Using GRASS and Spatial Explicit Population dynamics Modelling as a conservation tool to manage grey squirrel (*Sciurus*carolinensis) in northern Italy

Clara Tattoni*, Damiano G. Preatoni*, Peter W.W. Lurz[†], Steven P. Rushton[†], Guido Tosi*, Sandro Bertolino [‡], Lucas A. Wauters*

Spatially Explicit Population dynamics Models, GIS, conservation, grey squirrel, red squirrel

Abstract

A recently discovered population of the North American grey squirrel (*Sciurus carolinensis*), introduced to Ticino Park, Lombardy (N Italy), is likely to spread into continuous prealpine broadleaf forests of Lombardy and the south of Switzerland.

We used GRASS GIS and Spatially Explicit Population Dynamics Models as a conservation tool to predict the spread of grey squirrels and to test different management options in a 20000 $\rm km^2$ area around Ticino Park.

GRASS GIS has been used in two phases of the work: at first to build the habitat and the squirrel distribution maps to be processed by the model and finally to map the model output. Scripting in a Linux-shell environment allowed us to integrate the GIS capabilities with the population dynamics program, written in 'C' programming language, and assured the data stream from GRASS to the model and back.

The integrated approach of SEPM and GIS allowed us to predict grey squirrel expansion in the Ticino Regional Park and surrounding areas, including the Italian boundaries with Switzerland in a 40 years time frame. We were also able to evaluate the contemporary persistence of native red squirrels as the population of greys increase for the same time span. Results showed us that grey squirrels have the potential to reach Switzerland in the next two decades. Competition simulation showed also that greys spread will have a deep impact over the native red squirrels. We were able to produce predicted density map for both species. We then used the model to test the effect of different control strategies in order to suggest public administration a cost effective action plan to stop the invasion process.

1 Introduction

In many ecosystems, the introduction of invasive, alien species is claimed to be the second most important reason for loss of biodiversity, after the destruction and fragmentation of natural habitats, causing the extinction or decline of native species in the regions where they have been introduced [38] [46], [24, 19]. Alien species interfere with the native fauna by different ecological processes: predation, interspecific competition or acting as vector or reservoir of (new) diseases [16], [30], [4], [35], [17]. Introduced species not only present a serious ecological problem, but also a socio-economical, and political one [11], [31]. Many alien species cause direct economic damage to human activities (farming, forestry, zoo-technology, disease risk), but nevertheless their control often becomes an emotional issue, in particular with mammal pest species which often have a "charismatic" appeal [22], [45], [1], [2].

A well documented case of competition by an invasive alien species is the wide-scale replacement of the native Eurasian red squirrel (*Sciurus vulgaris*) by the introduced eastern grey squirrel (*Sciurus carolinensis*) in the British Isles and in parts of northern Italy. The rapid increase of the grey squirrel's distribution range, coincided with a dramatic

^{*} Dipartimento "Ambiente-Salute-Sicurezza", Università degli Studi dell'Insubria, Varese, Via J.H. Dunant 3, I-21100 Varese (VA), Italy tel. +39-0332-421538 Fax: +39-0332-421554 e-mail: clara@uninsubria.it, prea@uninsubria.it

[†] IRES, School of Biology, University of Newcastle upon Tyne, Devonshire Bldg, Newcastle Upon Tyne, NE1 7RU, UK

[‡] DI.VA.P.R.A. Entomology and Zoology, University of Turin, I-10095 Grugliasco (TO), Italy

decline of the range of the native red squirrel [16, 39], and the grey squirrel has now replaced the red squirrel over much of its range in Great Britain, Ireland, and in the fragmented landscapes it currently occupies in Piedmont, northern Italy [16],[39], [34], [23],[2]. An essential parameter to assess the risk of extinction of red squirrel populations, and plan effective management strategies for controlling the invasive species, is the rate at which replacement will occur, which mainly depends on factors that facilitate the spread of the alien species. For grey squirrels major factors are landscape structure (connectivity between good habitats) and abundant food supplies [6] [41], [27].

Spatially explicit population dynamics models (SEPM) have been developed to combine spatial variables and species' life-history traits. The drawback of these models is that their performance is sensitive to the accuracy of the estimates of the life-history parameters input, and, thus, the models can only be used for species for which detailed data of population parameters (fecundity, mortality, dispersal distance, density) in different habitat types are available ([28], [29]).

Fortunately, many studies on the population dynamics of red and grey squirrels have produced reliable estimates of these life-history traits under variable environmental (habitat) conditions (see Table 1 for references). Thus, accurate SEPM models can be applied to predict current and future distribution and population size, the effects of red and grey squirrel interspecific competition and of disease spread within and between grey and red squirrel populations ([28]; [29]; [23]).

The replacement of red by grey squirrels that is taking place in Piedmont, northern Italy, does not only have serious implications for red squirrel conservation in Italy, but also for the whole of Europe ([8]; [10]; [9]; [23]). Political concern about the lack of action in many countries has been expressed by the Permanent Commission of the Bern Convention, which has produced several recommendations (n. 57, 77 and 78 of 1997) urging countries to eradicate alien invasive species where possible.

Until now, no control has taken place, and recently grey squirrel populations have been discovered in mixed deciduous woodland belts along the Ticino river, the natural border between Lombardy (east) and Piedmont (Figure 1) [7], [2]. Since these woodlands connect with contiguous hardwood along the eastern side of Lake Maggiore and into Switzerland, immediate monitoring and control of this population is a priority for the local authorities responsible for wildlife management and conservation.

Here we use a spatially explicit population dynamics model (SEPM) linked to a Geographic Information System (GIS) which has been tested on grey squirrels in Britain and Piedmont, Italy [28], [23] to: (i) illustrate the potential expansion of this introduced species in and beyond the Ticino Regional Park, Lombardy, and (ii) test the effects of different control scenarios on the expansion rate, future distribution and population size of the grey squirrels. We propose effective control measures for the alien species and discuss the implications of our findings in relation to the survival of the native red squirrel in Europe.

2 Material and Methods

2.1 Study area and data collection

The Ticino Regional Park in Lombardy, North-Italy, extends for about 908 km² along the east-side of the Ticino river from where it leaves Lake Maggiore to its confluence with the Po river at Pavia (Figure 1). Our study area extended for 40 km in all directions from the park boundaries.

The current distribution of grey (and red) squirrels in the park was investigated using hair-tube surveys [15]. Twenty-one transects of 15 hair-tubes each were placed in various parts of the park and followed for a three year campaign (1999 - 2001) [7]. Hairs were identified as pertaining to red or grey squirrels using a reference collection and following methods in [15].

Since grey squirrel density (population size) in 2001 was not known, we assumed that in this early colonisation phase, none of the habitat blocks had reached carrying capacity,

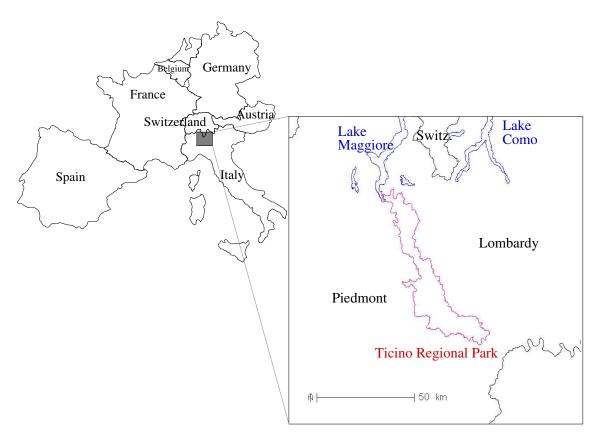


Figure 1: Study area location: Parco Lombardo della Valle del Ticino (boundaries in red), northen Italy, Europe.

and that squirrel occurred at the same (low) density of 0.33/ha in all colonised blocks. This extrapolated to an initial population size of 150 grey squirrels in nine habitat blocks (sub-populations, see Figure 2) and used as the starting point for the SEPM model.

2.2 Squirrel habitat suitability

The major areas utilised by grey squirrels are broad leaf and to some extend conifer woodlands and parks, although they will feed on maize in fields and on fruit in orchards ([13]; [14]; [39]; [41]).

In order to predict grey squirrel range expansion, we obtained land cover data for the regions of Piedmont and Lombardy in digitised format at 250 m resolution (CORINE Land Cover, [26]). Habitat types were classified using CORINE-biotopes, and were derived from different sources: the Ticino Regional Park forestry map (10 m resolution) for areas inside the park that are not in the Varese province (Lombardy), the vegetation map of the Varese province (10 m resolution, [36]), and CORINE Land Cover for the other areas of Lombardy. The Varese province covers the northern part of the park and surrounding areas, reaching the Swiss border. Land cover and vegetation type data were edited and a single habitat map, see figure 3, with a 250 m resolution was produced with the aid of the grass module r.mapcalc [33]. Each 250 m by 250 m cell was characterised by a single habitat type. As a result of the resolution scale of the land cover data, some small woodlands (< 3.2 ha) suitable for grey squirrels may not have been recognised as squirrel habitat, making model predictions of grey squirrel spread more conservative by reducing the total available habitat.

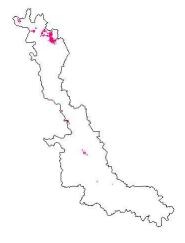


Figure 2: Grey squirrel initial distribution: the species is present in red blocks inside Ticino Park boundaries.

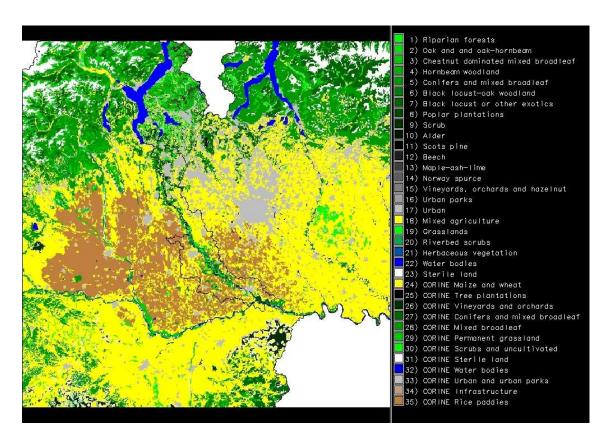


Figure 3: Habitat map used as input for the model. Types marked with the suffix CORINE apply only outside Park and Varese province boundaries.

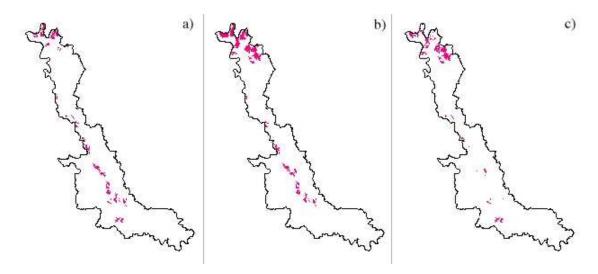


Figure 4: Habitat blocks (in red) where the management of grey squirrel take place in each of three simulated scenarios. a) 'Best habitat' scenario; b) 'Extended control' scenario; c) 'Target-area control' scenario.

2.3 Control maps

We assumed that the grey squirrel population would be be managed using the so called 'dispersal control', i.e. a fixed rate of individuals would be removed each year while the population was still small and spreading. We tested different schemes in the attempt to make a compromise between the effectiveness and the (logistic) feasibility of control. In all the runs squirrels were removed inside the park area and only in blocks covered by woodland, since these were more likely to host a squirrel population. Moreover, with a total park woodland cover of about 2000 ha and woodlot size ranging from 0.098 to 865 ha, we judged it impossible to trap squirrels in all woodlots. Therefore, we created three different control scenarios selecting different numbers of woodland blocks in which to trap grey squirrels according to different combinations of block size and woodland type.

- 'Best habitat' scenario: grey squirrels were removed only in good habitat blocks having a carrying capacity greater than 1/ha and larger than 60 ha, with 18 blocks, covering 2800 ha, occurring across the whole park's territory (Figure 4a).
- 'Extended control' scenario: we extended the control to habitat blocks with a carrying capacity greater or equal to 1 grey squirrel/ha (for habitat types see Table 1). Control was applied in 17 patches, each one larger than 60 ha, for a total trapping area of 4600 ha, with larger control blocks in the northern part of the park compared to the previous control scheme (Figure 4b).
- 'Target-area control' scenario: the same woodland habitat categories as in the previous scenario the blocks selected for control covered a smaller total area (2600 ha) and had an asymmetric distribution within the Park (Figure 4c).

2.4 Model outlines

The model used 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 4.2 [37] and GRASS 5 [33] were the GIS used to store and retrieve habitat information and the model outputs. The GIS undertakes data manipulation and abstraction and provides input for the second component, which consists of a program simulating the population dynamics of grey squirrels and their interactions and dispersal within the GIS-held landscape.

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. The model simulate also a random pattern of seed production among 2 poor, 2 good and one mast year. As squirrel life history parameters

Table 1: Habitat description and squirrel densities (squirrels/ha) based on field work and observations for the digitised landcover types (at 250 m resolution). Unsuitable habitats indicated by '-' had a value of zero in the model.

Land cover type	Grey squirrel	References	Red squirrel	References		
Dinanian famata	D_{max}	[2]	D_{max}	[2]		
Riparian forests 1.0 Oak and oak- 5.0		[3] [13]; [20]	0.3 0.8	[3] [20]; [42]		
hornbeam Hornbeam wood- land	2.5	Authors' estimates	0.4	Authors' estimates		
Black locust-oak woodland	1.0	Authors' estimates	0.2	[42]		
Black locust or other exotics	0.1	Authors' estimates	0.1	Authors' estimates		
Mixed broadleaf dominated by chestnut	5.0	[12]; [21]; [40]	1.1	[43]; [42]		
Mixed deciduous(CORINE)	2.0	[21]; [18]	0.4	[42]; Authors' estimates		
Beech	2.0	[12]	0.4	[5]; [43]		
Maple-ash-lime	5.0	Authors' estimates	1.1	Authors' estimates		
Conifers and mixed broadleaf	1.5	[12]; [13]; [18]	1.3	[43]		
Scots pine	0.3	[32]; Authors' estimates	0.5	Authors' estimates		
Norway spruce	0.2	[32]; Authors' estimates	0.35	[44]; Authors' estimates		
Poplar planta- tions	0.3	[3]	0.1	[39]; [41]; Authors' estimates		
Pastures (CORINE)	0.2	Authors' estimates	0.1	Authors' estimates		
Alder	0.1	Authors' estimates	0.1	Authors' estimates		
Cliffs, rock	-		-			
slides, riverbeds						
Scrub	-		-			
Herbaceous vege- tation	-		_			
Mixed agricul- ture	0.013	[3]; [23]	0.005	[3]		
Maize, wheat Rice	0.013	[3]; [23]	0.005	[3]		
Permanent grass- land	0.013	Authors' estimates	0.005	Authors' estimates		
Vineyards, or- chards and hazelnut woods	1.0	Authors' estimates	0.2	Authors' estimates		
Urban areas	0.013	Authors' esti- mates; [21]	0.013	[40]		
Urban parks Water bodies	1.0	Authors' estimates	0.02	Authors' estimates		
Sterile land	_		_			
Scrub, newly	_		_			
planted areas and uncultivated grassland						
Infrastructure	-		-			

7

like mortality and fecundity vary with annual tree seed abundance, we varied the life history parameters accordingly. A detailed description of the original model, used for investigating the spread of the grey squirrel and decline of the red squirrel in East Anglia, England, is given by Rushton (1997) [28]. The model was applied and fully tested in Piedmont, details are described in Lurz 2001 [23]. The population dynamics program was written in the programming language 'C' and integrated with the GIS component in a UNIX-shell environment.

GIS capabilities have been used to build the habitat map from different sources, the landscape in which squirrels can move figure 3, the initial distribution of the species and different pattern of control.

Suitable habitats were defined according to type and size, composition and distribution of habitat blocks was used to identify blocks in which the two squirrel species could be found. The carrying capacity, i.e. the number of individuals who can be supported by a given area [25], of each type of habitat for red and grey squirrels we relied on published estimates as shown in Table 1. When literature data were lacking, carrying capacity was estimated from values for similar habitats.

Some Land Cover and vegetation types are not suitable habitats for squirrels but animals can move through them when dispersing. Individuals were allowed to disperse to blocks of habitat that were below the carrying capacity for each species. In addition if there were no suitable habitat blocks available for occupation within the maximum dispersal distance of 10 km, dispersers were assumed to die. As some individuals are likely to move beyond the 10 km dispersal distance parameter used [21], model predictions of grey squirrel expansion were intentionally conservative.

From the habitat map we created a clump map of 18463 habitat blocks, and for each block area and centroids have been calculated. Species distribution and control raster maps were processed by r.volume using the habitat clump map in order to have all data referred to the same block frame.

Clumps are the key to pass data from GRASS to the model and back: a shell script has been used to rearrange the output of GRASS modules r.clump and r.volume in an ASCII file suitable for being processed by the population dynamic model. Each record in this file contains clump number, habitat type, number of squirrels, coordinates of clump centroids, clump size (i.e. number of cells) and a binary value for the control mechanism.

The spatial information and the biological parameters have been processed by the SEPM program who then outputs files that can be used for statistical analysis and for creating maps since they contain the clump number and the number of squirrels predicted for each replicate of the simulations. By the aid of another shell script run directly into GRASS we were able to display density maps for each year of the simulation.

3 Results

We run the the model through different scenarios, in order to: (i) predict grey squirrel expansion in the Ticino Regional Park and surrounding areas, including the Italian boundaries with Switzerland; (ii) predict contemporary persistence of native red squirrels; and (iii) test the effects of different control strategies.

All the runs started from the situation known in year 2001 and forecasted squirrel population dynamics for the following 40 years. As the model is a stochastic one, we ran it 10 times over for each set of inputs for 40 year time span. So for each scenario we then ran the models 400 times. Results presented are all averages of those multiple runs.

3.1 Grey squirrel spread

The landscape in and around Ticino Regional Park is very suitable for squirrels. If the starting population is not managed, our results indicate that grey squirrels are likely to spread over a wide area over the next 40 years. The model predicts 4103 sub-populations totalling approximately 370000 individuals (see also Table2). The spatial spread of grey squirrel population over the simulation period at ten year intervals is shown in Figure 5. The expanding population first occupies the northern part of the Park and during the

	-			•					
Year	No control	50%	SD	80%	SD	50%	SD	80%	SD
2001	150	150	-	150	-	-	-	-	-
2006	115	60	14	46	6	34	7	36	6
2011	247	73	16	41	11	31	8	26	5
2016	1639	58	9	14	9	33	7	20	9
2021	19311	125	38	10	13	48	10	9	10
2026	58485	200	72	8	12	107	37	7	10
2031	109720	145	52	2	5	102	47	2	4
2036	201521	200	114	0	0	91	61	0	0
2041	370237	205	171	0	0	64	37	0	0

Table 2: Average predicted grey squirrel population size in the 'no control' and in the 'target area control' scenarios. Results are presented at five years intervals. SD: standard deviation.

first ten years it occurs only in the mixed broad-leaf woodlands dominated by chestnut. During the next ten years it also spreads into the black locust woods (Figure 5a, b). Our predictions suggest that it will take more than twenty years for grey squirrels to start invading the southern part of the Park and to spread outside the Park boundaries reaching Switzerland (Figure 5c, d). Squirrels are predicted to show different patterns of spread: inside the Park dispersion tends to occur along the wooded riverbank of Ticino, while outside the spread has no preferential direction. The model simulations indicate that it will take up to 15 years to reach carrying capacity within Ticino Park. Dispersal beyond park boundaries may therefore be slow and the rapid implementation of control measures is likely to be successful in slowing or even preventing further spread.

3.2 Grey squirrel control scenarios

The same model has been used to predict grey squirrel dynamics according to different control schemes. A fixed level of control has been introduced as a further demographic factor inside the model (the others are birth rate, natural mortality, immigration, emigration) affecting the population in single habitat blocks. The number of replicates and the time frame used in the control simulations are the same used in the previous run, 10 replicates for 40 years and all the others parameters are left unchanged.

For each control scenario, the control maps previously defined, we tested the effect of a removal rate of 50% and 80% individuals. Squirrel removal starts in 2005 for each scenario, so for the first three years of the simulation no squirrels are removed. Comparing the surface to be managed in the different control scenarios shown in Figure 4 and the simulation outputs we were able to find the best compromise between effective management and number of patches to control. The scenario called "target control" best fitted those requests, results and comparison with the uncontrolled spread are presented in Table 2 while the "best habitat" scheme was proved to be ineffective.

3.3 Red and grey squirrel competition

To evaluate the effects of grey squirrel expansion on the native red squirrel population we also ran the competition model. This simulation runs in two steps: it calculates the number of squirrels for each species in each block according to the appropriate life history parameters and then applies competition effects of grey on red squirrels in the blocks where both species co-occur.

The number of red squirrels for the next run is the results of the competition interaction. We assumed red squirrel were present in the landscape at a density of 0.16 ind/hectare for each woodland block. As there was no information about the real density in the study we used an average density as a starting condition. Red squirrels start to go extinct in the park woodlands from 2020 as greys continue to expand and their numbers increase (see Figure 6). During the first 10-15 years red squirrel population is increasing from the an average density to carrying capacity. This is a model artefact related to input

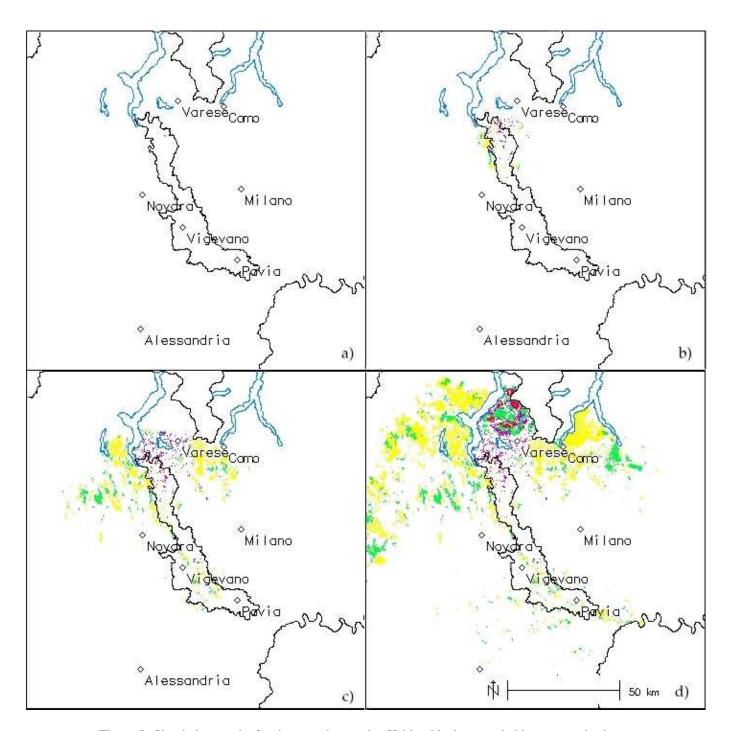


Figure 5: Simulation results for the spread scenario. Habitat blocks occupied by grey squirrels are evidenced in colour. Different colours represent the different densities (individuals per hectare) according to the legend below. a) year 2011; b) year 2021; c) year 2031; d) year 2041.

 Gray squirrel density Ind/hectar

 0.002
 1
 2
 3
 4
 5

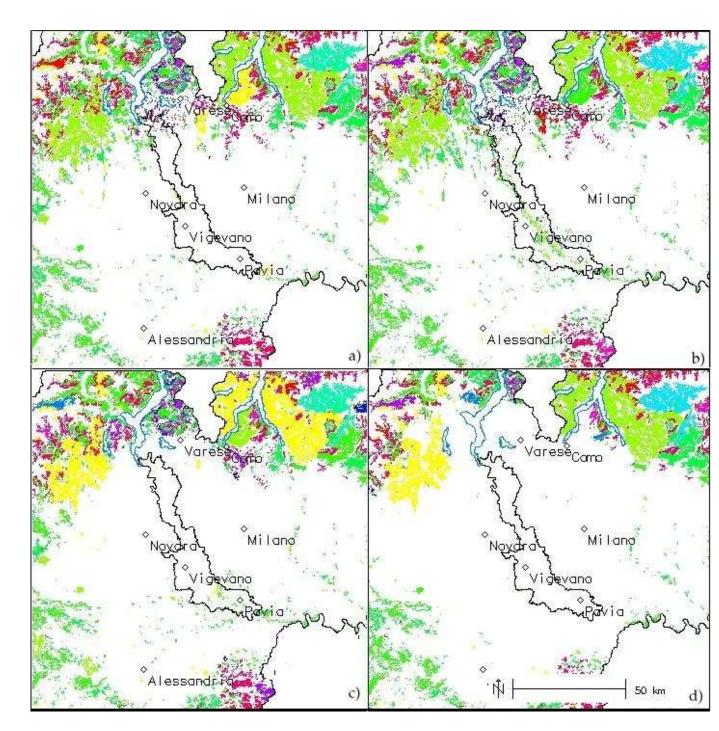


Figure 6: Contraction of red squirrel habitat in the competition scenario. Different colours represent the different predicted densities (individuals per hectare) according to the legend below. Pictures show the output at 10 year intervals. a) year 2011; b) year 2021; c) year 2031; d) year 2041.

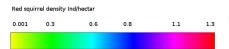


Table 3: Average predicted population size of grey and red squirrels for the competition model runs. Results are presented at five years intervals. SD: standard deviation.

	Individuals				Populations			
Year	Grey	SD	Red	SD	Grey	SD	Red	SD
2001	150	-		-		-		-
2006	112	15	206644	7984	6	2	2728	191
2011	274	87	267800	4307	9	5	4073	159
2016	1828	646	298100	512	40	17	4390	22
2021	21347	6138	284113	1270	492	116	4403	58
2026	61839	11446	274293	2693	1204	168	4020	98
2031	112908	13756	230043	6621	2047	182	3189	128
2036	208198	24588	221213	6753	3004	176	2805	180
2041	374636	19302	179204	10200	4120	131	1959	129

conditions at an average density for the whole landscape. Red squirrels reach equilibrium (based on carrying capacities for the different habitat types) in the landscape from the 10th to 20th year of simulation. The population is fluctuating around 280,000 individuals and the species is spread in all woodland blocks (Table 3). After the 20th year of simulation greys begin to be an impacting factor and the predicted 21,000 grey squirrels are likely to drive the red squirrel to extinction within the Park boundaries. Populations of red squirrels seems to persist longer in the northern part of the study area where the pre alpine mountains are covered with conifer forests (Fig. 6), and the habitat is slightly more suitable for reds than for greys. However, reds go extinct in the central and most of the southern part of the study area within the 40 yr-run simulations.

4 Discussion

Without control, grey squirrels will invade Switzerland within the next two decades, and, concomitantly, the size and distribution of local populations of native red squirrels will be reduced. Simulating different grey squirrel control or removal scenarios suggests that: (i) efficient control is possible and mainly determined by the spatial distribution and woodland size of the 'target' control areas; and (ii) immediate actions must be taken, since delay in grey squirrel control will result in the population increasing and spreading, which makes the problems of successful containment more difficult.

The coupled use of SEPM and GIS proved to be a useful tool in conservation as it allowed us to test the effectiveness of different strategies, including the no action option, providing wildlife managers with maps showing the consequences of each strategy. Control maps analysis allowed use to identify the best cost/effective action control plan to prevent the spread of the invasive grey squirrels. Those maps, theoretically, could already be used on the field to place traps. However caution must be used, as model scenarios were based on surveys that may underestimate the real distribution range and current population size of grey squirrels. In addition no information was available about the presence of the species outside the park boundaries, and so we assumed it was absent. For all these reasons our predictions can be conservative and we suggest a combination of grey squirrel monitoring and public participation survey to map grey squirrel presence, which may also help increase public awareness. Moreover future surveys can be used to improve model performance and to test the reliability of our predictions. Successful containment of further grey squirrel spread will require local co-operation between Italian and Swiss authorities involved in wildlife management.

Acknowledgements

The study was financed by Parco Regionale della Valle del Ticino Lombardo to Istituto Oikos, ONG, Varese. CT holds a fellowship from Fondazione Fratelli Confalonieri, Milano.

References

- [1] J.F. Barr, P.W.W. Lurz, M.D.F. Shirley, and S.P. Rushton. Evaluation of immuno-contraception as a publicly acceptable form of vertebrate pest species control: the introduced grey squirrel in britain as an example. *Environmental Management*, 30(342-351), 2002.
- [2] S. Bertolino and P. Genovesi. 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, 2003.
- [3] S. Bertolino, L.A. Wauters, L. De Bruyn, and G. Canestri-Trotti. Prevalence of coccidia parasites (protozoa) in red squirrels (*Sciurus vulgaris*): effects of host phenotype and environmental factors. *Oecologia*, 137:286–295, 2003.
- [4] A.E. Byrom. Dispersal and survival of juvenile ferrets *Mustela furo* in new zealand. *Journal of Applied Ecology*, 39:67–78, 2002.
- [5] M. Cagnin, G. Aloise, F. Fiore, V. Oriolo, and L.A. Wauters. Habitat use and population density of the red squirrel *Sciurus vulgaris meridionalis* in the sila grande mountain range (calabria, south italy). *Italian Journal of Zoology*, 67:81–87, 2000.
- [6] C.D. Fitzgibbon. The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. *Journal of Applied Ecology*, 30:736–742, 1993.
- [7] L. Fornasari, R. Galbussera, and M. Sacchi. Progetto per il monitoraggio e l'eradicazione dello scoiattolo grigio nel parco regionale della valle del ticino lombardo. Technical report, ., 2002.
- [8] P. Genovesi. Guidelines for eradication of terrestrial vertebrates: a european contribution to the invasive alien species issue. Council of Europe, tpvs65e-2000, 2000.
- [9] P. Genovesi and S. Bertolino. *The Great Reshuffling: human dimensions of Invasive Alien Species*, chapter Human dimension aspects in invasive alien species issues: the case of the failure of the Grey squirrel eradication project in Italy. IUCN, Gland, Switzerland and Cambridge, UK, 2001.
- [10] P. Genovesi and S. Bertolino. Linee guida per il controllo dello scoiattolo grigio (*Sciurus carolinensis*) in italia. *Quaderni di Conservazione della Natura*, 4(5-52), 2001.
- [11] L.M. Gosling and SJ. Baker. The eradication of muskrats and coypus from britain. *Biological Journal of the Linnean Society*, 38:39–51, 1989.
- [12] J. Gurnell. *The Handbook of British MammalsThe grey squirrel*, chapter The grey squirrel, pages 186–191. Blackwell Scientific Publications, Oxford, 1991.
- [13] J. Gurnell. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern england. *Journal of Applied Ecology*, 33:325–338, 1996.
- [14] J. Gurnell. *Thetford Forest Park: the ecology of a pine forest.*, chapter Conserving the red squirrel. Forestry Commission, Edinburgh, 1996.
- [15] J. Gurnell, P.W.W. Lurz, and H. Pepper. *Practical techniques for surveying and monitoring squirrels*. Forestry Commission Practical Notes.
- [16] J. Gurnell and H. Pepper. A critical look at conserving the british red squirrel *Sciurus vulgaris. Mammal Review*, 1993.
- [17] J. Gurnell, L.A. Wauters, P.W.W. Lurz, and G. Tosi. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology*, 73:26–35, 2004.
- [18] J. Gurnell, L.A. Wauters, D.G. Preatoni, and G. Tosi. Spacing behaviour, kinship and dynamics of the grey squirrel in a newly coolnised deciduous woodland in north italy. *Canadian Journal of Zoology*, 79:1533–1543, 2001.
- [19] IUCN, Gland, Switzerland. Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species.

[20] R.E. Kenward, K.H. Hodder, R.J. Rose, C.A. Walls, T. Parish, J.L. Holm, P.A. Morris, S.S. Walls, and F.I. Doyle. Comparative demography of red squirrels (*Scirurus vulgaris*) and grey squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *Journal of Zoology, London*, 224, 1998.

- [21] J.L. Koprowski. Sciurus carolinensis. American Society of Mammalogists, 1994.
- [22] J.A. Lever. Competing values and moral imperatives: An overview of ethical issues in biological control. *Agriculture and Human Values, London*, 1994.
- [23] P.W.W. Lurz, Rushton S.P., L.A. Wauters, S. Bertolino, I. Currado, P. Mazzoglio, and M.D.F. Shirley. Predicting grey squirrel expansion in north italy: a spatially explicit modelling approach. *Landscape Ecology*, 16, 2001.
- [24] R.N. Mack, D. Simberloff, WM. Londsdale, H Evans, M. Clout, and F.A. Bazzaz. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, 10, 2000.
- [25] E.P. Odum. Ecology. Holt Rinehart and Winston, 1975.
- [26] Commission of the European Communities. Corine. land cover, guide technique. Directorate of Environement, Nuclear Safety and Civil Protection, Office of Official Publications of the European Communities Luxembourg., 1993.
- [27] A. Rodriguez and H. Andrén. A comparison of eurasian red squirrel distribution in different fragmented landscapes. *Journal of Applied Ecology*, 36, 1999.
- [28] S.P. Rushton, P.W.W. Lurz, R. Fuller, and P.J. Garson. 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, 1997.
- [29] S.P. Rushton, P.W.W. Lurz, R. Fuller, and J. Gurnell. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the uk? *Journal of Applied Ecology*, 37, 2000.
- [30] A.W. Sainsbury, P. Nettleton, J. Gilray, and J. Gurnell. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. *Animal Conservation*, 3, 2000.
- [31] C. Shine, N. Williams, and GÃijndling. A guide to designing legal frameworks on alien invasive species. IUCN. Environmental Policy and Law Paper No. 40. IUCN, Gland, Switzerland.
- [32] D. Smith and J. Gurnell. *The Conservation of Red Squirrels* Sciurus vulgaris, chapter The ecology of the grey squirrel in conifer forest. People's trust for Endangered Species, London, 1997.
- [33] GRASS. Development Team. *GRASS. 5.0 Users Manual*. ITC. IRST, Trento, Italy, 2002.
- [34] D. O' Teangana, S. Reilly, W.I. Montgomery, and J. Rotchford. The distribution and status of the red squirrel (*Sciurus vulgaris*) and grey squirrel (*Sciurus carolinensis*) in ireland. *Mammal Review*, 30.
- [35] D.M. Tompkins, A.W. Sainsbury, P. Nettleton, D. Buxton, and J. Gurnell. Parapoxvirus causes a deleterious disease in red squirrels associated with uk population declines. *Proceedings of the Royal Society, London B*, 269, 2002.
- [36] G. Tosi and A. Zilio. Conoscenza delle risorse ambientali della provincia di varese – progetto sit fauna. Technical report, Provincia di Varese, Settore Politiche per l'Agricoltura e Gestione Faunistica, Varese, Italy, 2002.
- [37] U.S.Army. *GRASS. 4.1 Reference Manual*. U.S. Army Corps of Engineers, Construction Engineering Research Laboratories, Champaign, Illinois, 1993.
- [38] P.M. Vitousek, C.M. D'Antonio, L.L. Loope, and R. Westbrook. Biological invasions as global environmental change. *American Scientist*, 84, 1996.
- [39] L.A. Wauters, I. Currado, P.J. Mazzoglio, and J. Gurnell. *The Conservation of Red Squirrels*, Sciurus vulgaris, chapter Replacement of red squirrels by introduced grey squirrels in Italy: evidence from a distribution survey. People's trust for Endangered Species, London, 1997.

- [40] L.A. Wauters and J. Gurnell. The mechanism of replacement of red by grey squirrels: a test of the interference competition hypothesis. *Ethology*, 105, 1999.
- [41] L.A. Wauters, J. Gurnell, I. Currado, and P.J. Mazzoglio. rey squirrel *Sciurus carolinensis* management in italy squirrel distribution in a highly fragmented land-scape. *Wildlife Biology*, 3, 1997.
- [42] L.A. Wauters, J. Gurnell, D.G. Preatoni, and G. Tosi. Effects of spatial variation in food availability on spacing behaviour and demography of eurasian red squirrels. *Ecography*, 24, 2001.
- [43] L.A. Wauters and L. Lens. Effects of food availability and density on red squirrel *Sciuris vulgaris* reproduction. *Ecology*, 76, 1995.
- [44] L.A. Wauters, P.W.W. Lurz, and J. Gurnell. 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, 2000.
- [45] P.C.L. White and S.J. Whiting. Public attitudes towards badger culling to control bovine tuberculosis in cattle. *Veterinary Record*, 147, 2000.
- [46] M. Williamson. Biological invasion. Chapman and Hall, London, 1996.