

APPLICATION OF MODELLING TECHNIQUES
TO MANAGE A POPULATION OF GREY SQUIRRELS
(*SCIURUS CAROLINENSIS*) IN LOMBARDY, NORTHERN
ITALY, AND ANALYSIS OF PARAMETERS ESTIMATES
USED IN SIMULATIONS

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ABSTRACT - Grey squirrel (*Sciurus carolinensis*), an invasive alien species, is currently replacing the native Eurasian red squirrel (*Sciurus vulgaris*) in British Isles and north-west Italy. Grey squirrel has recently been reported in the Ticino Park (Lombardy region, NW Italy) and the species is likely to spread in the woodlands connecting Italy to other European countries. We used GRASS Geographical Information System (GIS) and Spatially Explicit Population Dynamics Models (SEPM) as a conservation tool to predict the spread of grey squirrels and to test different management options in the Ticino Regional Park and surrounding areas in a 40 years time frame. The integrated approach of SEPM and GIS allowed us to suggest public administration a cost effective action plan to stop the invasion process. We also analyse the parameters used in the model highlighting some missing data in literature: we can address future field study with the aim to improve model performance.

Key words - Geographic Information Systems, grey squirrel, red squirrel, simulation, Spatially Explicit Population Dynamics Models

RIASSUNTO - *Modelli per la gestione di una popolazione di Scoiattolo grigio (Sciurus carolinensis) in Lombardia e stima dei parametri usati nelle simulazioni.* La sostituzione da parte dello Scoiattolo grigio (*Sciurus carolinensis*), specie alloctona e invasiva, dello Scoiattolo rosso (*Sciurus vulgaris*), specie autoctona Europea, é attualmente in corso nelle Isole Britanniche e nell'Italia nord occidentale. Lo Scoiattolo grigio é stato recentemente segnalato nel Parco Lombardo della Valle del Ticino (Italia nord occidentale) ed é probabile che di diffonda nelle foreste che connettono l'Italia agli altri paesi europei. In questo lavoro il Sistema Informativo Geografico GRASS e i modelli denominati *Spatially Explicit Population Dynamics Models* sono stati usati come strumento per prevedere la diffusione dello Scoiattolo grigio e per verificare differenti opzioni gestionali all'interno del Parco del Ticino e nell'area circostante, per un periodo di tempo di 40 anni. Questo approccio integrato ha permesso di formulare un piano di azione efficace da proporre alle autorità competenti per fermare il processo di colonizzazione. Inoltre sono stati valutati criticamente i

parametri utilizzati nel modello, evidenziando alcuni dati mancanti in letteratura fornendo suggerimenti per studi futuri finalizzati ad accrescere l'accuratezza del modello.

Parole chiave - Geographic Information Systems, Scoiattolo grigio, Scoiattolo rosso, simulazione, Spatially Explicit Population Dynamics Models

INTRODUCTION

The introduction of species from a different ecosystem in another environment is claimed to be the second most important reason for loss of biodiversity, after the destruction and fragmentation of natural habitats, leading to extinction or decline of native species (Vitousek *et al.*, 1996; Williamson, 1996; IUCN, 2000). Alien species interfere with the native fauna by different ecological processes: predation, interspecific competition or acting as vector or reservoir of diseases (Sainsbury *et al.*, 2000; Gurnell *et al.*, 2004). Many introduced species can also cause direct economic damage to human activities (impact on farming, forestry, agriculture, animal husbandry; disease risk), and socio-economical problems sum with the ecological one (Shine *et al.*, 2000). 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 grey squirrel (*Sciurus carolinensis*) in the British Isles and in parts of northern Italy. The rapid increase of grey squirrel's distribution, coincided with a dramatic decline of the range of the native red squirrel (Wauters *et al.*, 1997a), at the point that greys have now almost replaced reds in Great Britain and Ireland (Gurnell and Pepper, 1993) and in a small area in Piedmont region, NW

Italy. (Bertolino and Genovesi, 2003). Recently, other grey squirrel populations have been discovered in mixed deciduous woodland belts along the Ticino river (Fornasari *et al.*, 2002). The competition of red and grey squirrels in northern Italy has serious implications for red squirrel conservation in Europe (Genovesi and Bertolino, 2001a, b), because of the vicinity of France and Switzerland (Fig. 1). 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. In order to assess the risk of extinction of red squirrel populations, and plan effective management strategies for controlling the invasive species, it is necessary to know the rate at which replacement will occur, which mainly depends on landscape structure (connectivity between good habitats) and abundant food supplies (Wauters *et al.*, 1997b). We used an integrated approach of GRASS GIS with SEPM (Spatially Explicit Population Dynamics Models) that has been tested on grey squirrels in Britain and Piedmont region, Italy (Rushton *et al.*, 1997; Lurz *et al.*, 2001). The aims of this work are: i) evaluate grey squirrel expansion in the Ticino Regional Park and surrounding areas, ii) suggest an

effective control strategy, iii) evaluate model parameters and address future studies.

METHODS

1. Study species

The mechanisms of interspecific competition between grey and red squirrels have recently been understood, at least in part: in broadleaf woodlands where the two species are temporarily syntopic, they show a high niche overlap, both from a trophic and from a spatial point of view. In fact both species select the same tree seed species as food resource, have similar space use and activity patterns, and eventually grey squirrels seem to pilfer many of the seeds scatterhoarded by the congener (Wauters and Gurnell, 1999; Wauters *et al.*, 2001a, 2002a, b). In deciduous woods grey squirrels heavily feed on acorns, while red squirrels feed much less on this often abundant seed supply, resulting in an advantage of the introduced species in terms of energy requirements satisfaction (Kenward and Holm, 1993; Gurnell, 1996a; Kenward *et al.*, 1998; Wauters *et al.*, 2001a, b). In conifer forests, some degree of niche separation seems to exist, but red squirrels tend to avoid the habitat patches with the highest food availability, occupied by greys, being often found at low densities in poor quality patches of exotic spruce species (Gurnell, 1996b; Wauters *et al.*, 2000; Bryce *et al.*, 2002). Overall, interspecific competition for primary food resources results for the red squirrel in reduced body growth, juvenile recruitment and reproductive success (Wauters *et al.*, 2001a; Gurnell *et al.*, 2004), which will eventually cause density to decline and push red squirrels to local extinction (Gurnell *et al.*, 2004). Moreover, at least in the UK, grey squirrels seem to act as vector for a poxvirus which causes a lethal disease in red squirrels

(Sainsbury *et al.*, 2000; Tompkins *et al.*, 2002). There are no known competitive effects of red squirrels on greys (Rushton *et al.*, 1997; Gurnell *et al.*, 2004).

2. Study area and data collection

The Ticino Regional Park (Lombardy region), covers about 900 km² along the east bank of the Ticino river, from Lake Maggiore to its confluence with the Po river at Pavia (Fig. 1). Our study area enclosed the park area plus a 40 km buffer zone, extended in all directions from the park boundaries.

The distribution of grey (and red) squirrels in the park was investigated using 21 transects of 15 hair-tubes each, placed in various parts of the park (Gurnell *et al.*, 2001; Fornasari *et al.*, 2002).

To predict grey squirrel range expansion, we obtained land cover data for Piedmont and Lombardy regions in digitised format at 250 m spatial resolution, and further refined the base dataset (CORINE Land cover; Commission of the European Communities, 1993) adding data derived from two other sources: the Ticino Regional Park forestry map (10 m spatial resolution) for areas inside the park that are not in the Varese province (Lombardy), and the vegetation map of the Varese province (10 m spatial resolution, Tosi and Zilio, 2002). We produced a final habitat map at 250 m spatial resolution where each cell was characterised by a single habitat type (predominant land cover type, Tab. 1). As a result of the spatial resolution 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.

3. Modelling approach

The model used for simulating the distribu-

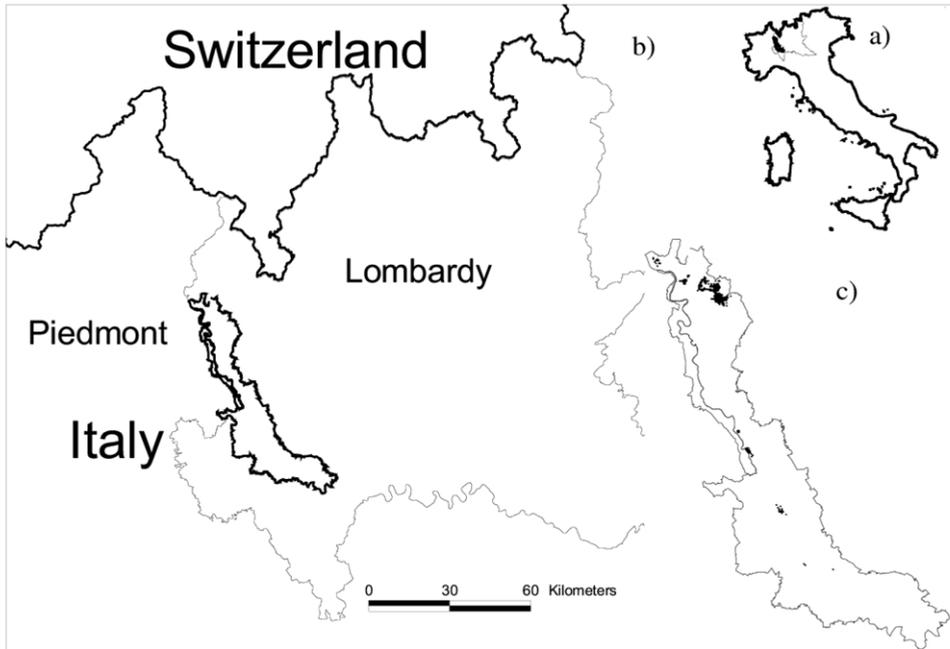


Figure 1 - a) Position of the study area relative to the Italian peninsula. b) “Parco Regionale della Valle del Ticino Lombardo”, solid back line, Piedmont and Lombardy region boundaries, grey line. The scalebar is relative to the b) part of the image. In c) the black blocks represent the habitat patches in which grey squirrel has been detected inside the boundaries of “Parco Regionale della Valle del Ticino Lombardo”.

tion of grey squirrels in the landscape has two main components. The first is a geographical information system (GIS) which stores habitat and animal population information. GRASS 4.2 (U.S. Army, 1993) and GRASS 5 (GRASS Development Team, 2002) 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 second component is a population dynamics model that predicts the distribution of squirrels by simulating the life history processes of births, deaths, home range formation and dispersal in yearly time steps. 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 *et al.*, 1997. The model was applied and fully tested in Piedmont (details are described in Lurz *et al.*, 2001). 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 initial distribution of the species and the patterns for control. Suitable habitats were defined according to the carrying capacity (CC), i.e. the number of individuals who can be supported by a given area (Odum, 1975). Each habitat type received a CC value based on published estimates.

All the simulation runs started from the sit-

Modelling grey squirrel in northern Italy

Table 1 - Habitat description and squirrel maximum densities (Dmax, ind./ha) derived from literature, for the digitised land cover classes. Unsuitable habitats are: Cliffs, rock slides and riverbeds, Scrub, Herbaceous vegetation, Rice fields, Water bodies, Sterile land, Scrub, newly planted areas and uncultivated grassland, and Infrastructure. They all received a value of zero in the model; G. s. = grey squirrel; R.s. = red squirrel.

Land cover type	Dmax G.s.	References	Dmax R.s.	References
Riparian forests	1.0	Bertolino <i>et al.</i> , 2003	0.3	Bertolino <i>et al.</i> , 2003
Oak and oak-hornbeam	5.0	Gurnell 1996a Kenward <i>et al.</i> , 1998	0.8	Kenward <i>et al.</i> , 1998 Wauters <i>et al.</i> , 2001b
Ostreti	2.5	Authors' estimate	0.4	Authors' estimate
Black locust-oak woodland	1.0	Authors' estimate	0.2	Wauters <i>et al.</i> , 2001b
Black locust or other exotics	0.1	Authors' estimate	0.1	Authors' estimate
Mixed broadleaf dominated by chestnut	5.0	Gurnell, 1991; Koprowski, 1994 Wauters and Gurnell, 1999	1.1	Wauters and Lens, 1995 Wauters <i>et al.</i> , 2001b
Mixed deciduous (CORINE)	2.0	Koprowski, 1994 Gurnell <i>et al.</i> , 2001b	0.4	Wauters <i>et al.</i> , 2001b Authors' estimate
Beech	2.0	Gurnell, 1991	0.4	Cagnin <i>et al.</i> , 2000 Wauters and Lens, 1995
Maple-ash-lime	5.0	Authors' estimate	1.1	Authors' estimate
Conifers and mixed broadleaf	1.5	Gurnell, 1991; 1996a Gurnell <i>et al.</i> , 2001b	1.3	Wauters and Lens, 1995
Scots pine	0.3	Smith and Gurnell, 1997 Authors' estimate	0.5	Authors' estimate
Norway spruce	0.2	Smith and Gurnell, 1997	0.35	Wauters <i>et al.</i> , 2000
Poplar plantations	0.3	Bertolino <i>et al.</i> , 2003	0.1	Wauters <i>et al.</i> , 1997a, b
Pastures (CORINE)	0.2	Authors' estimate	0.1	Authors' estimate
Alder	0.1	Authors' estimate	0.1	Authors' estimate
Mixed agriculture	0.013	Bertolino <i>et al.</i> , 2003 Lurz <i>et al.</i> , 2001	0.005	Bertolino <i>et al.</i> , 2003
Maize, wheat	0.013	Bertolino <i>et al.</i> , 2003 Lurz <i>et al.</i> , 2001	0.005	Bertolino <i>et al.</i> , 2003
Permanent grassland	0.013	Authors' estimate	0.005	Authors' estimate
Vineyards, orchards and hazelnuts	1.0	Authors' estimate	0.2	Authors' estimate
Urban areas	0.013	Authors' estimate Koprowski, 1994	0.013	Wauters and Gurnell, 1999
Urban parks	1.0	Authors' estimate	0.02	Authors' estimate

uation known for 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 ran the models 400 times overall. Results presented are averages of those multiple runs. A detailed description of all the runs can be find in Tattoni *et al.*, 2005.

4. Parameter estimation

An individual based model requires a good estimate of all the parameters used into the model itself in order to produce a reliable output.

The main drawback of these models is that a sound knowledge of both life-history parameters and habitat preferences is required and, thus, SEPM can only be used for species for which detailed data of population parameters in different habitat types

(such as fertility, litter size, etc.) commonly referred as life history parameters (Tab. 2) and ecological parameters, such as carrying capacity in different habitat types (Tab. 3).

For some habitat types no published data were available so we provided an estimate based on comparison with similar habitats and field experience. Over a total of 29 habitat types present on the study area, we have been able to find literature estimates of CC for red squirrel in 21 habitat classes and in 20 for grey squirrel. Red squirrel literature reports CC estimates in Scots pine (*Pinus sylvestris*) forests, while the same estimate is not available for grey squirrel (Tab. 1). This tree species is absent in north America, so the behaviour of the grey squirrel in this kind of forest is not known. The other habitats with unavailable CC in literature for both species are mainly anthropic habitats (orchards, urban areas,

Table 2 - Red (R. s.) and grey (G. s.) squirrel life history parameters in relation to annual changes in tree seed crops. Fecundity is the average litter size (Bertolino and Genovesi, 2003), survival is the percent of individuals surviving to the next year according to two age classes and food availability (Gurnell, 1996a). Reproducing females is the percent of adult females who reproduce each year once (first litter) or twice (second litter) (Rushton *et al.*, 1997).

Paramete	Poor year		Good year		Mast year	
	R.s.	G.s.	R.s.	G.s.	R.s.	G.s.
Fecundity	2	1.5	2.8	2.5	3.5	3.5
Adult survival	0.55	0.55	0.6	0.6	0.75	0.65
Juvenile survival	0.25	0.25	0.3	0.3	0.4	0.4
Reproducing females (first litter) (%)	67	87	67	87	67	87
Reprodoucing females (second litter) (%)	26	42	26	42	26	42

are available (Rushton *et al.*, 1997 and 2000). 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.

Two main kind of parameters are needed to run simulations: individual linked parame-

urban parks, pastures, permanent grassland). We proposed a very low CC instead of a null value because these habitats can be used by squirrels of both species to move through. A null CC implies that in the simulation any squirrel dies when passing over these habitats: we considered this option unrealistic.

Alien species invasiveness is often related to their sudden introduction into habitats where they have not co-evolved with the biological community (White, 1997): interaction with local species is not predictable, the scene becomes then more and more complex when more than one alien species is present. Our study area is a good example, since here we can find European and American squirrels in a habitat composed by North American tree species. Wauters *et al.* (2001b) recently estimated the carrying capacity for red squirrel in black locust (*Robinia pseudoacacia*) mixed with oaks forests, while for a black locust mixed with other exotic species there is not an estimate yet. The only natural habitats for which we provided a personal estimate are alder, hornbeam and maple-ash-lime woodlands. Even with some author's estimates, we relied on our model outputs. In fact the total area covered by the habitats with no CC in literature is only 18% of the total study area (Tab. 3).

RESULTS

1. Grey squirrel spread

The landscape in and around “Parco Regionale della valle del Ticino Lombardo” 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 approximately 370000 individuals (see also Fig. 2 and Fig. 3). 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 (Fig. 2c, d). Squirrels are predicted to show different patterns of spread: inside the Park dispersion tends to occur along the wooded riverbank of Ticino river, 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 boundaries. 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.

2. Grey squirrel control scenarios

We tested the effect of two different removal rate, namely 50% and 80% of the individuals present at a given time over three different control scenarios

Table 3 - Surface (km²) of habitat types with a carrying capacity (CC) estimated by authors for both red and grey squirrels.

Habitat class with CC estimated by authors	Habitat types	Area km ²	% of study area
Natural	Alder, maple-ash-lime and scots pine	156.50	1.77
Anthropic	Orchards, urban parks, pastures	1308.56	14.77
Exotic	Black locust-oak and black locust and other exotic species	153.25	1.73
Total		1618.31	18.26
Total (study area)		8861.63	

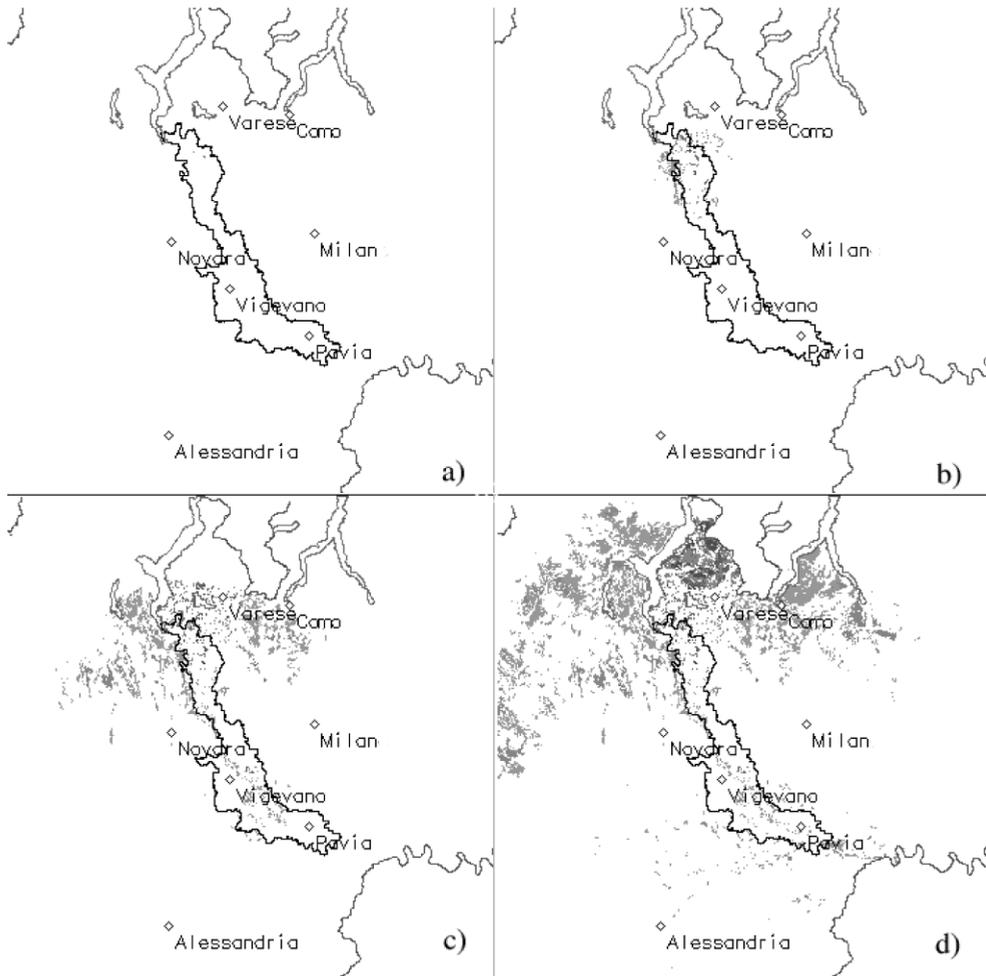


Figure 2 - The spatial spread of grey squirrel population at ten year intervals a) 2011; b) 2021; c) 2031; d) 2041.

(Tattoni *et al.*, 2005). Squirrel removal starts in 2005 for each scenario, so for the first three years of the simulation no squirrels are removed. From the simulation outputs we were able to find the best compromise between effective management and number of patches to control. This is confirmed in this scenario where an effective control can be achieved on a relatively small area (2600 ha with respect to 4600 ha) if

proper target areas are defined. We find that 80% removal rate results in total eradication in 30 years. Average yearly removal is around 50 individuals per year for the first 10 years, dropping to less than ten squirrels per year afterwards (Tattoni *et al.*, 2005). These results show that it is possible to face the spread of grey squirrels if policy makers and wildlife managers take immediate actions to control the alien

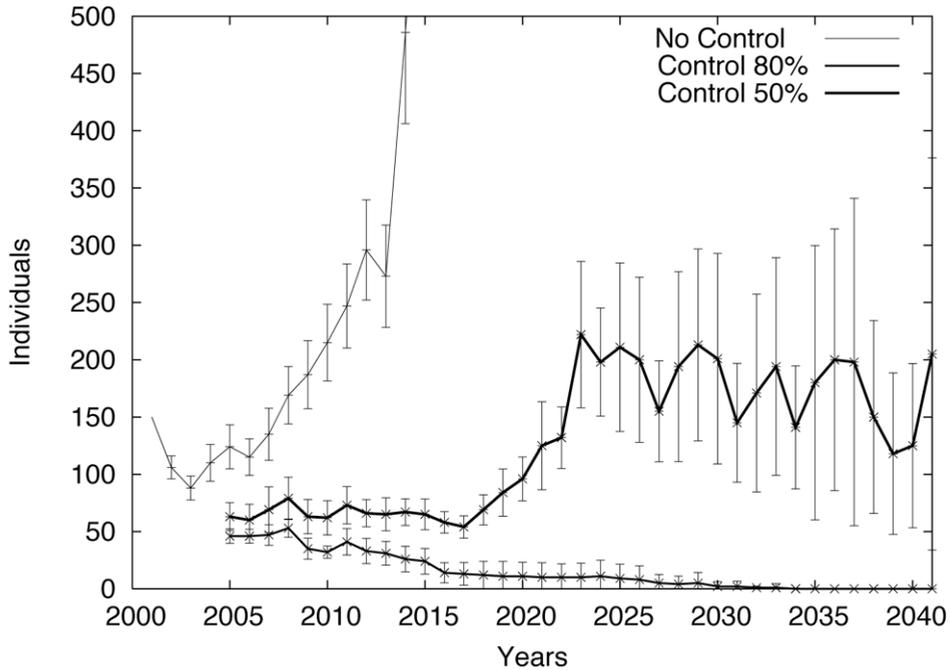


Figure 3 - Grey and red squirrel population dynamics as predicted by the competition scenario. Each line represents average values calculated over 10 simulation runs. Bars indicate standard deviation.

species and plan a carefully designed control scheme, with selective choice of target areas, controlling only a small portion of the landscape. However, for control to be efficient, even on a small area, new hair-tube surveys, covering all woodlands inside the park (and those just outside the northern border) must be carried out immediately to reveal the present distribution. We also produce a first map for hair tube survey (Fig. 4), and future trapping campaign should be adjusted on the field according to the surveys results.

3. Competition scenario

We also ran the model with both squir-

rel species to evaluate competition. Red squirrels start to go extinct in the park woodlands from year 2020, as greys continue to expand and their numbers increase (Fig. 3). During the first 10-15 years red squirrel population increases from an average density to carrying capacity. This is an artefact related to input conditions, defined at an average density for the whole landscape. Red squirrels reach equilibrium from the 10th to 20th year of simulation. The population is fluctuating around 280000 individuals and the species is spread in all woodland blocks. After the 20th year of simulation greys begin to be an impacting factor and the predicted 21000 grey squirrels are likely to drive

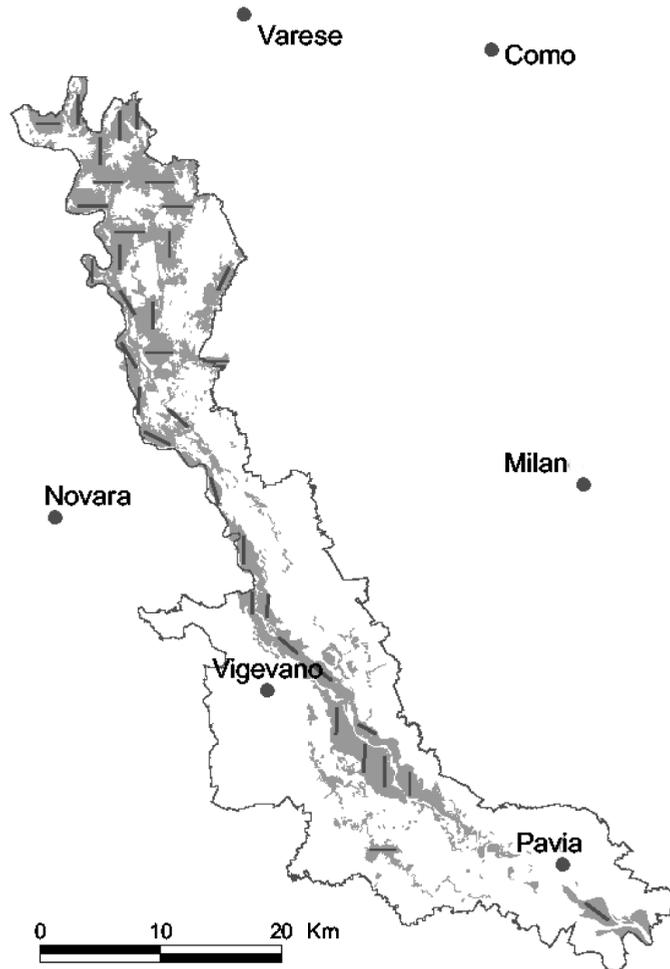


Figure 4 - Proposed hair tube survey scheme; each transect (bold line) is about 2 km length. Surveys are planned to take place in woodland patches.

the red squirrel to extinction within the Park boundaries. Populations of red squirrels seem to persist longer in the northern part of the study area where the prealpine mountains are covered with conifer forests, 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 40 years.

DISCUSSION

Without control, grey squirrels could invade Switzerland woodlands within the next two decades. Simulating different grey squirrel control or removal scenarios suggests that: (i) efficient control is possible and mainly determined by the spatial distribution and woodland patch size of the 'target' con-

trol 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 a 'no action' option, providing wildlife managers with maps showing the consequences of each strategy. Control maps analysis allowed us 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 range and current population size of grey squirrels. In addition, no information was available on 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. A successful containment of further grey squirrel spread will in fact require local cooperation of Park authorities with the Regional Parks and Wildlife Services of the Regions of Lombardy and Piedmont. Furthermore, also the Swiss authorities of the Ticino District must take an active role in counteracting

grey squirrel invasion within the next 20-30 years (potentially sooner when dispersing individuals are considered). We also highlight the lack of studies on both species in some habitat types: future field study may consider to investigate species behaviour in black locust, alder, hornbeam and maple-ash-lime woodlands.

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REFERENCES

- Bertolino S. and 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. *Biol. Conserv.*, 109: 351-358
- Bertolino S. Wauters L.A., De Bruyn L. and Canestri-Trotti G. 2003. Prevalence of coccidia parasites (Protozoa) in red squirrels (*Sciurus vulgaris*): effects of host phenotype and environmental factors. *Oecologia*, 137: 286-295
- Bryce J., Johnson P.J. and MacDonald D.W. 2002. Can niche use in red and grey squirrels offer clues for their apparent coexistence? *J. Appl. Ecol.*, 39: 875-887
- Cagnin M., Aloise G., Fiore F., Oriolo V. and Wauters L.A. 2000. Habitat use and population density of the red squirrel,

- Sciurus vulgaris meridionalis*, in the Sila Grande mountain range (Calabria, South Italy). *It. J. Zool.*, 67: 81-87
- Commission of the European Communities 1993. CORINE Land cover, Guide technique. Directorate-General Environment, Nuclear Safety and Civil Protection, Office for Official Publications of the European Communities, Luxembourg.
- Fornasari L., Galbusera R. and Sacchi M. 2002. Progetto per il monitoraggio e l'eradicazione dello scoiattolo grigio nel Parco Regionale della Valle del Ticino Lombardo. Unpublished technical report.
- Genovesi P. 2000. Guidelines for Eradication of Terrestrial Vertebrates: a European Contribution to the Invasive Alien Species Issue. Council of Europe, tpsv65e-2000, 61 pp.
- Genovesi P. and Bertolino S. 2001a. Linee guida per il controllo dello scoiattolo grigio (*Sciurus carolinensis*) in Italia. *Quaderni di Conservazione della Natura*, 4: 5-52
- Genovesi P. and Bertolino S. 2001b. Human dimension aspects in invasive alien species issues: the case of the failure of the Grey squirrel eradication project in Italy. In: Mcneely J.A. (ed.), *The Great Reshuffling: human dimensions of Invasive Alien Species*, IUCN, Gland, Switzerland and Cambridge, UK, 113-119.
- Genovesi P. and Shine C. 2003. European Strategy on Invasive alien species. Council of Europe, T-PVS (2003): 7.
- Gurnell J. 1991. The grey squirrel. In: Corbet G.B. and Harris S. (eds), *The Handbook of British Mammals*. Blackwell Scientific Publications, Oxford, 186-191.
- Gurnell J. 1996a. The effects of food availability and winter weather on the dynamics of a grey squirrel population in southern England. *J. Appl. Ecol.*, 33: 325-338.
- Gurnell J. 1996b. Conserving the red squirrel. In: Ratcliffe P. and Claridge J. (eds), *Thetford Forest Park: the ecology of a pine forest*. Forestry Commission, Edinburgh, 132-140.
- Gurnell J. and Pepper H. 1993. A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal Review*, 23: 125-136.
- Gurnell J., Lurz P.W.W. and Pepper H. 2001a. Practical techniques for surveying and monitoring squirrels. Forestry Commission Practical Notes, 11: 1-12.
- Gurnell J., Wauters L.A., Lurz P.W.W. and Tosi G. 2004. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *J. An. Ecol.*, 73: 26-35.
- Gurnell J., Wauters L.A., Preatoni D. and Tosi G. 2001. Spacing behaviour, kinship and dynamics of the grey squirrel in a newly colonised deciduous woodland in north Italy. *Can. J. Zool.*, 79: 1533-1543.
- GRASS Development Team 2002. GRASS. 5.0 Users Manual, Edited by ITC. IRST, Trento, Italy.
- Hughes B. 1996. The Ruddy Duck *Oxyura jamaicensis* in the Europe and the threat to the White-headed Duck *Oxyura leucocephala*. *Oxyura*, VIII(1): 51-64.
- IUCN 2000. Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species. IUCN, Gland, Switzerland.
- Kenward R.E. and Holm J.L. 1993. On the replacement of the red squirrel in Britain: a phytotoxic explanation. *Proceedings of the Royal Society, London*, B 251: 187-194.
- Kenward R.E., Hodder K.H. Rose R.J. Walls C.A., Parish T., Holm J.L., Morris P.A., Walls S.S. and Doyle F.I. 1998. Comparative demography of red squirrels (*Sciurus vulgaris*) and grey

Modelling grey squirrel in northern Italy

- squirrels (*Sciurus carolinensis*) in deciduous and conifer woodland. *J. Zool.*, London, 224: 7-21.
- Koprowski J.L. 1994. *Sciurus carolinensis*. Mammalian Species 480, American Society of Mammalogists, 9 pp.
- Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P. and Shirley M.D.F. 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. *Land. Ecol.*, 16: 407-420.
- Odum E.. 1975. Ecology. Edited by Holt Rinehart and Winston.
- Rushton S.P., Lurz P.W.W., Fuller R. and Garson P.J. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *J. Appl. Ecol.*, 34: 1137-1154.
- Rushton S.P., Lurz P.W.W., Fuller R. and Gurnell J. 2000. 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? *J. Appl. Ecol.*, 37: 997-1012.
- Sainsbury A.W., Nettleton P., Gilray J. and Gurnell J. 2000. Grey squirrels have high seroprevalence to a parapoxvirus associated with deaths in red squirrels. *Anim. Conserv.* 3: 229-233.
- Shine C., Williams N. and Gündling L. 2000. A guide to designing legal frameworks on alien invasive species. IUCN Environmental Policy and Law Paper No. 40, IUCN, Gland, Switzerland, 138 pp.
- Smith D. and Gurnell J. 1997. The ecology of the grey squirrel in conifer forest. In: Gurnell J and Lurz P.W.W. (eds), The Conservation of Red Squirrels, *Sciurus vulgaris* L. People's Trust for Endangered Species, London, 109-119.
- Tattoni C., Preatoni D.G., Bertolino S., Martinoli A., Tosi G., Wauters L.A. 2005. Modelling the expansion of grey squirrels (*Sciurus carolinensis*) in Lombardy, northern Italy: implications for squirrel control. In: Nentwig, W., Bacher S., Cock M.J.W, Dietz H., Gigon A. and Wittenberg R. (eds), Biological Invasions - From Ecology to Control. *NEOBIOTA*, 6: 149-164.
- Tompkins D.M., Sainsbury A.W., Nettleton P., Buxton D. and Gurnell J. 2002. Parapoxvirus causes a deleterious disease in red squirrels associated with UK population declines. Proceedings of the Royal Society, London, B 269: 529-533.
- Tosi G. and Zilio A. 2002. Conoscenza delle risorse ambientali della provincia di Varese – Progetto SIT Fauna. Provincia di Varese, Settore Politiche per l'Agricoltura e Gestione Faunistica, Varese, Italy, 297 pp.
- U.S. Army 1993. GRASS. 4.1 Reference Manual. U.S. Army Corps of Engineers, Construction Engineering Research Laboratories, Champaign, Illinois.
- Vitousek P.M., D'Antonio C.M., Loope L.L. and Westbrook R. 1996. Biological invasions as global environmental change. *American Scientist*, 84: 468-478.
- Wauters L.A., Currado I., Mazzoglio P.J. and Gurnell J. 1997a. Replacement of red squirrels by introduced grey squirrels in Italy: evidence from a distribution survey. In: Gurnell J. and Lurz P.W.W. (eds), The Conservation of Red Squirrels, *Sciurus vulgaris* L. People's Trust for Endangered Species, London. 79-88.
- Wauters L.A. and 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., Gurnell J., Currado I. and Mazzoglio P.J. 1997b. Grey squirrel *Sciurus carolinensis* management in Italy – squirrel distribution in a highly fragmented landscape. *Wildl. Biol.*, 3: 117-124.

- Wauters L.A., Gurnell J., Martinoli A. and Tosi G. 2001a. Does interspecific competition with introduced grey squirrels affect foraging and food choice of Eurasian red squirrels? *Anim. Behav.*, 61: 1079-1091.
- Wauters L.A., Gurnell J., Martinoli A. and Tosi G. 2002b. Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur? *Behav. Ecol. Sociobiol.*, 52: 332-341.
- Wauters L.A., Gurnell J., Preatoni D. and Tosi G. 2001b. Effects of spatial variation in food availability on spacing behaviour and demography of Eurasian red squirrels. *Ecography*, 24: 525-538.
- Wauters L.A. and Lens L. 1995. Effects of food availability and density on red squirrel (*Sciurus vulgaris*) reproduction. *Ecology*, 76: 2460-2469.
- Wauters L.A., Lurz P.W.W. and 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. *Ecol. Res.*, 15: 271-284.
- White, P.S. 1997 Exotic Pests of Eastern Forests, Conference Proceedings - April 8-10, 1997, Nashville, TN, Edited by: Kerry O. Britton, USDA Forest Service & TN Exotic Pest Plant Council
- Williamson M. 1996. Biological invasion. Chapman and Hall, London, 244 pp.