into Switzerland. This means that the grey squirrel would find good habitat over a wide area, between Italy and the Canton Ticino in Switzerland. These areas would support high population densities. It is obvious that the small population along the Ticino river poses the biggest risk with regard to spread to Switzerland (Tattoni *et al.*, 2005; Tattoni *et al.*, in press).

Our predictions suggest that it will take 40-50 years for the grey squirrel to colonise the area along the Ticino and the Lake Maggiore (Figs. 3.3.1.a,b). The first populations in Switzerland are predicted in 2051-2066, with an increasing probability of grey squirrel presence(higher percentage of replicates with grey squirrels in Switzerland). As previously reported in the modelling results of the grey's spread in Italy, the two populations of Piedmont and Ticino ill meet between 2060 and 2080 (Figs. 3.3.1.b,c). The map of year 2076 shows a high probability of a large range of the species in most of Piedmont and the western part of Lombardy, in the area of Varese, Como and north of Milan.

The spread of the grey squirrel in Switzerland will start in the Canton Ticino, in the area south of the Swiss part of the Lake Maggiore, around the Lake of Lugano. The species will then continue to spread between 2066-2096 and reach the area of Bellinzona and Locarno (Figs. 3.3.1.b,c).

The model predicts a maximum of 8,436 sub-populations totalling over 2 million individuals at the end of the simulation period (Figs. 3.3.2.). The fluctuations in population size between years are small until year 30-40 and then increase progressively. This is an effect related to the annual changes in the tree seed crops that we have modelled. Population size is predicted to remain under 1 million until 2065, and then increases with a peak of 2.4 million in year 2095. This is accompanied by a large fluctuation in numbers and followed by a drop to 7-800,000 animals a few years later.

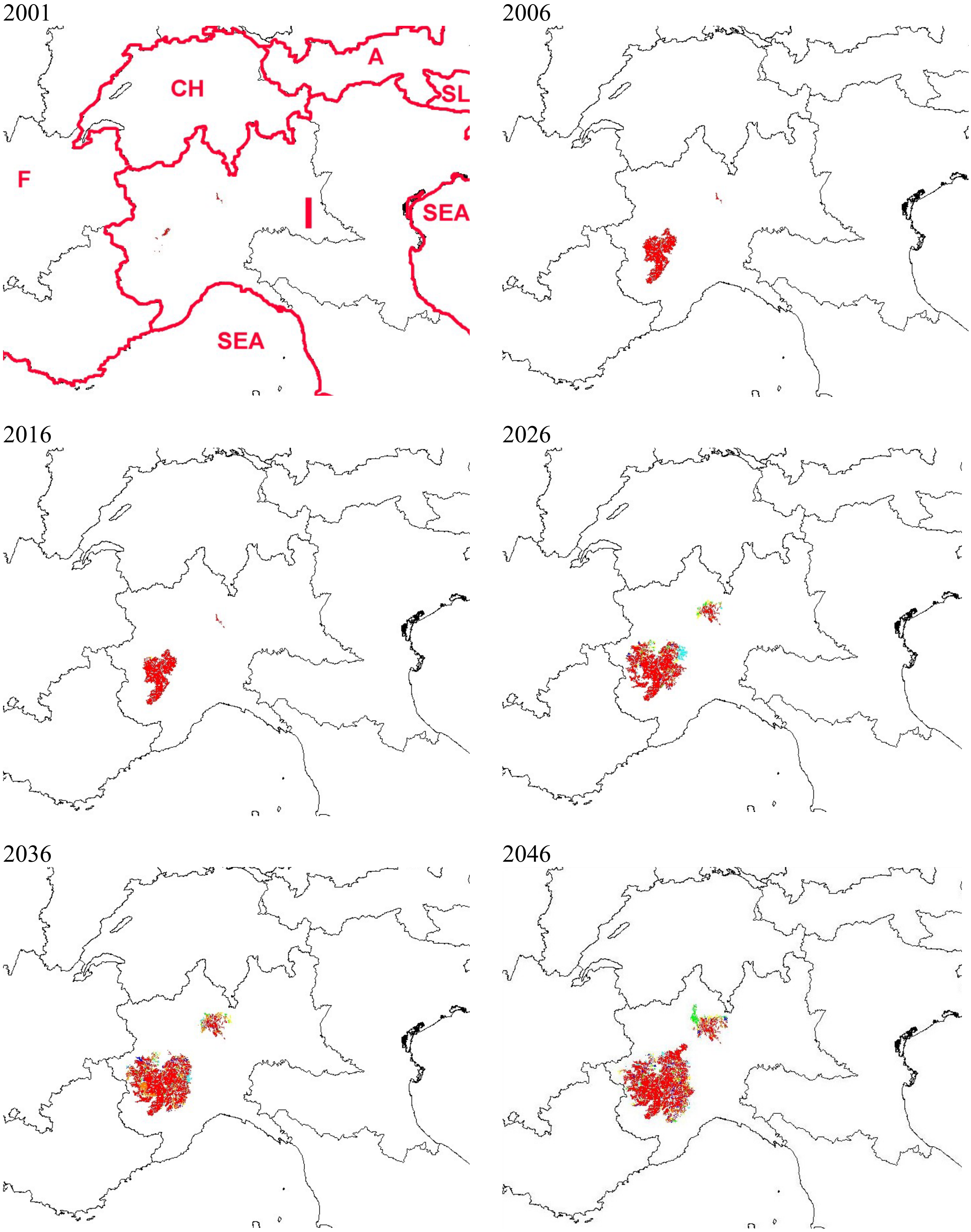


Figure 3.3.1.a. Simulation results illustrating the grey squirrel spread in Switzerland from 2001 to 2046 in a scenario with a random pattern of poor, good and mast year seed crops. The source populations were in Piedmont and the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%. F = France, Ch = Switzerland, SL = Slovenia, I = Italy.

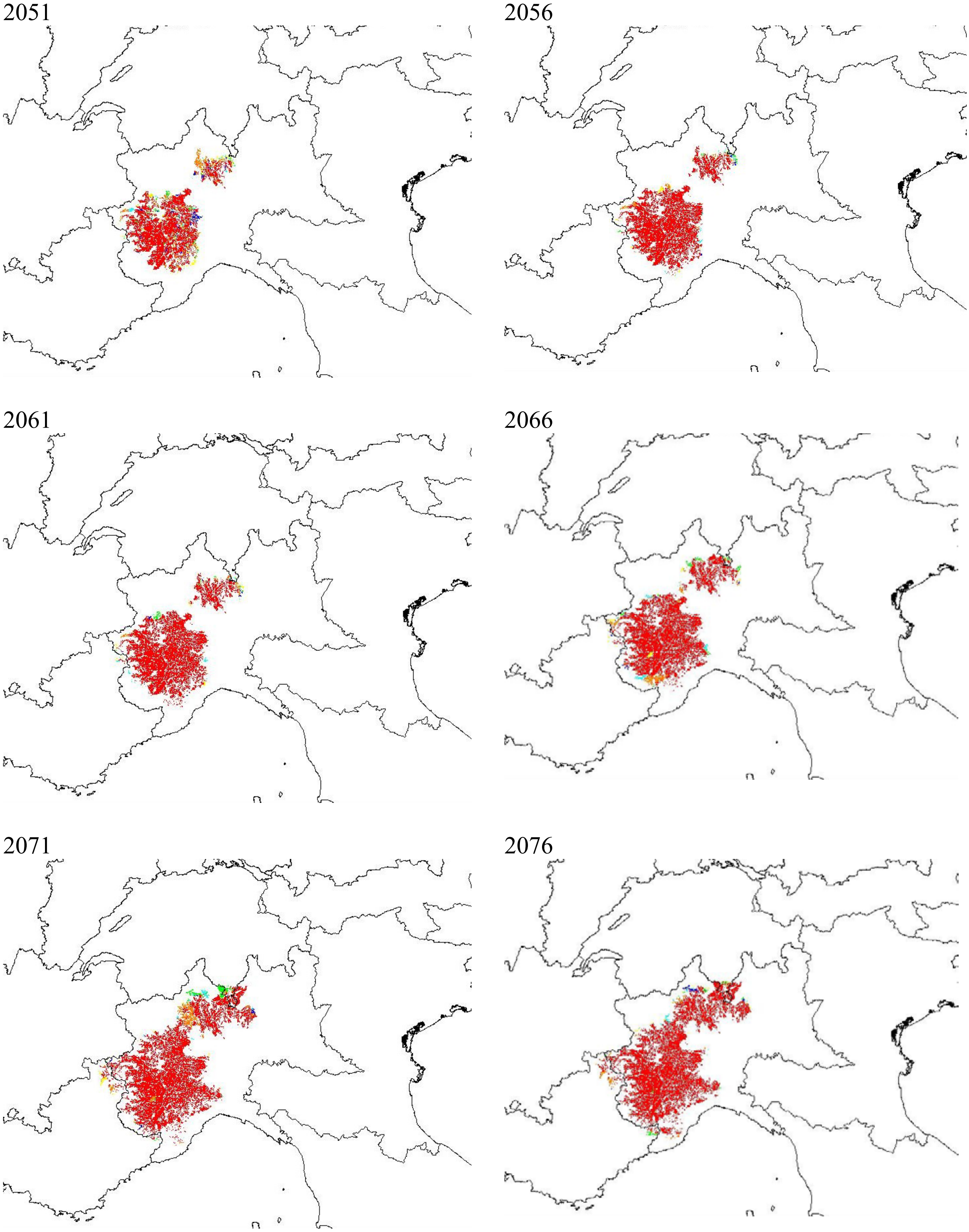


Figure 3.3.1.b. Simulation results illustrating the grey squirrel spread in Switzerland from 2051 to 2076 in a scenario with a random pattern of poor, good and mast year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%.

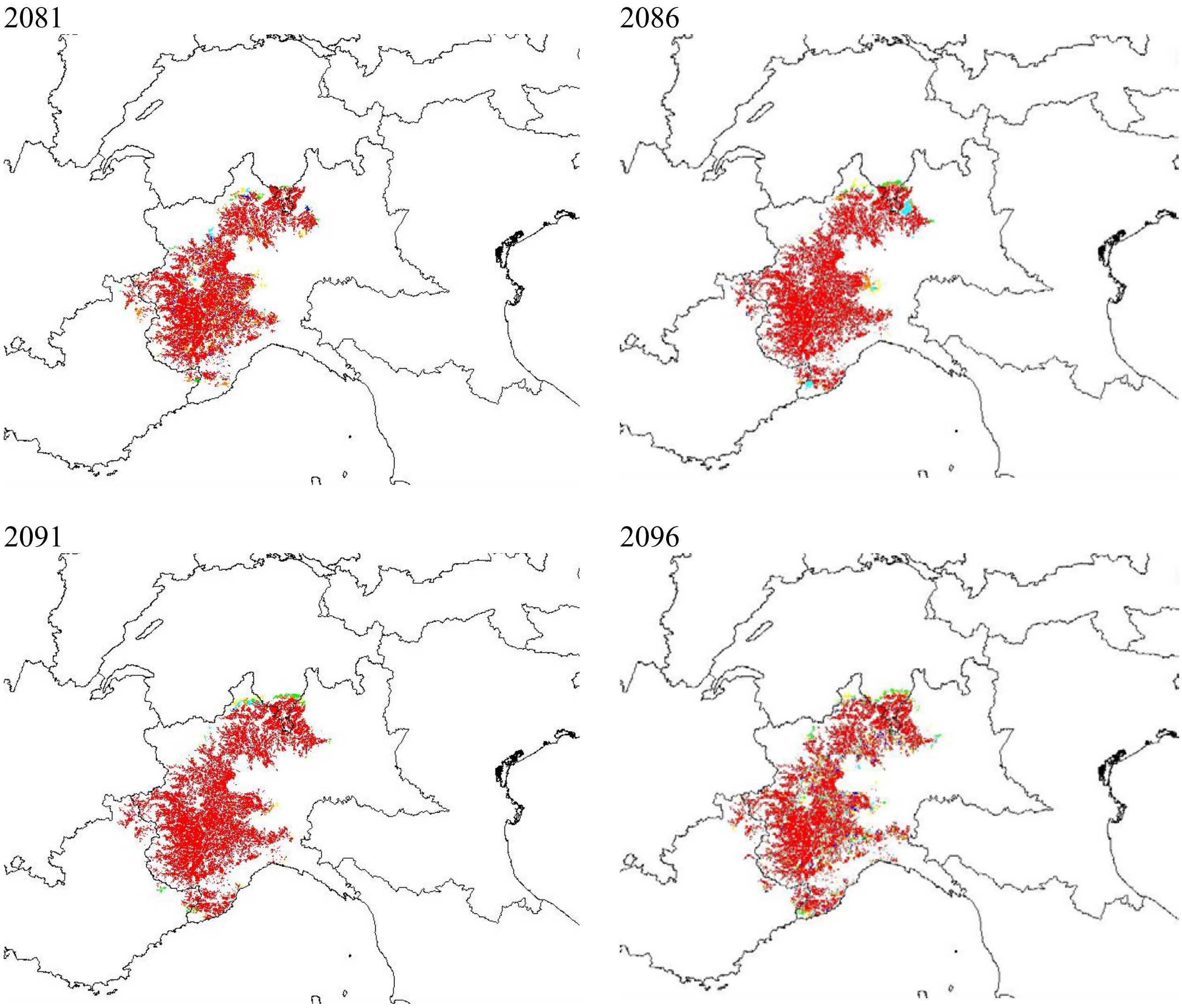


Figure 3.3.1.c. Simulation results illustrating the grey squirrel spread in Switzerland from 2081 to 2096 in a scenario with a random pattern of poor, good and mast year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%.

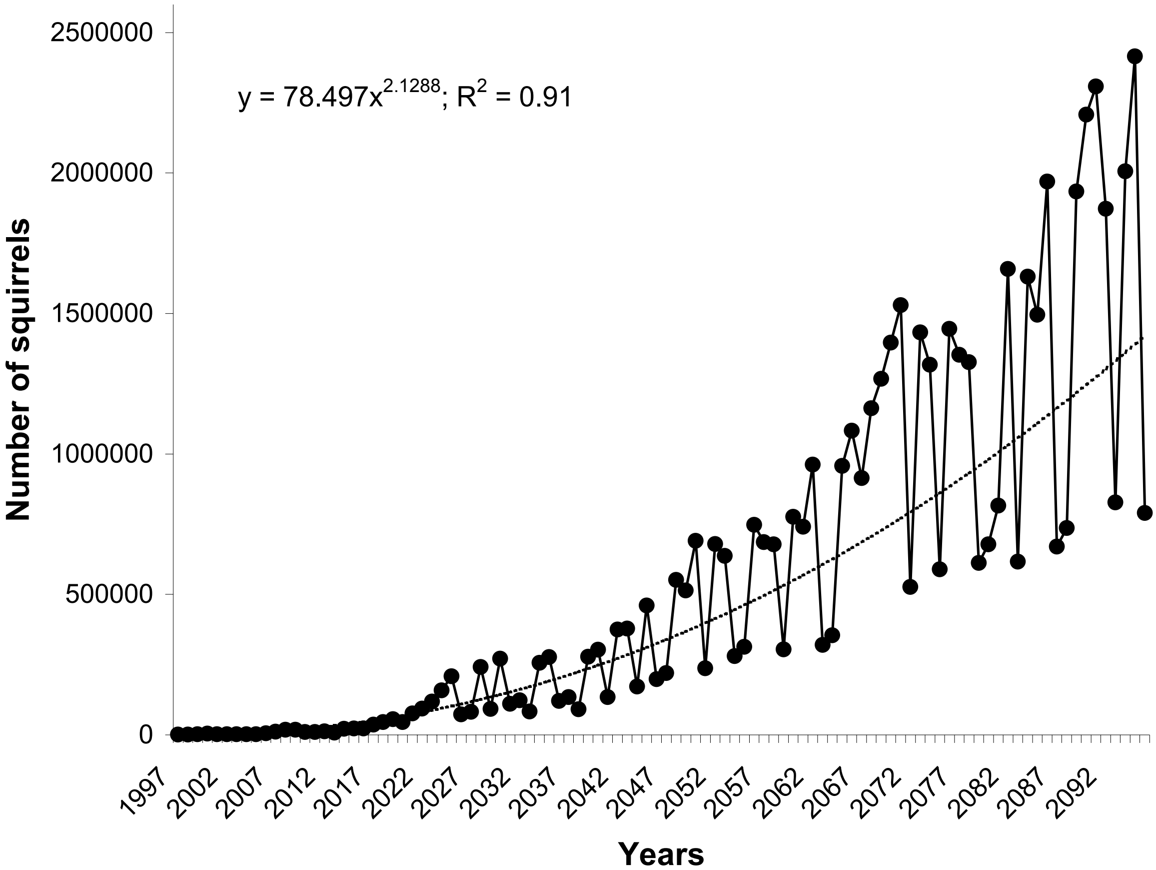


Figure 3.3.2. Average predicted grey squirrel population size in the scenario which simulated the grey squirrel spread in Switzerland from the source populations in Piedmont and the Ticino river. A random pattern of poor, good and mast year seed crops was used.

3.3.1. “Worst case” scenario

We also considered a second scenario without poor years in the random pattern of seed crops (worst case) in order to see the response of grey squirrels in a high quality habitat situation. According to this scenario the spread will be much faster and it will take only 20 years for the grey squirrel to colonise the area along the Ticino and the Lake Maggiore (Figs. 3.3.3.a,b). First populations in Switzerland are predicted in 2031-2041, with a progressively higher probability of grey presence in the model predictions. The two populations of Piedmont and Ticino are likely to join up between 2041 and 2051 (Figs. 3.3.3.b,c). The map of year 2076 shows a high probability for a large range expansion of the species covering most of Piedmont, Aosta Valley, and the western part of Lombardy.
The spread of the grey squirrel in Switzerland will start in the Canton Ticino, in the area south of the Swiss part of the Lake Maggiore, around the Lake of Lugano. Then, it will continue in a northerly direction in the Lepontine Alps, covering most of the Canton Ticino. In the last years of the simulation, the grey squirrel will also spread in a westerly direction in the area of the Pennine and Bernese Alps.
This simulation also illustrates the spread into France (south-eastern) that was reported previously.
The model predicts a maximum of 15,670 sub-populations totalling over 3.5 million individuals at the end of the simulation period (Fig. 3.3.4.). The fluctuations in population size between years are narrower than in the previous simulation. This is an effect related to the annual changes in the tree seed crops that in this case did not include poor years. Population size is predicted to remain below 1 million until 2018, and then to increase to over 3 million at the end of the simulation.

Switzerland is a mountainous country with good forestry cover (Fig. 3.3.5). Therefore, it is likely that in the future the grey squirrel would spread to all of the country, continuing afterwards to Austria and the rest of central and eastern Europe, where the species will find good habitats. Simulation of such a long period was beyond the scope of this report, however it must be pointed out that from Italy, France, and Switzerland the colonisation of Eurasia is only a matter of time.

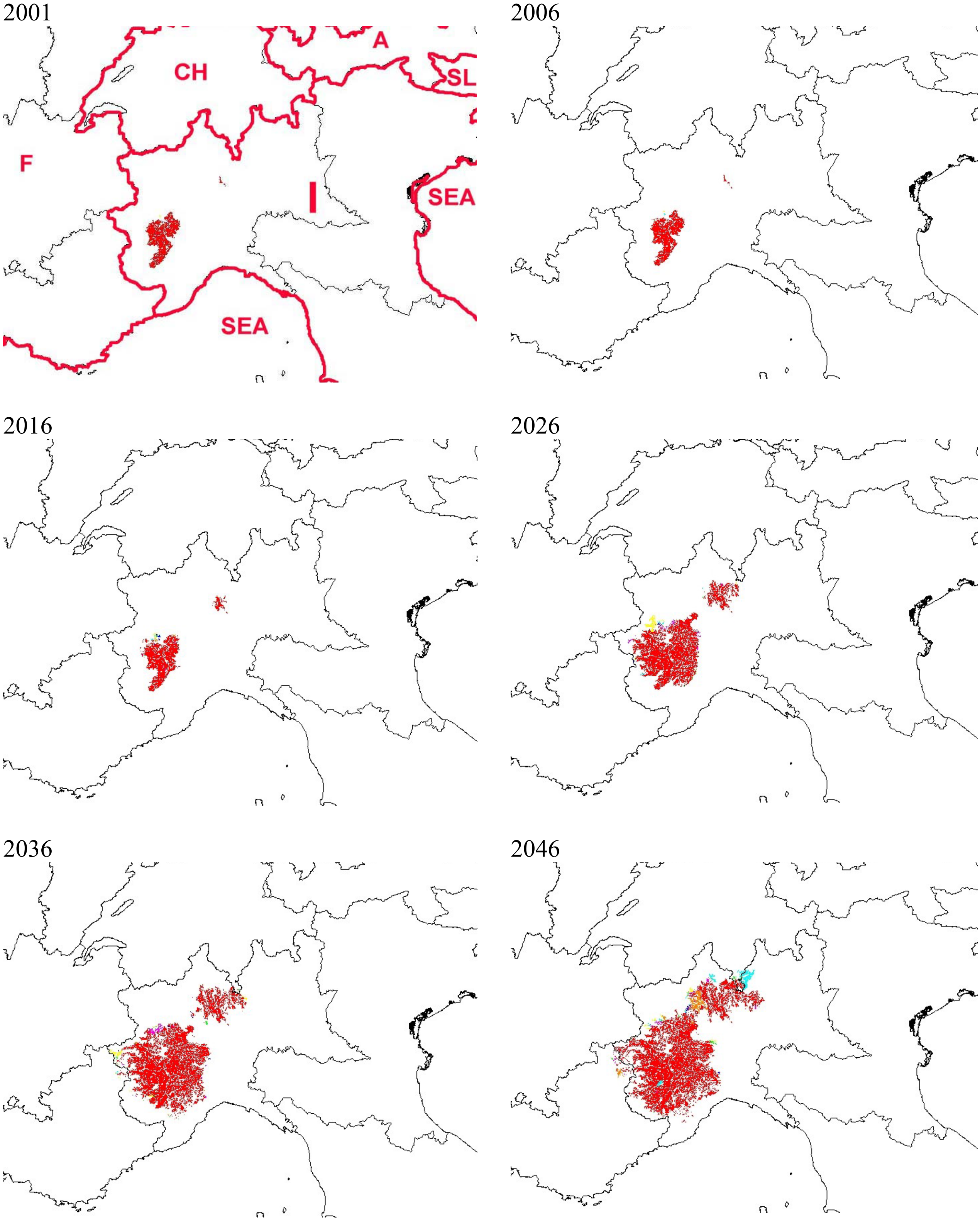


Figure 3.3.3.a. Simulation results illustrating the grey squirrel spread in Switzerland from 2001 to 2046 in a scenario with a random pattern without poor year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%. F = France, Ch = Switzerland, SL = Slovenia, I = Italy.

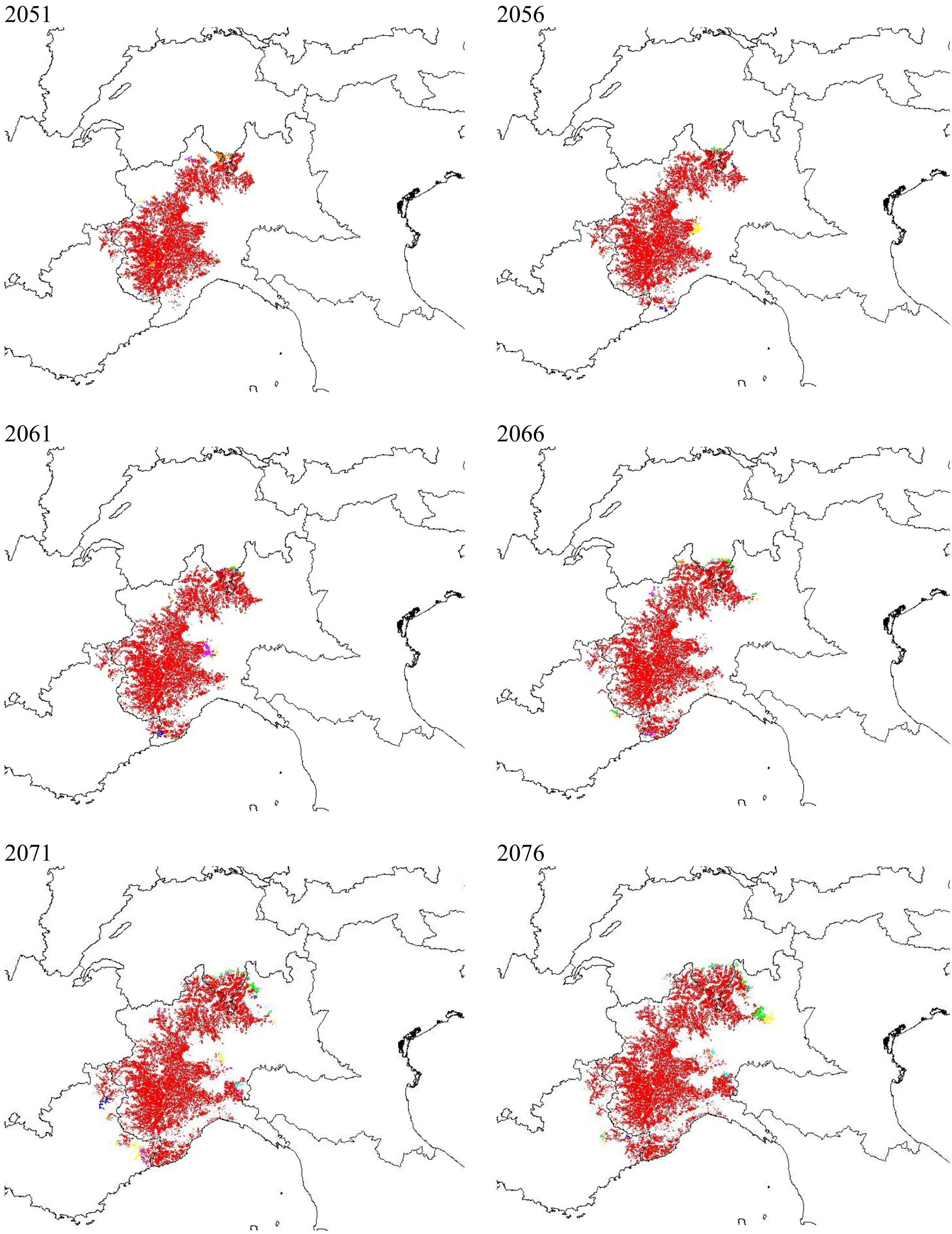


Figure 3.3.3.b. Simulation results illustrating the grey squirrel spread in Switzerland from 2051 to 2076 in a scenario with a random pattern without poor year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%.

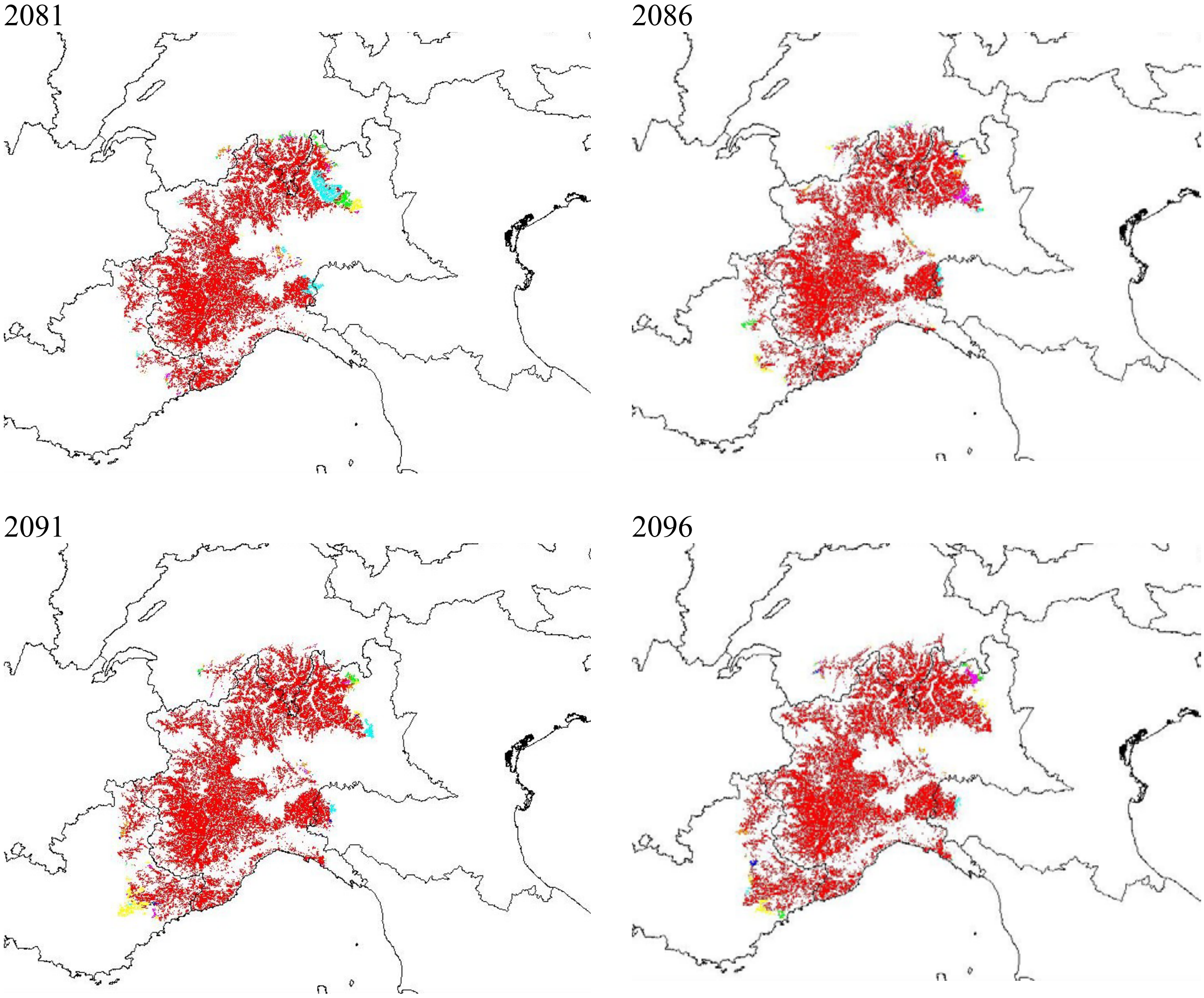


Figure 3.3.3.c. Simulation results illustrating the grey squirrel spread in Switzerland from 2081 to 2096 in a scenario with a random pattern without poor year seed crops. The source populations were in Piedmont and along the Ticino. Colour scheme: yellow 10-20% probability of grey squirrels colonising, green 30-40%, blue-40-60%, orange 70%, magenta 80%, red 90-100%.

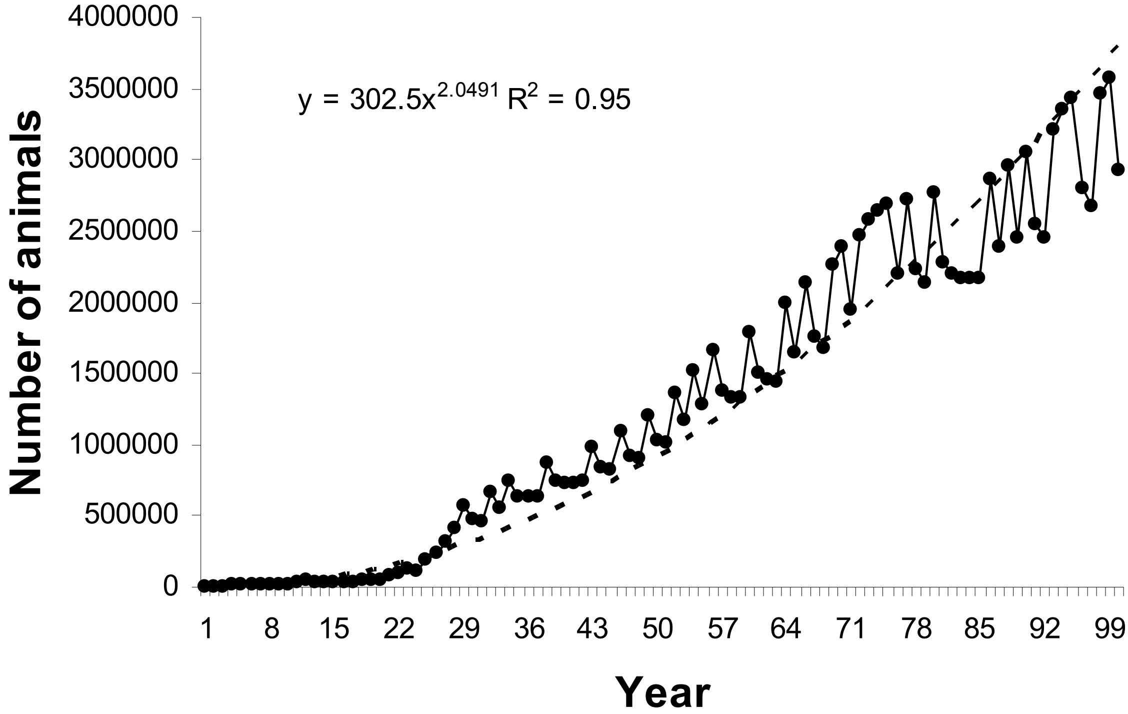


Figure 3.3.4. Average predicted grey squirrel population size in the scenario which simulated the grey squirrel spread in Switzerland from the source populations in Piedmont and the Ticino river. A random pattern without poor year seed crops was used.

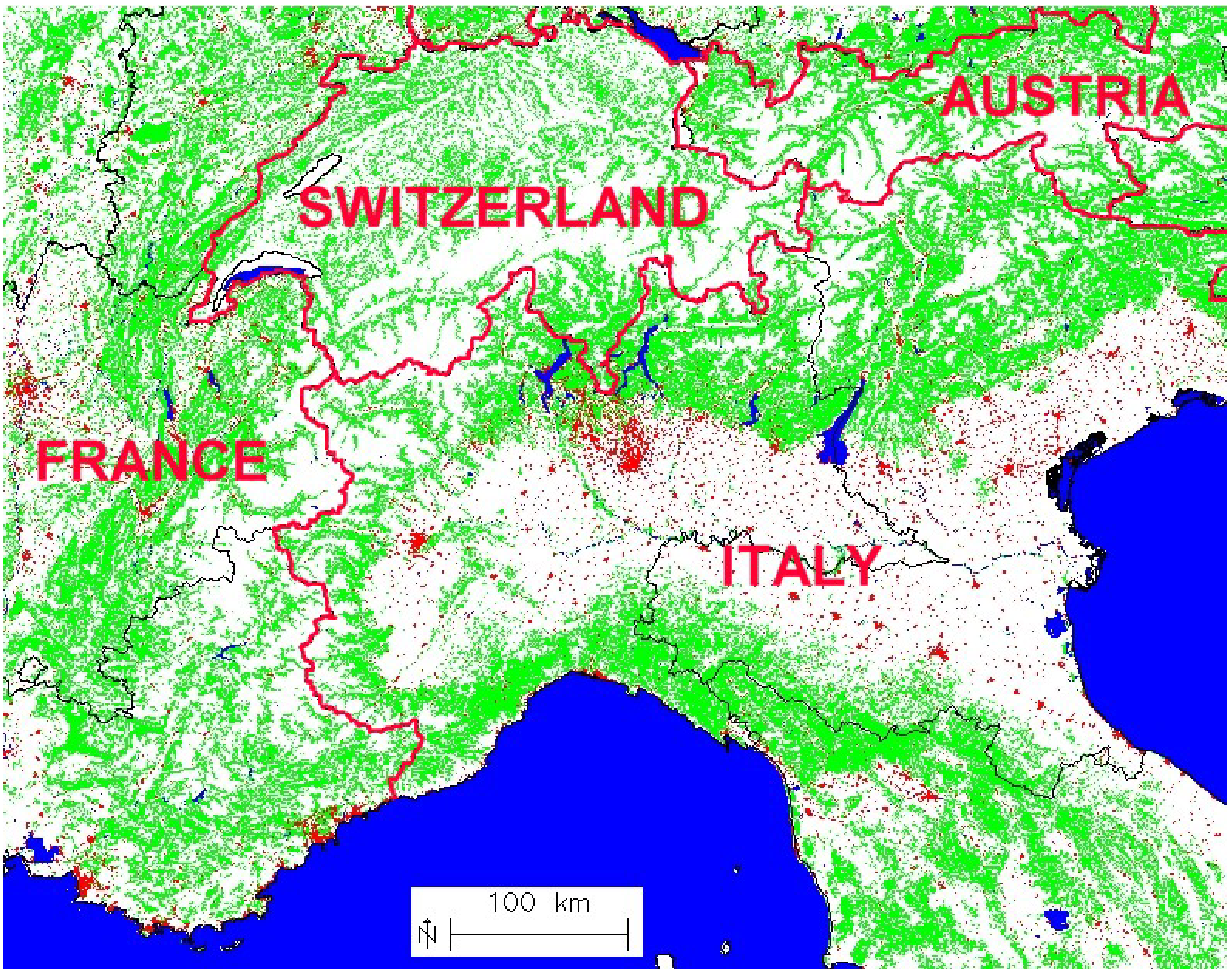


Figure 3.3.5. Forest cover (in green colour) in Switzerland and adjacent countries

3.4. Removing the small populations along the Ticino and in Genoa

The extent of the distribution of the two grey squirrel populations present along the Ticino and in Genoa Nervi is still small (Tattoni *et al.*, 2005; Venturini *et al*., 2005). The spread of the population in Genoa is considered difficult (Venturini *et al*., 2005) and currently there is no discussion about the possibility to control or eradicate it. The presence of the animals in a public park, where people are used to see and feed them, would make any intervention difficult from a social point of view. Any attempt would need a parallel effort in public education on the problems grey squirrels cause and the need to remove them. The situation along the Ticino is different, and the risk for Switzerland was highlighted in the past and is shown with more detail in this report. The National Wildlife Institute is presently co-ordinating a working group with the task to evaluate costs and the people and organisations that should be involved in the eradication of the population. This is finally happening after years in which an intervention was discussed only as a theoretical proposal.
If the eradication programme will go ahead, it is possible that the population will be removed in the next years. This is important, not only to eliminate the present risk for Switzerland, but also to create in Italy a test case in which a population of an alien species is removed. The experience would also be useful as a pilot study, to get information to prepare a more general control programme for the species.

In this last simulation, we wanted to evaluate the effect of the removal of the two populations in Genoa and Ticino on the spatial dynamics of the grey squirrel and the timescale of invasion of France and Switzerland. We thus compared the spread of the three populations (Piedmont, Ticino, and Genoa, Figs. 3.4.1.a,b, on the left), with a case where only the population in Piedmont remained (Figs. 3.4.1.a,b on the right).
Figure 3.4.1 illustrates the likely spread with and without the grey squirrel populations in Genoa and Ticino. The eradication of the population along the Ticino removes the risk of invasion of Switzerland for the next 100 years. The Piedmontese population will eventually spread to the region, entering Lombardy through a south-easterly direction, reaching the area of the Ticino only at the end of the century. If the eradication of the Ticino population can be achieved, it would approximately take 90 years from today for the grey squirrel to colonise the area again. This would postpone the risk for Switzerland for a century.
The effect of the removal of the population in Genoa for France is more limited. In the first 50-60 years the colonisation of France is due mainly to the westward spread of the Piedmontese population that will enter the country from the Alps, and then from the south. It is only after this period that the species will reach France also from Genoa (shaded orange in the maps). This has the effect of increasing the overall population size and the speed of spread. According to our predictions, in order to eliminate the risk for France, both populations of Piedmont and Genoa would have to be eradicated or at least controlled.
However, removing the population in Genoa will drastically reduce the spread in Italy in a south-easterly direction. The potential colonisation of the Apennine between Emilia-Romagna and Tuscany is predicted to be entirely due to the spread from Genoa, and without this population the grey squirrel will reach the very first part of the Apennine only at the end of the century. It must be underlined that in the Apennines there are two native subspecies of red squirrel, *S.v. italicus* and *S.v. meridionalis* (Toschi, 1965) that would be endangered by the spread of the grey squirrel. Thus, the removal of the American species from Genoa would be important to safeguard them.

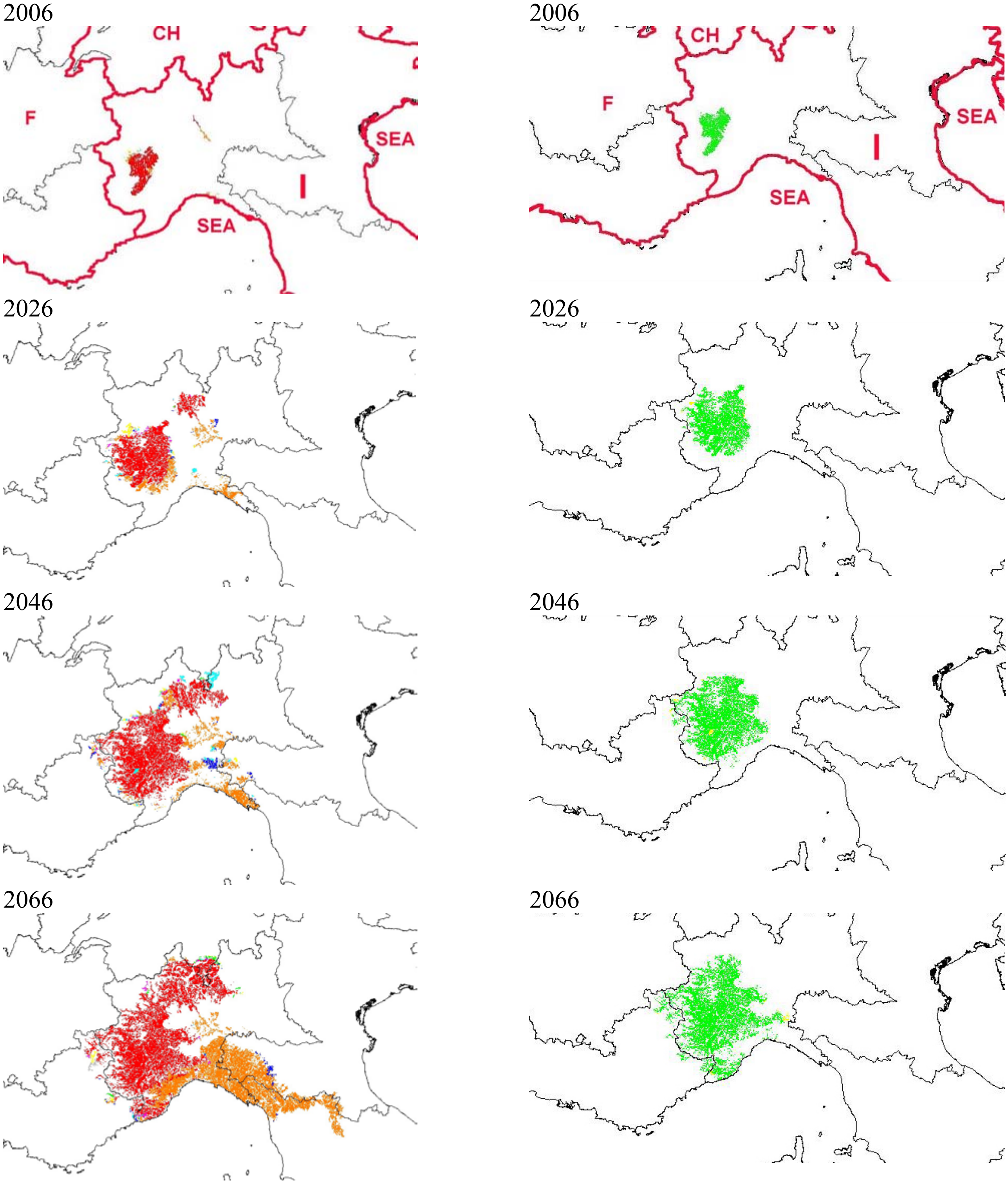


Figure 3.4.1.a. Simulation results comparing the grey squirrel spread from 2006 to 2066, in a scenario with no poor year seed crops, and where the three populations are spreading (left) or when the populations along the Ticino and in Genoa are removed (right). Maps on the left combine 2 scenarios based on different runs to better illustrate the effect of single populations. In maps on the left red and orange colours indicate high chance of grey squirrels colonising, blue intermediate, green and yellow low and grey very low probabilities. In maps on the right green indicate high chance of colonising, yellow intermediate, and grey very low probabilities.

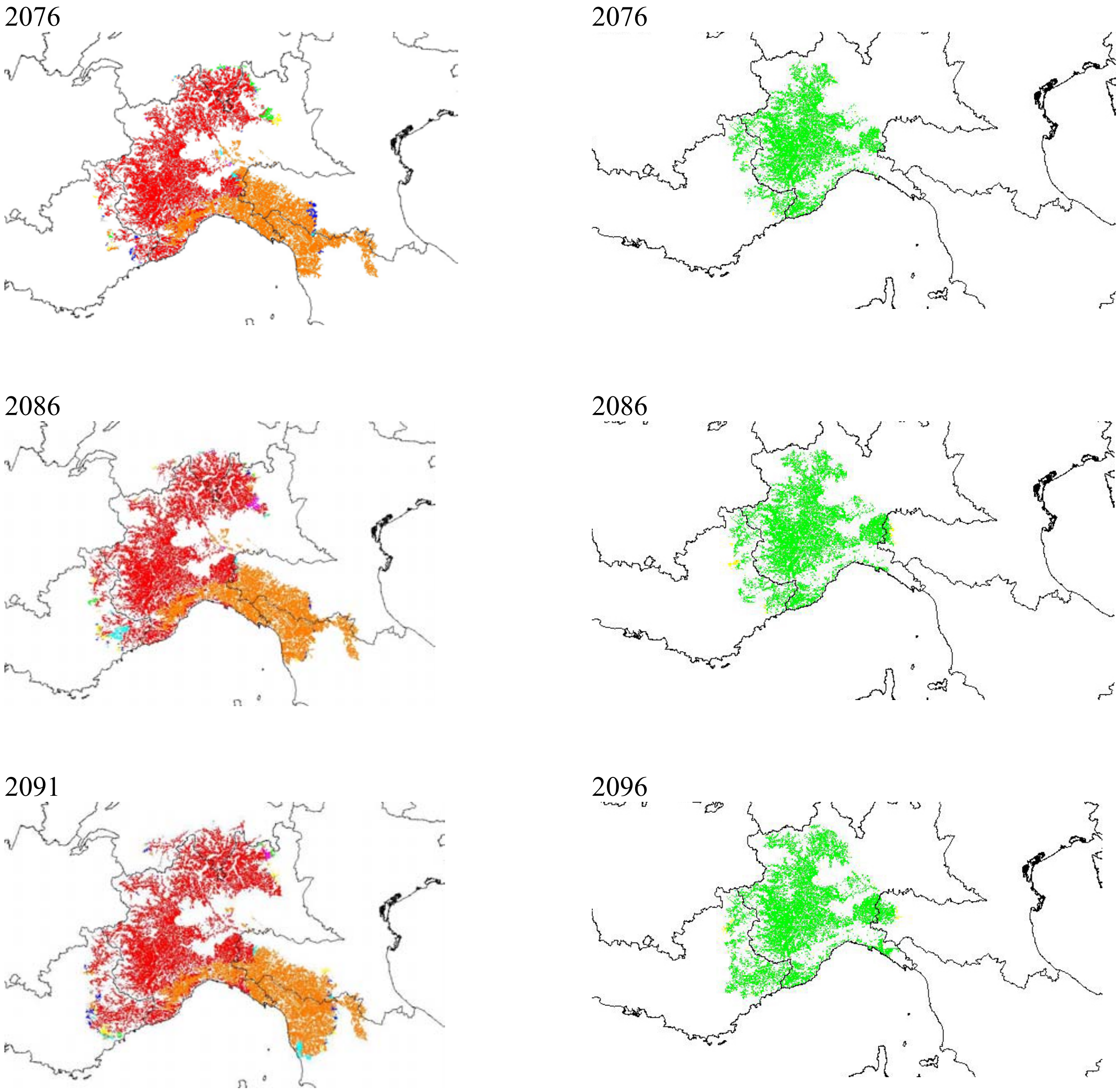


Figure 3.4.1.b. Simulation results comparing the grey squirrel spread from 2076 to 2096, in a scenario with no poor year seed crops, and where the three populations are spreading (left) or when the populations along the Ticino and in Genoa are removed (right). Maps on the left combine 2 scenarios based on different runs to better illustrate the effect of single populations. In maps on the left red and orange colours indicate high chance of grey squirrels colonising, blue intermediate, green and yellow low and grey very low probabilities. In maps on the right green indicate high chance of colonising, yellow intermediate, and grey very low probabilities.

4. DISCUSSION

Previous studies applying SEPM of grey squirrel expansion in Northern Italy predicted an increasing rate of spread in the next 20-30 years, with a dramatic increase of population size after colonisation of continuous broad-leaf forests in the Prealps (Lurz *et al*., 2001; Tattoni *et al*., 2005). In this work we simulated the future spread of the species in Italy, France and Switzerland. For the first time, the expansion of all three extant populations in Piedmont, Ticino, and Genoa were considered and simulated together.
Simulations were performed considering two possible scenarios: in a “best case” scenario we considered a random pattern of seed production, with poor, good and mast years, and varying the life history parameters accordingly. A second “worst case” scenario did not included years with poor seed crop. If the habitat is diverse (i.e. woodlands are composed of different tree species) grey squirrels may not experience poor years like established populations The more diverse tree species composition, the more likely that one of the species is producing seeds in any given year.

4.1. The spread in Italy

The first simulation of the grey squirrel spread in Italy did not include the population in Genoa Nervi. This population is still localised in an urban area and the spread in the nearby hilly area is considered difficult, although not impossible (Venturini *et al*. 2005). Thus, we considered a first scenario where the grey squirrels could not spread from Genoa Nervi. SEPM simulations indicate that in sixty years grey squirrels will colonise the western Alps, the internal hilly system in Piedmont, and the area along the Ticino river from Switzerland to the confluence in the Po river. Between 2060 and 2080 the two populations will join and then the expansion will continue in all of Piedmont, part of Liguria and western part of Lombardy.
According to our simulations, it will take a few years for the grey squirrel to colonise the hilly area of Monferrato and Langhe in Piedmont. In part of this area the forestry cover is quite extensive and composed of mixed broadleaf trees (De Biaggi *et al*., 1990), a good habitat for the grey squirrel. This hilly area is characterised by the presence of extensive hazelnut plantations, and the economy of some districts relies entirely on this production. Hazelnut growers already suffer a loss of production due to feeding by the edible dormouse (*Glis glis*), a native nocturnal arborial rodent. The loss where the hazelnut plantations are near woodlands, a situation that is quite common, could range between 10-30% (Currado & Scaramozzino, 1989; Giraudo, 1991; Piero Bertone AscoPiemonte pers. comm.). The arrival of the grey squirrel could probably increase the damage to a level that may influence the profitability of the production and the survival of this activity, at least in some areas. Considering the proximity to the hilly area of the grey squirrel range recorded in 1999/2000, when the last survey on the species was conducted, we urge the necessity to start a new survey, in order to check the spread of the species in the last years.
In the Ticino, dispersal tends to occur along the wooded banks of the river, and it would take about 15-30 years for the grey squirrel to colonise the park and the surrounding areas. A previous study applying SEPM of grey squirrel expansion in the Ticino valley already predicted the spread of the grey squirrel in the Italian part (Tattoni *et al*., 2005). The model forecasted the spread of grey squirrels in the whole study area within the next 40 years and the concomitant reduction of native red squirrels if no action is taken. An efficient control was considered still possible, and the result was considered mainly determined by the spatial distribution and total woodland size of the ‘target’ trapping areas. The main result of that

simulation was that immediate actions have to be taken, as a delay in grey squirrel control will result in the population augmenting and spreading beyond the park borders, which would increase the logistic problems of a successful containment of grey squirrels. However, at the moment, a local control programme is still under discussion.
The population size of the two joint populations (Piedmont and Ticino) remains under 1 million in the first 70 years, and then increases to 2 million at the end of the simulation. The situation will be worse if the population in Genoa Nervi will spread outside the urban area. In this case, the squirrel will colonise the eastern part of the Ligurian region until 2070 and part of the region toward Emilia-Romagnia and Tuscany, in a south-east direction, towards 2068-2073. The size of the three populations from Piedmont, Ticino and Genoa, could reach in this case up to 4 million animals.
In the worst case scenario, where seed production was modelled with no poor years, the output maps show that the spread will be faster. At the end of the simulations, the Piedmontese region will be colonised completely, as well as Liguria, the western part of Lombardy, and the northern part of the Apennines.

4.2. The spread in the Alps and in France

The landscape in the Alps is suitable for squirrels, and grey squirrels are likely to spread over a wide area in the next decades. Alpine forests are continuous and composed at a lower altitude of mixed broad-leaves, sometimes with conifers, that are a good habitat for squirrels. Only in the upper part of the valleys, coniferous forests replace the broadleaves, constituting a large sub-optimal area for grey squirrels. The grey squirrel is considered more adapted to deciduous forests, thus it may reach lower densities in coniferous forests where cones are more difficult to handle (Lurz *et al.* 1995). However, considering the ability of the grey squirrel to colonise coniferous forests or plantations in England and Scotland (Wauters et al., 2000), we would also predict the colonisation of the continuous alpine coniferous forests, especially in areas connected to deciduous forest.
In the western Alps, larch (*Larix decidua*) is the main species, sometimes mixed with spruce. Less frequent are mixed forests with spruce and silver fir, or composed of Scots pine. Larch cones are difficult to handle and, in general, cones are less suitable than the fruits of deciduous trees. However, Scots pine forests may act as a stepping stone in the colonisation of these valleys, due to the energy content and size of seeds that may be manipulated more easily by grey squirrels. Furthermore, the presence of mixed forests could assure a continuous food availability. For example, tree seed crop in spruce changes heavily from year to year, with a random pattern that foresees a mast crop year, usually followed by a year with crop failure and 2-3 years with an intermediate production (Mencuccini *et al.*, 1995). The tree seed production in larch is lower but with a reduced fluctuation between years (Wauters *et al.*, 2005). Thus, in mixed forests with larch and spruce, the main coniferous forest on the western Italian Alps, squirrels could respond to a cone crop failure in spruce adapting their behaviour and foraging more frequently on larch (Wauters et al., 2005). At present we do not know exactly, how the grey squirrel could perform in alpine coniferous forests, because the species is not yet present there. But, considering the information available from other areas, it is reasonable to assume that the species would adapt to this new habitat.
Our predictions suggest that it will take 30-40 years for grey squirrels to start invading the Alps up to the coniferous forests and about 70-75 years, since 1996, to cross the border between Italy and France. Squirrels get close to the border much sooner, but the alpine habitats (size/type of patch) make for a very slow crossing. The expansion will progressively cover all the valleys in the province of Turin south of the Valley of Lanzo, the alpine valleys

in the province of Cuneo, and the north-eastern part of Liguria. Considering a situation with no poor seed years in the simulation (worst scenario) the spread is faster. In 20 years the grey squirrels are predicted to colonise the western Alps in the provinces of Turin and Cuneo, and in about 30 years they will reach France

4.3. The spread in Switzerland

The SEPM simulation of grey squirrel expansion along the Ticino river woodlands confirm the risk posed by this population. According to our simulations, the grey squirrels will invade Switzerland in 40-50 years in the best case scenario, and in 25-30 years in the worst case. The spread of this species northwards will be into contiguous deciduous forests along the east bank of Lake Maggiore, including southern parts of Switzerland (Canton Ticino).

In the scenario with no poor years, the spread is predicted to continue in a north direction in the Lepontine Alps, covering most of the Canton Ticino, and then reaching the Pennine and Bernese Alps in a western direction.

A previous SEPM simulation indicated that the implementation of a control plan could significantly reduce grey squirrel expansion, and that complete extirpation of the Ticino population is still possible, if the trapping areas are carefully planned. Hence, it is absolutely essential and urgent to determine the current distribution of grey squirrels along the two rivers of the Ticino and to implement a control programme for this species. It must be underlined that probably the population along the Ticino is still small, and that a success in the eradication here could be used as an example for similar action in other areas. A broad political support, at community, international (Switzerland – Italy), national and regional (Lombardy, Piedmont) levels is essential for a successful control campain in the Ticino Parks.

Considering the forestry cover in Switzerland, in the future the grey squirrel would spread in all the country, continuing afterwards to Austria and the rest of Europe. Simulation of such a long period was beyond the scope of this report, also because increasing the time involved increases the uncertainty of the model outputs. However, it must be pointed out that from Italy, France, and Switzerland the colonisation of Eurasia is only a matter of time.

5. CONCLUSION

The only effort of grey squirrel eradication from Italy was attempted in 1997, but it failed (Bertolino & Genovesi, 2003). Since then, in spite of many attempts to illustrate the dangers of grey squirrel spread (Lurz *et al*. 2001; Bertolino & Genovesi, 2003, 2005; Tattoni *et al*. 2005; Genovesi & Bertolino, 2001; Recommendation No. 78/1999 and Recommendation December 2005 from the Bern Convention) and urging the necessity to do something to stop the spread of this species, no action has been taken.

Modelling the range expansion of an alien species over large time and spatial scales limits the accuracy of predictions. Habitat maps such as the Corine landcover data only contain broad habitat types and lack detailed information on species composition or age structure. This means that assumed carrying capacities for grey squirrels and life history parameters have to be based on averages. The suitable forest habitat is also likely to change considerably over the time frame of the model simulations. Nor were we able to consider the likely impacts of possible climate change on vegetation composition. The results should therefore be seen as an illustration of possible spread based on currently available habitat and life history data.

In the period considered by our simulations (100 years since 1996), the grey squirrel is likely to spread to the north-western part of Italy, and colonise areas in France and Switzerland. SEPM simulations indicated that grey squirrel spread across Europe will not be like an epidemic that will sweep through Italy, France and Switzerland but a slow process potentially measured in decades. It will speed up if seed crops are good or if people translocate grey squirrels (a process we cannot predict) as happened in other cases (Aloise & Bertolino, 2005). However, given the predicted population growth, there is a need to act soon. Once populations exceed 2 million squirrels as in some scenarios and they have spread into the alpine belt or in large hilly areas covered by mixed deciduous woodlands, it will be logistically difficult to effectively control them. France may have the option for a while to control them in the alpine passes in the future, but once grey squirrels spread along the coast this attempt may become very difficult.

This also applies to Switzerland. The low altitude of the areas that connect Italy to Switzerland along the Ticino and the Lake Maggiore, and the compositon of the forest with mixed deciduous woodlands, will make the control very difficult. There is an urgent need for action there while the population of grey squirrels is still localised.

The SEPM presented here supports the conclusion that the grey squirrel could successfully colonise large part of northern Italy, France and Switzerland and, in a long term, a wide area of continental Eurasia. This expansion of the alien species on a continental scale could threaten the survival of the red squirrel and have a severe impact on the woodland ecosystems and on economic timber production. The successful containment of further grey squirrel spread will require local cooperation of the Park's authorities, such as the Ticino Park in Lombardy and Piedmont, with the Regional Parks and Wildlife Services of the Regions of Lombardy and Piedmont, and, at the national level, the Department of the Environment (Nature Conservation Service) and the National Wildlife Service. Furthermore, the Swiss and the French authorities must be told of the risk of grey squirrel invasion and the establishment of grey squirrel populations within their countries in the next 30-70 years, and potentially sooner, when dispersing individuals and further translocations are considered.

The National Wildlife Institute is presently co-ordinating a working group with the task to organize the eradication of the population along the Ticino. Our simulations indicated that the eradication of this population removes the risk of invasion of Switzerland for the next 100 years. The Piedmontese population will eventually spread entering Lombardy, but reaching again the Ticino only at the end of the century. Removing the population at Genoa will drastically reduce the spread in Italy in a south-easterly direction along the Apennines between Emilia-Romagna and Tuscany, safeguarding two native subspecies of red squirrel, *S.v. italicus* and *S.v. meridionalis*. However, this is not enough to eliminate the risk for France. The colonisation of this country is due mainly to the westward spread of the Piedmontese population that will enter the country from the Alps, and then from the south. In order to eliminate the risk for France, both populations of Piedmont and Genoa would have to be eradicated or at least controlled.

6. REFERENCES

Aloise G., Bertolino S., 2005. Free-ranging population of the Finlayson's squirrel *Callosciurus finlaysonii* (Horsfield, 1824) (Rodentia, Sciuridae) in South Italy. Hystrix It. J. Mamm. (n.s.) 16 (1) (2005): 70-74.

Bertolino S., Genovesi P, 2003. Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia. Biological Conservation 109: 351-358.

Bertolino S., Genovesi P., 2005. The application of the Euroepan strategy on invasive alien species: an example with introduced squirrels. Hystrix Italian Journal of Mammalogy, 16 (1): 59-69.

Bertolino S., Currado I., Mazzoglio P.J., Amori G., 2000. Native and alien squirrels in Italy. Hystrix, Italian Journal of Mammalogy, 11 (2): 49-58.

Currado I., Scaramozzino P.L., 1989. Modificazioni ambientali e danni da roditori arboricoli in Piemonte. Mus. Reg. Sci. Nat. Torino: 255-258.

Currado I., Scaramozzino P.L., Brussino G., 1987. Note sulla presenza dello Scoiattolo grigio (*Sciurus carolinensis* Gmelin) in Piemonte. Annali della Facolta di Scienze Agrarie dell'Universita di Torino 14: 307-331.

Genovesi P., Bertolino S., 2001. Linee guida per il controllo dello Scoiattolo grigio (*Sciurus carolinensis*) in Italia. Quaderni Conservazione della Natura 4. Min. Ambiente - Ist. Naz. Fauna Selvatica, pp 52.

Giraudo A., 1991. Danni da Ghiro ai noccioleti dell'Alta Langa. Alba Pompeia, XII (II): 47-54

Dagnall J, Gurnell J, Pepper H. 1998. Bark-stripping by gray squirrels in state forests of the United Kingdom: a review. In: Steele MA, Merritt JF, Zegers DA, (Ed). Ecology and Evolutionary Biology of Tree Squirrels. Virginia Museum of Natural History, Special Publication, n. 6: 249-261.

De Biaggi E., Stoppa T., Scotta M., 1990. Proposta per una suddivisione del Piemonte in settori eco-geografici. Rivista Piemontese di Storia Naturale, 11.

Gurnell J., 1983. Squirrel numbers and the abundance of tree seed supplies. Mamm. Rev. 13: 133-148.

Gurnell J., 1987. The natural history of squirrels. Helm, London, 1987.

Gurnell J., 1991. The grey squirrel. In: Corbet GB, Harris S, (eds). The Handbook of British Mammals. Blackwell Scientific Publications, Oxford: 186-191.

Gurnell J., 1996. The effects of food availability and winter weather on the dinamics of a grey squirrel population in southern England. Journal of Applied Ecology 33: 325-338.

Gurnell J., Pepper H., 1993. A critical look at conserving the British red squirrel *(Sciurus vulgaris*). Mammal Rev. 23: 127-137.

Gurnell J., Wauters L.A., Lurz P.W.W., Tosi G., 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. J. Anim. Ecol. 73: 26-35.

Hewson C.M., Fuller R.J., 2003. Impacts of grey squirrels on woodland birds: an important predator of eggs and young? BTO Research Report No. 328, British Trust for Ornithology and Woodland Heritage.

Kenward RE, Hodder KH, Rose RJ, Walls CA, Parish T, Holm JL, Morris PA, Walls SS, Doyle FI, 1998. Comparative demography of red squirrels (*Sciurus vu*lgaris) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. J. Zool. Lond. 244: 2-21.

Koprowski J.L., 1991. Response of fox squirrels and gray squirrels to a late spring early summer food shortage. Journal of Mammalogy 72: 367-372.

Koprowski J.L. 1994. *Sciurus carolinensis*. Mammalian Species 480. American Society of Mammalogists.
Lurz P.W.W., Garson P.J., Rushton S.P. 1995. The ecology of squirrels in spruce dominated plantations: implications for management. Forest Ecology and Management 79: 79-90.
Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P., Shirley, M.D.F. 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. Landscape Ecology 16: 407-420.
Mencuccini M, Piussi P, Zanzi Sulli A, 1995. Thirty years of seed production in a subalpine Norway spruce forest: Patterns of temporal and spatial variation. Forest Ecology and Management 76: 109-125.
Montgomery S.D., Whelan J.B., Mosby H.S. 1975. Bioenergetics of a woodlot grey squirrel population. J. Wildl. Manage. 39: 709-717.
Mosby H.S. 1969. The influence of hunting on the population dynamics of a woodlot grey squirrel population. J. Wildl. Manage. 33: 709-717.
Rushton S.P., Lurz P.W.W., Fuller R., Garson P.J. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. Journal of Applied Ecology 34: 1137-1154.
Rushton S.P., Lurz P.W.W., South A.B., Mitchell-Jones A. 1999. Modelling the distribution of red squirrels (*Sciurus vulgaris*) on the Isle of Wight. Animal Conservation 2: 111-120.
Sainsbury AW, Nettleton P, Gilray J, Gurnell J, 2000. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. Animal Conservation 3: 229-233.
Shorten M., 1951. Some aspects of the biology of the grey squirrel (Sciurus vulgaris) in Great Britain. Proceedings of the Zoological Society, London 121: 427-459.
Smith, D.F.E. 1999. Grey squirrel, *Sciurus carolinensis*, population dynamics and feeding biology in a conifer forest. Ph.D. Thesis Queen Mary & Westfield College, University of London, UK.
Smith D, Gurnell J, 1997. The ecology of grey squirrels in conifer forests: population ecology and feeding. In: Gurnell J, Lurz PWW (eds) The conservation of red squirrels, *Sciurus vulgaris* L. People Trust for Endangered Species: 109-119.
Tattoni C., Preatoni D.G., Bertolino S., Martinoli A., Tosi G., Wauters L.A., 2005. Modeling the expansion of grey squirrels (Sciurus carolinensis) in Lombardy, northern Italy: implications for squirrel control. In: Nentwig W. et al. (Eds.), Biological Invasions - From Ecology to Control. NEOBIOTA 6: 149-164.
Tattoni C., Preatoni D.G., Lurz P.W., Rushton S. P., Tosi G., Martinoli A., Bertolino S., Wauters L.A. (In press). Modelling the expansion of grey squirrels (Sciurus carolinensis) in Lombardy, Northern Italy: implications for squirrel control. Biological Invasion.
Thompson D.C. 1978. The social system of the grey squirrel. Behaviour 64: 305-328.
Toschi, A., 1965. Fauna d'Italia VII. Mammalia: Lagomorpha, Rodentia, Carnivora, Ungulata, Cetacea. Calderini, Bologna.
Venturini M., Franzetti B., Genovesi P., Marsan A., Spanò S. 2005. Distribuzione e consistenza della popolazione di Scoiattolo grigio *Sciurus carolinensis* Gmelin, 1788 nel levante genovese. Hystrix It. J. Mamm. (n.s.) 16 (1) (2005): 53-58
Wauters LA, Gurnell J, 1999. The mechanism of replacement of red by grey squirrels: a test of the interference competition hypothesis. Ethology 105: 1053-1071.
Wauters L.A., Lurz P.W.W., Gurnell J. 2000. The interspecific effects of grey squirrels (*Sciurus carolinensis*) on the space use and population demography of red squirrels (*S. vulgaris*) in conifer plantations. Ecological Research 15: 271-284.
Wauters LA, Currado I, Mazzoglio PJ, Gurnell J, 1997a. Replacement of red squirrels by introduced grey squirrels in Italy: evidence from a distribution survey. In: Gurnell J, Lurz

PWW, (eds) The Conservation of Red Squirrels, *Sciurus vulgaris* L. . People Trust for Endangered Species: 79-88.

Wauters L., Gurnell J., Currado I., Mazzoglio P.J., 1997b. Grey squirrel *Sciurus carolinensis* management in Italy – squirrel distribution in a highly fragmented landscape. Wildlife Biology 3: 117-124.

Wauters L.A., Bertolino S., Adamo M., Van Dongen S., Tosi G. 2005. Food shortage disrupts social organization: the case of red squirrel in conifer forests. Evolutionary Ecology 19: 375-404.

Westervelt J.M., Shapiro M., Goran W., Gerdes D. 1990. Geographic Resource Analysis Support System, Version 4.0 User's Reference manual, USACERL ADP Report N-87/22.