POXVIRUS, RED AND GREY SQUIRREL DYNAMICS: IS THE RECOVERY OF A COMMON PREDATOR AFFECTING SYSTEM EQUILIBRIA? INSIGHTS FROM A PREDATOR-PREY ECOEPIDEMIC MODEL

ELENA TRAVAGLIA
Dipartimento di Matematica “Giuseppe Peano”
Università di Torino, via Carlo Alberto 10,
10123, Torino, Italy

VALENTINA LA MORGIA¹, EZIO VENTURINO*,²
¹Institute for Environmental Protection and Research (ISPRA),
via Ca’ Fornacetta 9,
40064, Ozzano Emilia (BO), Italy
²Dipartimento di Matematica “Giuseppe Peano”
Università di Torino, via Carlo Alberto 10,

(Communicated by )

ABSTRACT. In Europe, the Eastern grey squirrel is an allochthonous species causing severe impacts on the native red squirrel. The invasive species establishes complex relationships with the native one, out-competing it through resource and disease-mediated competition. However, recent research shed light on the potential role of a predator, the pine marten, in reversing the outcome of the competition between squirrels. Here, we investigate this hypothesis developing a one predator-two prey ecoepidemic model, including disease (squirrel poxvirus) transmission. We assess the equilibria of the dynamical system and investigate their sensitivity to ecosystem parameters changes through numerical simulations.

Our analysis reveals that the system is more likely to evolve toward points where the red squirrels thrive than toward a disease-and-red-squirrels-free point. Although the disease is likely to remain endemic in the system, the introduction of the pine marten destabilizes previous equilibria, favouring the native squirrel and facilitating wildlife managers in their efforts to protect it. Nevertheless, the complete eradication of grey squirrels could be achieved only for specified values of the predation rates and pine marten carrying capacity. The active management of grey squirrel populations remains therefore necessary to try to eradicate the invader from the system.

1. Introduction. The Eastern grey squirrel (Sciurus carolinensis Gmelin, 1788) is an arboreal mammal, native to the eastern United States and adjacent southern Canada. It lives mainly in deciduous and mixed forests, but thanks to its ecological flexibility it thrives in many different habitats, including city parks and floodplains, [1]. From North America, it was introduced into Europe (in the British Isles, mainly from 1890 onwards, [2, 3], and in Italy, from 1948, [4]), where
it started to compete with the native Eurasian red squirrel (Sciurus vulgaris Linnaeus, 1758) for habitat and trophic resources. According to available data, [5, 6, 7, 8, 9], no niche partitioning occurs between the two species and the interspecific competition may affect red squirrel population dynamics, leading to the replacement of the red species by the grey squirrel, [10].

The interspecific competition can also be disease- or parasite-mediated. In the United Kingdom, a squirrel poxvirus (SQPV) of the Chordopoxviridae genus, [11, 12], was introduced with the grey squirrel, [12], which represents a reservoir host. While having no impacts on greys, the virus causes a debilitating disease in red squirrels. Several studies suggested that the disease transmission should therefore be taken into account to explain the observed replacement rate between red and grey squirrels, [13, 14]. Indeed, considering reference values for population parameters [3, 15], a model developed in [16] confirmed that a system made up of grey, red and infected red squirrels is likely to evolve toward a grey-only situation, with the disappearance of the red species in a timespan that depends on the red squirrel overall mortality. In [17] it is also observed that the introduced grey squirrels harbour an impoverished parasite community compared to their native range. In any case, grey squirrels introduced in Italy the North American nematode Strongyloides robustus, which then spilled over to the native red squirrel. In the presence of the invader, the native squirrel also seems to have a reduced ability to cope with other parasitic infections.

Thus, in the European range in which it is now present, the grey squirrel establishes complex relationships with the native red species and out-competes it through several mechanisms. Unquestionably, the European red squirrel suffers from the resource competition, and its population dynamics may be severely affected by the poxvirus transmission from the grey squirrels. On the other hand, the invasive advantage of the Eastern grey squirrel partly follows from its opportunistic diet and trophic adaptability [18], from its high reproductivity and behaviour, e.g., relatively high reproductive rate and capacity to live at high densities; [19, 20, 21, 22, 15, 23], and from the reduced parasite pressure, enemy-release hypothesis, [17]. Finally, in spite of the existence of a wide range of potential predators of the grey squirrel, e.g., raptores, red fox, martens, feral and domestic cats, in Europe none of them exerted a significant impact, [10], but see also [24], so that until now the species has not been truly limited in its establishment and spread.

However, the pine marten (Martes martes), a predator of both red and grey squirrels, recently started recovering. For instance, in England, in the late 1980s, there were probably fewer than 100 pine martens. The population decline was the result of hunting of martens for their fur, loss of habitat, and poisoning. However, the recovery started in the 1940s, thanks to reduced persecution, slow natural spread, and translocations. As a consequence, while the remnant pine marten populations at one time overlapped almost exclusively with the red squirrel populations, [25], in recent years the predator started to appear more frequently in grey squirrel areas, too.

Indeed for the first time in [26] reports of pine marten predation on grey squirrels appeared. The authors in [26] also observed that the pine marten could have an impact on some grey squirrel populations of Ireland, and this led to the revision of the idea that pine marten predation could represent an option to control grey squirrels and favour native ones, [27, 25]. More recently, [28] suggested that enemy-mediated relationships involving grey and red squirrels together with the pine marten as common predator should be taken into account to evaluate the potential evolution of the grey-red squirrel system in the UK or, more generally, in areas where the three species occur. According to these authors, in Britain native red and invasive grey squirrels are linked by (a) resource competition, (b) SQPV disease-mediated apparent competition, and (c) enemy-mediated relationships involving the pine marten as a shared predator. They observed that non-native grey squirrel occupancy is strongly negatively affected by exposure to pine martens and that exposure to predation has an indirect positive effect on red squirrel populations. With their study, they thus supported the hypothesis of a highly asymmetrical pine marten impact, and they suggested that the presence of the shared predator could reverse the outcome of the competition between the red and grey squirrel.

Taking into account these recent findings and hypotheses, we develop here a one predator-two prey ecopidemic model, including SQPV transmission. In this paper we extend the analysis performed by [16] in the absence of pine martens. The aim is to understand under which conditions this ecosystem could evolve toward a situation favourable to the native species, considering various parameter configurations. Ultimately we would like to assess the role of the shared predator in the shaping of the system equilibria.

2. Model set-up. We consider three populations, and the SQPV induced disease. However, as discussed in the Introduction and to keep the mathematics treatable, we assume that the grey
squirrels, $G$, are asymptomatic carriers of the virus, while the red squirrel population is partitioned among susceptibles, $R$, and infected $I$. This implies that the grey squirrels are in fact infected, so that they can propagate the disease to the native population. In addition we consider the pine martens, $M$.

The model reads as follows:

$$\begin{align*}
\frac{dG}{dt} &= G(d - rG - fR - uM - zI) \\
\frac{dR}{dt} &= R[a - bR - cG - sM - wI - \lambda I - \beta G] \\
\frac{dI}{dt} &= I(\lambda R - \mu - vM) + \beta RG \\
\frac{dM}{dt} &= M[g - hM + e(sR + uG + vI)]
\end{align*}$$

Its Jacobian is

$$J = \begin{pmatrix}
d - 2rG - fR - uM - zI & -fG & -zG & -uG \\
-(c + \beta)R & J_{22} & -(w + \lambda)R & -sR \\
\beta R & \lambda I + \beta G & \lambda R - \mu - vM & -vI \\
euM & esM & evM & J_{44}
\end{pmatrix}$$

with

$$J_{22} = a - 2hR - (c + \beta)G - sM - (w + \lambda)I,$$

$$J_{44} = g - 2hM + esR + euG + evI.$$

The first equation of (1) describes the grey squirrels dynamics: they grow logistically with net growth rate $d$ and intraspecific competition $r$, the competition with healthy and infected red squirrels occurring at respective rates $f$ and $z$; they are finally subject to hunt by the pine marten, at rate $u$.

The second equation describes the healthy red squirrel, that also grow logistically, their net reproduction rate being $a$, the intraspecific competition $b$. They are subject to competition with the infected and the grey ones, at respective rates $w$ and $c$ and are hunted by the pine marten at rate $s$. They can be infected by contact with other infected red squirrels at rate $\lambda$ or by contact with the grey squirrels, that are all assumed to be disease-carriers, at rate $\beta$.

The third equation describes the infected red squirrels, recruited via "successful" contacts from the susceptible red squirrels, as described above for the first equation. The are subject to natural plus disease-related mortality $\mu$ and are hunted at rate $v$.

The final equation contains the pine marten dynamics: once more it is of logistic type due to the implicit presence of other possible resources, at net reproduction rate $g$ and intraspecific competition $h$. The three kinds of hunted squirrels are turned into newborns at rates proportional to the respective hunting rates, scaled by a conversion factor $e$.

All the parameters are non-negative. Let us further assume that the grey squirrels are more subject to predation by pine marten than the red squirrels are, and competitively they outperform the red squirrels, for which the following restrictions are in order:

$$u > s, \quad r < c, \quad f < b. \quad (2)$$

3. **Equilibria.** We now analyse the steady states of the ecosystem (1).

The origin $E_0 = (0, 0, 0, 0)$ is an unstable equilibrium, in view of the Jacobian eigenvalues $a > 0$, $d > 0$, $g > 0$, $-\mu$.

The squirrel-free equilibrium point $E_1 = (0, 0, 0, M_1) = (0, 0, 0, gh^{-1})$ is always feasible, the eigenvalues are explicitly found as

$$\frac{ah - gs}{h}, \quad \frac{dh - gu}{h}, \quad -g < 0, \quad -\frac{h\mu + gv}{h} < 0,$$

providing the stability conditions

$$ah - gs < 0, \quad dh - gu < 0. \quad (3)$$
The grey-squirrel-only point $E_2 = (G_2,0,0,0) = (d r^{-1}, 0, 0, 0)$ is again always feasible and has also explicit eigenvalues:

$$\frac{ar - cd - d \beta}{r} - d < 0, \quad \frac{gr + du}{r} > 0, \quad -\mu < 0,$$

from which its unconditional instability follows.

The disease-and-red-squirrels-free point

$$E_3 = (G_3, 0, 0, M_3) = \left( \frac{hd - gu}{rh + eu^2}, 0, 0, \frac{ewd + rg}{rh + eu^2} \right)$$

is feasible under the condition

$$dh - gu > 0. \quad (4)$$

A comparison with (3) indicates the presence of a transcritical bifurcation between this point and the squirrel-free equilibrium, which originates when the pine marten invades the system.

Two eigenvalues are explicitly calculated: $a - (c + \beta)G_3 - sM_3, -\mu - vM_3 < 0$. The Routh-Hurwitz conditions applied to the remaining minor $A_3$ are satisfied: $-\text{tr}(A_3) = rG_3 + hM_3 > 0, \quad \text{det}(A_3) = rhG_3M_3 + eu^2G_3M_3 > 0$. Thus stability depends only on the first eigenvalue and yields the condition

$$bd - 0, det(I) > 0.$$  

The next equilibrium is $E_4 = (0, R_4, 0, 0) = (0, ab^{-1}, 0, 0)$ always feasible. The eigenvalues are explicitly obtained as $-a < 0, (bd - af)b^{-1}, (bg + ae)f b^{-1} > 0, (a\lambda - bg)b^{-1}$, showing its unconditional instability.

We then find $E_5 = (0, R_5, I_5, 0)$, with

$$R_5 = \frac{\mu}{\lambda}, \quad I_5 = \frac{a\lambda - b\mu}{\lambda(w + \lambda)}.$$

so that its feasibility condition is

$$a\lambda - b\mu > 0. \quad (6)$$

Two eigenvalues are explicit, but although the Routh-Hurwitz conditions on the remaining minor $A_5$ would be satisfied, $-\text{tr}(A_5) = br_{R_5} > 0, \quad \text{det}(A_5) = \lambda(w + \lambda)R_5I_5 > 0$, one of their values is positive, $d - f R_5 - z I_5$ and $g + es R_5 + ev I_5 > 0$, which is enough to imply the equilibrium unconditional instability.

The point $E_6 = (0, R_6, 0, M_6)$,

$$R_6 = \frac{ah - gs}{bh + es^2}, \quad M_6 = \frac{bg +aes}{bh + es^2}$$

is feasible for

$$ah - gs > 0. \quad (7)$$

Again two explicit eigenvalues are $d - f R_6 - u M_6$ and $\lambda R_6 - \mu - v M_6$, the Routh-Hurwitz conditions on the remaining minor $A_6$ are satisfied, $-\text{tr}(A_6) = br_{R_6} + h M_6 > 0, \quad \text{det}(A_6) = bh R_6 M_6 + es^2 R_6 M_6 > 0$, so that $E_6$ is stable if

$$\frac{d - u M_6}{f} < R_6 < \frac{\mu + v M_6}{\lambda},$$

i.e. explicitly for

$$\frac{d(bh + es^2) - u(bg - a es)}{f} < ah - gs < \frac{\mu(bh + es^2) + v(bg + aes)}{\lambda}. \quad (8)$$

We then find the grey-squirrel-free point by solving for $R$ the third equilibrium equation, substituting into the remaining ones and solving for $M$ as function of $I$ the second one, the first one provides the value of $I$, so that we finally obtain

$$E_7 = (R_7, 0, I_7, M_7) = \left( \frac{\mu + v M_7}{\lambda}, 0, I_7, \frac{a\lambda - b\mu - I_7(w + \lambda)\lambda}{bv + s\lambda} \right)$$

with

$$I_7 = \frac{bgv + gs\lambda - ah\lambda + bh\mu + es^2\mu + aesv}{esuv - hw\lambda - \lambda^2 - bev^2}.$$

To have nonnegative populations, we must impose the condition

$$0 \leq I_7 \leq \frac{a\lambda - b\mu}{\lambda(w + \lambda)}, \quad (9)$$

$$\frac{ar - cd - d \beta}{r} - d < 0, \quad \frac{gr + du}{r} > 0, \quad -\mu < 0,$$
together with either one of the following two alternative sets of inequalities
\[ bgv + gs\lambda + es^2\mu + aev = h(a\lambda - b\mu), \quad esvw > hw\mu + h\lambda^2 + bev^2; \quad (10) \]
\[ bgv + gs\lambda + es^2\mu + aev \leq h(a\lambda - b\mu), \quad esvw < hw\mu + h\lambda^2 + bev^2. \quad (11) \]

One eigenvalue is \( d - fR_T - uM_T - zT \), for the remaining minor \( A_T \) we seek conditions for which \(-A_T\) is positive definite. In fact, calculating its principal minors, we find
\[ bR_T > 0, \quad (bh + es)R_T M_T > 0, \quad \det(-A_T) = hw\lambda + h\lambda^2 + bev^2 - esvw. \]

Thus stability is ensured in case (11) holds, provided also the following condition is satisfied,
\[ d < fR_T + uM_T + zT. \quad (12) \]

We also find the predator-free environment,
\[ E_8 = (R_S, G_S, I_S, 0). \]
The population values can be obtained solving for \( G \) from the second equilibrium equation
\[ G = \frac{1}{r}[d - zI - fR] \quad L = z(c + \beta) - r(w > +\lambda) \quad (13) \]
and substituting it into the first one to get \( R \),
\[ R = \frac{1}{F}(B + IL), \quad F = br - f(c + \beta), \quad B = ar - d(c + \beta), \quad L = z(c + \beta) - r(w > +\lambda). \quad (14) \]
Solving for \( G \) after substitution of (14) also into the third equilibrium equation, we obtain
\[ G = \Psi(I) = \frac{F \mu}{\beta(B + LI)} - \frac{\lambda}{\beta}. \]
Substitution of (14) into the expression for \( G \) in (13) gives
\[ G = \Phi(I) = \frac{(f(w + \lambda) -bz)I + bd - af}{br - f(c + \beta)}. \]
The existence and feasibility of the equilibrium could be ensured by possible intersections in the first quadrant of \( \Psi \) and \( \Phi \). However, we do not explore further this situation because, evaluating the Jacobian at this point, one explicit eigenvalue is \( g + e(sR_S + \mu G_S + vI_S) > 0 \), implying the unconditional instability of this equilibrium.

Then, the summary of the situation is contained in Table 1.

**Table 1. Possible ecosystem’s equilibria other than coexistence**

| Equilibria | Feasibility  | Stability   |
|------------|--------------|-------------|
| \( E_0 = (0, 0, 0, 0) \) | unconditional | unstable |
| \( E_1 = (0, 0, 0, M_1) \) | unconditional | (3)        |
| \( E_2 = (G_2, 0, 0, 0) \) | unconditional | unstable |
| \( E_3 = (G_3, 0, 0, M_4) \) | (4)         | (5)        |
| \( E_4 = (0, R_4, 0, 0) \) | unconditional | unstable |
| \( E_5 = (0, R_5, I_5, 0) \) | (6)         | unstable   |
| \( E_6 = (0, R_6, 0, M_6) \) | (7)         | (8)        |
| \( E_7 = (0, R_7, I_7, M_7) \) | (9), (10), (11)| (10), (12)|
| \( E_8 = (G_8, R_8, I_8, 0) \) | conditional | unstable   |

There are transcritical bifurcations between \( E_1 \) and \( E_6 \) and between \( E_1 \) and \( E_3 \) respectively when
\[ a^1 = gsh^{-1}, \quad d^1 = guh^{-1}. \quad (15) \]
Note further that \( E_7 \) is achievable if and only if the conditions (9), (10), (12) hold.
Our goals are prevention of the native population and possibly the eradication of the invaders, conditions that mathematically amount to requiring \( R \rightarrow 0 \), and if possible, \( G \rightarrow 0 \). Thus we should ensure that equilibria \( E_1 \) and \( E_3 \) do not arise, by rendering their stability conditions impossible to be satisfied, so that they do not hold, while we should strive instead to satisfy the feasibility and stability conditions of \( E_6 \) and \( E_7 \), with a preference for the former, since at this point in the phase space also the disease is eradicated. Thus conditions should be possibly put on the parameters so that \( ah > gs \), i.e. \( a \geq a^1 \) and (8) both hold, or, as a second choice, so that (9), (10), and (12) are satisfied.
4. Discussion on the conditions and simulations. In this section, we discuss the feasibility and stability conditions of the equilibria $E_1$, $E_3$, $E_6$ and $E_7$. We also investigate the sensitivity of the system with respect to the choice of the ecosystem parameters, through simulations carried out by standard MATLAB routines for the integration of ordinary differential equations. For the simulations, we allowed variation in a chosen pair of parameters at a time, keeping all the other ones at fixed values determined from selected available literature on the grey, red and pine marten demography and ecology. For the squirrel populations and the epidemiological parameters we adopted the same values used in [16] (see references therein), while for the pine marten we considered information reported in [29, 30, 31]. The set of basic parameter values used in all the simulations is the following one:

$$r = 1, \ d = 1.25, \ f = 0.61, \ u = 1, \ z = 0.4, \ a = 1,$$
$$b = 1, \ c = 0.165, \ s = 0.1, \ w = 0.1, \ \lambda = 3.27, \ \mu = 1.1,$$
$$v = 0.7, \ \beta = 3.27, \ g = 1.1, \ h = 1.7, \ e = 0.2.$$  

To better describe the feasibility and stability conditions from the ecological viewpoint, letting $P$ denote a generic population, we can introduce the “relative killing” $K_P$ or “relative intraspecific competition” $C_P$ rates as follows. For the grey squirrel, the red squirrel and the pine marten are respectively given by

$$K_G = \frac{u}{d}, \quad K_R = \frac{s}{a}, \quad C_M = \frac{h}{g}, \quad C_R = \frac{h}{a}.$$  

Note that the “relative intraspecific competition” $C_P$, represents essentially the reciprocal of the population $P$ carrying capacity.
For the squirrel-free equilibrium point \( E_1 = (0, 0, 0, M_1) = (0, 0, 0, gh^{-1}) \) the stability conditions (3) imply
\[
C_M < \min\{K_R, K_G\},
\]
i.e. that the pine marten relative intraspecific competition rate should not exceed the relative killing rates of both types of squirrels. Also, the transcritical bifurcations (15) in terms of these quantities become
\[
C_M = K_R, \quad C_M = K_G.
\]
Conditions (18) could be met if the predation rates (\( s \) and \( u \)) were large and if the pine marten intraspecific competition was limited with respect to the net reproduction rate. However, this is unlikely to be the case. In particular, the condition involving the red squirrel killing rate is not met with the realistic parameter values used in the simulations.

In view of the transcritical bifurcations found for \( E_1 \), the system is thus more likely to evolve toward \( E_3 \) (disease-and-red-squirrel-free point) or \( E_6 \) (disease-and-grey-squirrel-free point), depending on the condition involving the grey squirrel killing rate. Indeed, the disease-and-grey-squirrel-free point \( E_3 = (G_3, 0, 0, M_3) \) is feasible when condition (4) holds, which now can be rephrased as follows
\[
C_M > K_G.
\]
Figure 1 shows that the survival of the grey squirrel occurs if \( u < h \), which is probably the case in natural conditions. Note indeed that in the simulations the base parameter values were indeed fixed at 1 and 1.7, for \( u \) and \( h \) respectively.

The grey squirrel population could go extinct for small to moderate \( u \) values, only if \( h < 2 \).

In order to move toward a more favourable situation for the red squirrel, the \( u \) values should
be slightly larger than $h$, although in this case the disease remains endemic in the system. The persistence of the predator is achieved for small and moderate $h$ values, independently from $u$.

With small or moderate $u$, and small $h$, so that $h < u$, the grey-squirrel-free point corresponding to $E_7$ could indeed be achieved. For this point, $E_7 = (R_7, 0, I_7, M_7)$ to have nonnegative populations, we must impose the feasibility condition (9), which involves both epidemiological parameters, $\lambda$ and $\mu$, namely the intraspecific disease transmission rate for red squirrels and the red squirrels’ natural plus disease-related mortality respectively. It can be rephrased by observing that it provides an epidemiological upper bound on the relative intraspecific competition rate for the red squirrel, namely

$$\frac{\lambda}{\mu} \geq C_R. \quad (20)$$

This can be achieved only for large values of $\mu$.

Finally, the point $E_6 = (0, R_6, 0, M_6)$, is feasible for the condition (7), which becomes now

$$C_M \geq K_R. \quad (21)$$

In this case, the condition is met with the chosen parameter values, but compare also the above discussion for $E_1$. Thus the relative killing rate on the red squirrels must not exceed the pine marten relative intraspecific competition rate. This latter equilibrium represents the most desirable outcome from the conservation perspective. In order to drive the system toward this configuration, $h$ appears to be a critical parameter, but its real value is highly uncertain. Moreover, our simulations highlight the fact that a too much larger value of $h$ could lead to the pine marten extinction.
EFFECTS OF PINE MARTEN ON SQUIRRELS DYNAMICS

Figure 4. Equilibria behaviour in the $h - \mu$ parameter space. The height of the surface represents the value of each population at equilibrium; clockwise from top left $G, R, I, M$.

very large $h$ will then bring the system back to a particular subsystem, the one investigated in [16], whose outcomes were mostly in favour of the grey squirrel.

Through our simulations, we thus assessed the behaviour of the system for a wide range of $h$ values. We found that favourable conditions, i.e. red squirrel and pine marten persistence, with disease eradication or kept at an endemic low level could be obtained in different situations. These outcomes occur if $h < 2$ even if the grey squirrel intraspecific competition rates were reduced (Figure 2), or alternatively for smaller values of $h$ ($h < 1$) with different levels of red squirrel intraspecific competition (Figure 3). A positive outcome could also be achieved with small $h$ and if the red squirrels' natural plus disease-related mortality $\mu$ is large (Figure 4). An inspection of Figures 2 and 3 reveals that there is a wide range of $h$ values for which the grey squirrel could disappear from the system and the analysis of (8) suggests that the whole system could actually evolve toward $E_6$, for $0 < h < 2$.

Note that $c$ and $\mu$ also represent arbitrary parameters. As in [16], here we observe again that large $\mu$ values are favourable for the red squirrels, in that their population increases more sharply (Figure 5 and 4). In the absence of the pine marten, moreover in [16] it is found that the red squirrel could outcompete the alien species and at the same time eradicate the disease if it had much more weight in the interspecific competition (small $c$). In the system that includes the predator, reducing the interspecific competition between the squirrel species would result in a more marked decrease in the grey population. This would also help the red squirrels recovery, without wiping out neither the disease nor the predator (Figure 6).

Finally, concerning the direct impact of the pine marten on the grey squirrel, $u$, which is of course of primary interest, we note that its value should be large, as expected, in order to wipe out
Figure 5. Equilibria behaviour in the $\mu - r$ parameter space. The height of the surface represents the value of each population at equilibrium; clockwise from top left $G$, $R$, $I$, $M$.

5. Conclusions. Our analysis reveals that the ecosystem in consideration has different equilibria. They include a squirrel-free point ($E_1$) that could originate if the predator invaded the ecosystem. However, this point represents an unlikely outcome. Its conditions could only be met if the pine marten exerted a high predation pressure on both squirrel species and if the carrying capacity of the predator was large. In reality, no predator has an actual advantage in extinguishing its prey. In this case, in particular, the predation rate of the marten on the squirrels is not thought to be a direct threat to squirrel population viability [25], also because adult pine martens are solitary and territorial animals [32], living at low densities, [31] and showing an opportunistic trophic behaviour, [32]. However, direct predation of the pine marten on squirrels has been verified in natural conditions, and the predation pressure is likely higher on greys than reds. In the Irish Midlands, where both red and grey squirrels were present, the percentage frequency of occurrence of grey squirrels in pine marten diet was significantly higher than that of red squirrels, [33]. The different predation rate
Figure 6. Equilibria behaviour in the $u-c$ parameter space. The height of the surface represents the value of each population at equilibrium; clockwise from top left $G$, $R$, $I$, $M$.

may be due to differences in the ecology of the two squirrels: grey squirrels are less arboreal than red squirrels [34], and they typically occur at much higher densities, [35]. Predation could thus be easier on the grey ones, also because the pine marten predation rate is likely to be proportional to the rate at which the predator and the prey meet. Moreover, the presence of the predator could have detrimental impacts on greys populations through several, complex mechanisms. Namely, the hypothesis of a ‘landscape of fear’ has been advocated [32], considering that the grey squirrel has no predators similar to the pine marten in its natural range (‘prey naivety’, [38]). Under this scenario, we expect the grey squirrels to be predated more frequently, although at moderate rates, than reds, and in general we expect them to lose or at least reduce their ecological advantage to the red squirrel. Overall, it could be inferred that the native species may benefit in the presence of the pine marten due to the removal of competitive pressure [36] (i.e., reduced $c$ in our model) and the risk of epizootic disease spread (i.e., reduced $\beta$) from grey squirrels, [37].

Our results are indeed consistent with all these considerations. Assuming a higher predation rate on greys than on reds, and analysing the feasibility and stability conditions of the equilibria, we found that the system is more likely to evolve toward points including the red squirrels ($E_6$ and $E_7$) than toward the disease-and-red-squirrels-free point ($E_3$). Comparing our results with those obtained by [16] in the absence of the predator, we also note that the introduction of the pine marten into the system destabilises all the equilibria of the subsystem including only grey, healthy and infected red squirrels.

The presence of the pine marten thus drives the system toward conditions that are more favourable to the native squirrel species, although the disease is likely to remain endemic. Favourable conditions are found for several values of the intraspecific competition rate of the predator, $h$, that
is, ultimately, for different pine marten carrying capacities. However, the eradication of the invader from the ecosystem could occur for small, realistic values of $u$ only if $h < 2$. This agrees with the finding that the negative effect of the predator on the grey squirrel, as observed in Ireland, may be dependent on marten density exceeding the threshold of 3 martens/km$^2$, [38]. In particular, the most favourable conditions for the red squirrels arise when $u > h$. Taking into account available information on pine marten and grey squirrel ecology as synthesised above, this scenario is not very likely, and from a conservation and wildlife management perspective decreasing $h$ seems particularly difficult. Nevertheless, efforts could be exerted to increase the marten predation pressure on grey squirrels. In the presence of the predator the wildlife managers would be facilitated in their attempts to reduce the grey squirrels and favour the red ones, but, ultimately, the presence of the predator alone could not guarantee the eradication of the invader from the system. Efforts should still be made to control grey squirrel populations, increasing $u$ and reducing $d$, as also suggested in [16].

**Acknowledgments.** This research has been carried out within the framework of the LIFE U-SAVEREDS Project (LIFE13 BIO/IT/000204), funded by the LIFE+ Biodiversity Programme of the European Commission.

**REFERENCES**

[1] F Cassola. *Sciurus carolinensis, Eastern Gray Squirrel. The IUCN Red List of Threatened Species*, pages 1–8, 2018.
Figure 8. Equilibria behaviour in the $u-s$ parameter space. The height of the surface represents the value of each population at equilibrium; clockwise from top left $G$, $R$, $I$, $M$.

[1] A. D. Middleton. 38. The Ecology of the American Grey Squirrel (Sciurus carolinensis Gmelin) in. the British Isles. Proceedings of the Zoological Society of London, 100(3):809–843, October 1930.

[2] M Shorten Mrs. Vizoso and C Elton. Some aspects of the biology of the grey squirrel ($Sciurus carolinensis$) in Great Britain. Proceedings of the Zoological Society of London, 121(2):427–459, August 1951.

[3] A Martinoli, S Bertolino, Damiano G Preatoni, Andrea Balduzzi, Andrea Marsan, P Genovesi, G Tosi, and Lucas A Wauters. Headcount 2010: the multiplication of the grey squirrel populations introduced to Italy. Hystrix, the Italian Journal of Mammalogy, 21(2):127–136, December 2010.

[4] John Gurnell. Squirrel numbers and the abundance of tree seeds. Mammal Review, 13(2-4):133–148, June 1983.

[5] Luc A Wauters and John Gurnell. The Mechanism of Replacement of Red Squirrels by Grey Squirrels: A Test of the Interference Competition Hypothesis. Ethology, 29(6):1053–1071, December 1999.

[6] Luc A Wauters, John Gurnell, A Martinoli, and G Tosi. Interspecific Competition between Native Eurasian Red Squirrels and Alien Grey Squirrels: Does Resource Partitioning Occur? Behavioral Ecology and Sociobiology, 52(4):332–341, 2002.

[7] L Wauters, G Tosi, and John Gurnell. Interspecific competition in tree squirrels: do introduced grey squirrels ($Sciurus carolinensis$) deplete tree seeds hoarded by red squirrels ($S. vulgaris$)? Behavioral Ecology and Sociobiology, 51(4):360–367, 2002.
[9] Luc A Wauters, Peter W W Luiz, and John Gurnell. Interspecific effects of grey squirrels (Sciurus carolinensis) on the space use and population demography of red squirrels (Sciurus vulgaris) in conifer plantations. Ecological Research, 15(3):271–284, 2000.

[10] S Bertolino, A Martinoli, and L A Wauters. Risk Assessment for Sciurus carolinensis (grey squirrel). In H Roy, editor, Invasive alien species - framework for the identification of invasive species of EU concern, page 298. Natural Environment Research Council, June 2014.

[11] K Thomas, D M Tompkins, A W Sainsbury, A R Wood, R Dalziel, P F Nettleton, and C J McInnes. A novel poxvirus lethal to red squirrels (Sciurus vulgaris). Journal of General Virology, 84(12):3337–3341, 2003.

[12] Colin J McInnes, Ann R Wood, Kathryn Thomas, Anthony W Sainsbury, John Gurnell, F Joshua Dein, and Peter F Nettleton. Genomic characterization of a novel poxvirus contributing to the decline of the red squirrel (Sciurus vulgaris) in the UK. Journal of General Virology, 87(8):2115–2125, August 2006.

[13] J C Reynolds. Details of the Geographic Replacement of the Red Squirrel (Sciurus vulgaris) by the Grey Squirrel (Sciurus carolinensis) in Eastern England. The Journal of Animal Ecology, 54(1):149–162, February 1985.

[14] S.P. Rushton, P.W.W. Luiz, J. Gurnell, and R. Fuller. 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, 37:997–1012, 2000.

[15] P W W Luiz, S P Rushton, 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(5):407–420, 2001.

[16] F. Barbara, V. La Morgia, V. Parodi, G. Toscano, and E. Venturino. Analysis of the incidence of poxviruses on the dynamics between red and grey squirrels. Mathematics, 6:113, 2018.

[17] C Romeo, L A Wauters, and N Ferrari. 11. Parasite of grey squirrels: an additional threat to red squirrels in Italy? In The Grey Squirrel Ecology and Management of an Invasive Species in Europe, pages 193–209. ESI, European Squirrel Initiative, 2016.

[18] M.A. Steele, and L.A. Wauters. Diet and food hoarding in Eastern grey squirrels (Sciurus carolinensis): implications for an invasive advantage. In The Grey Squirrel Ecology and Management of an Invasive Species in Europe, pages 97–114. ESI, European Squirrel Initiative.

[19] Henry S Mosby. The Influence of Hunting on the Population Dynamics of a Woodlot Gray Squirrel Population. The Journal of Wildlife Management, 33(1):709–717, 1969.

[20] Samuel D Montgomery, James B Whelan, and Henry S Mosby. Bioenergetics of a Woodlot Gray Squirrel Population. The Journal of Wildlife Management, 39(4):709, October 1975.

[21] A Okubo, P K Maini, M H Williamson, and J D Murray. On the spatial spread of the grey squirrel in Britain. Proceedings of the Royal Society of London. Series B, Biological sciences, 238(1291):113–125, 1989.

[22] John 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(2):325–338, April 1996.

[23] S Bertolino. Attivazione di un progetto di monitoraggio estensivo ed intensivo dello Sciattolo grigio (Sciurus carolinensis) in Piemonte. Technical report, Regione Piemonte, 2004.

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

[25] S Harris, C D Soulsbury, and G Iossa. Is culling grey squirrels a viable tactic to conserve red squirrel populations? Technical report, Advocates for animals, 2006.

[26] Emma Sheehy and C Lawton. Population crash in an invasive species following the recovery of a native predator: the case of the American grey squirrel and the European pine marten in Ireland. Biodiversity and Conservation, 23:753–774, 2014.

[27] J J Rowe. Squirrel management. Mammal Review, 13:173–181, 1983.

[28] Emma Sheehy, Chris Sutherland, Catherine O’Reilly, and Xavier Lambin. The enemy of my enemy is my friend: native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. Proceedings of the Royal Society B: Biological Sciences, 285(1874):20172603–9, 2018.

[29] S Harris, Pat Morris, Stephanie Wray, and Derek Yalden. A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. Technical report, Joint Nature Conservation Committee, Peterborough, 1995.
[30] L. Boitani, S. Lovari, and A. Vigna Taglianti. Fauna d’Italia. Mammalia III. Carnivora - Artiodactyla. Edizioni Calderini de Il Sole-24 Ore, Bologna, 2003.

[31] A. Zalewski and W. Jedrzejewski. Spatial organisation and dynamics of the pine marten Martes martes population in Białowieża Forest (E Poland) compared with other European woodlands. *Ecography*, 29(1):31–43, February 2006.

[32] J.L. MacPherson, H. Denman, D. Tosh, C. McNicol, and E.C. Halliwell, E.C. A review of the current evidence for impacts of the pine marten (Martes martes) on non-native and native squirrel populations. In *The Grey Squirrel Ecology and Management of an Invasive Species* in Europe, pages 289–304. ESI, European Squirrel Initiative.

[33] E. Sheehy, D.B. O’Meara, C. O’Reilly, A. Smart, and C. Lawton, C. A non-invasive approach to determining pine marten abundance and predation. *European Journal of Wildlife Research*, 60:223–236, 2013.

[34] R.E. Kenward, and J.M. Tonkin, J.M. Red and grey squirrels: some behavioural and biometric differences. *Journal of Zoology*, 209:279–281, 1986.

[35] J. Gurnell. *The Natural History of Squirrels*. Helm, London.

[36] J. Gurnell, L.A. Wauters, and P. Lurz, P. Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. *Journal of Animal Ecology*, 73:26–35, 2004.

[37] J. Chantrey, T.D. Dale, J.M. Read, S. White, F. Whitfield, D. Jones, C.J. McInnes, and M. Begon, M. European red squirrel population dynamics driven by squirrelpox at a gray squirrel invasion interface. *Ecology and Evolution*, 4:3788–3799.

[38] E. Sheehy, and C. Lawton, C. Predators of red and grey squirrels in their natural and introduced range. In *Red Squirrels Ecology, Conservation Management in Europe*, pages 83–96. ESI, European Squirrel Initiative.

Received xxxx 20xx; revised xxxx 20xx.

E-mail address: elena.travaglia@unito.it
E-mail address: valentina.lamorgia@isprambiente.it; valentina.lamorgia@unito.it
E-mail address: ezio.venturino@unito.it