

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

A model for voles interference in cultivated orchards

This is a pre print version of the following article:

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1945248> since 2023-12-01T13:44:42Z

Published version:

DOI:10.1016/j.mbs.2023.109107

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

A Model for Voles Interference in Cultivated Orchards

Alberto Viscardi^{a,*}, Sandro Bertolino^b, Ezio Venturino^a

^a*Dipartimento di Matematica “Giuseppe Peano”, Università degli studi di Torino*

^b*Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università degli studi di Torino*

Abstract

We consider a dynamical system involving seven populations to model the presence of voles in a cultivated orchard. The plant population is stratified by age (three groups) and by health status (being damaged or not). The last equation models the voles with a modified logistic equation with Allee effect, where the modification takes into account the disturbance provided by the human activity on the orchard. Both an analytical investigation and numerical simulations on a case study are presented. The latter support the observed differences in the literature, in terms of number of voles, between cultivated and uncultivated fields.

Keywords: population dynamics; subpopulations structured by age groups; rodents on cultivated areas; Allee effect

1. Introduction

Fossorial and semi-fossorial rodent species are important agricultural pests worldwide [3]. Voles of the genus *Microtus* can cause severe damage in European agroecosystems to crops and orchards [18, 28, 32]. During outbreaks, populations of *M. arvalis* and *M. agrestis* can reach densities of up to 2000 individuals per hectare, which could lead to enormous damage to crops [3, 22, 24]. In Italy, the most widespread *Microtus* species is the Savi’s pine vole (*Microtus savii*) which is responsible for extensive damage in arable lands [4, 23].

The Savi’s pine vole feeds on annual and perennial herbaceous wild and cultivated plants, generally within 10 m from the burrow exit hole [13, 32]. When herbaceous plants are strongly reduced in winter, voles search for alternative food sources and could debark trunks and roots just above and below ground level. Debarking allows the animals to reach the phloem, which is rich in nutrients. Bark-stripping reduces the phloem flow and thus affects the plant’s productivity; if the animals remove an entire circular band of bark, it could also cause the tree to die off [4].

The burrow system of Savi’s pine vole comprises several chambers connected by a network of corridors with primary and secondary entrances. These nests can be occupied by multiple individuals either simultaneously or sequentially. Savi’s pine voles also modify and utilize pre-existing mole burrows (*Talpa* spp.). Furthermore, in orchards, the tunnels of both species are often shared with white-toothed shrews (*Crocidura* spp.) and *Arvicola italicus* [6, 12, 33].

Despite its economic importance, Savi’s pine vole demographic studies are nearly absent [32]. Occasional observations have suggested that population densities may show seasonal and multiannual fluctuations without however extreme outbreaks [10]. The only published demographic study reported densities from 3 to 32 in/ha, with a peak in October, after reproduction, and the lowest values in February–April [11]. Studies on the factors affecting the Savi’s pine vole dynamics and damage level in croplands and orchards are also very limited [1, 32].

*Corresponding author

Email addresses: alberto.viscardi@unito.it (Alberto Viscardi), sandro.bertolino@unito.it (Sandro Bertolino), ezio.venturino@unito.it (Ezio Venturino)

Considering the general lack of information on the demography of the Savi's pine vole, a mathematical simulation could help managers to better understand the species dynamics in crop fields and orchards. Mathematical modeling is a basic theoretical tool for understanding the dynamics of biological and ecological systems (see, e.g., [25, 35]). It has been successful for the study of different phenomena, from the spread of diseases and infections [7, 19] to various interactions between predators and prey [14, 15, 20, 34, 36], in different contexts, from aquatic environments [8, 9] to cultivated areas [31]. In such situations, the study of the dynamics of ecological systems can provide useful insights about the consequences of strategies aimed at curbing certain phenomena, such as an outbreak of pests [2]. This paper considers a population of Savi's pine voles living in an orchard, digging tunnels close to the surface and damaging the trees through debarking of the roots [5, 11]. Agricultural practices however disturb the vole population, preventing explosive outbreaks. In Section 2, we present the model and its theoretical study, while Section 3 is devoted to the numerical simulation of the model on a peach orchard, based on the available data in the literature. Section 5 contains final considerations and remarks.

2. The proposed model

We consider a large monoculture orchard where a population of voles lives, digging tunnels close to the surface and in the process damaging the roots of the trees. We need to account for the plants and the animal populations. In order to model the trees, we use six different compartments. On one hand, we denote by T_y , T_a and T_o the trees not damaged by the voles. We partition them into the three demographic groups ("young" y , "adult" a and "old" o , respectively) that cohabit the orchard. The adult trees are the ones at their fruit production peak. On the other hand, we similarly define three populations of damaged trees: D_y , D_a and D_o .

We denote by $g_{ya} > 0$ and $g_{ao} > 0$ the growth rates of the trees which respectively move from T_y to T_a and from T_a to T_o . Trees in the old category T_o have then a mortality rate of $m > 0$. We model mortality as if it is affecting only old trees. We are not considering other damaging effects than the voles, hence a tree death in the younger classes is a rather rare event and we can interpret it as a "fast migration" into the oldest tree class followed by quick death.

We work under the assumption that the owner of the orchard plants a new tree in T_y as soon as an older one dies, thereby keeping the total number of trees in the orchard constant, $w > 0$. We also assume that the orchard's owner plants the trees in a way as to avoid competition between trees for the resources of the soil, so that the corresponding terms can be neglected in the model.

Each time the voles meet an undamaged tree in T_y , T_a or T_o there is a chance, respectively modeled by the parameters ν_y , ν_a , $\nu_o > 0$, that the tree will migrate into the corresponding damaged class. The damage inflicted by the voles is assumed to be permanent.

Since it is very difficult to quantify how much the voles' damage impacts the fruit production and the tree life, we make the following choice. We assume that, for the damaged trees, the parameters g_{ya} , g_{ao} , m become $g_{ya}(1 - \epsilon_{ya})$, $g_{ao}(1 + \epsilon_{ao})$, $m(1 + \epsilon_{oy})$, respectively, for some $\epsilon_{ya} \in [0, 1]$ and ϵ_{ao} , $\epsilon_{oy} > 0$. In this way, on one hand, young damaged trees take more time to become adults, while, on the other one, damaged adults and damaged old trees take less time to respectively age and die. Therefore, the overall population of adult trees is reduced by the presence of the voles and, since the bulk of the fruit production is given by adult trees, this is reflected in a reduction of the fruits produced by the orchard.

Remark 2.1. *The assumption on the mortality of trees could sound inadequate, since it is not possible for young and adult trees to die until they grow old, whether they are healthy or sick. However, this choice is reasonable from different point of views. On one hand, no data are available for damages caused to young tree individuals by the *M. savi* and for other species, the damage is dependent on too many factors (type of trees, voles density, type of agricultural practices applied on the soil, type of environment surrounding the orchard, etc.). Trying to be more accurate about this feature would make the model too complex to be studied.*

On the other hand, the assumption on the automatic replacement of dead individuals in the young class is already taking into account the matter. If a young healthy tree dies because of the damages caused by

the voles, it should be subtracted by the T_y population but then immediately added back to it because of the replacement assumption on the orchard trees, and the two terms would cancel out. For adult trees, instead, we have even less evidences of deaths caused by voles damage and so, on average, we can include them in the augmented growth rate and death rate given by the factors $g_{ao}(1 + \epsilon_{ao})$ and $m(1 + \epsilon_{oy})$ for the damaged adult trees class and the damaged old trees class, respectively.

Lastly, for the vole population, we start with a logistic equation with Allee effect (see, e.g., [16]), i.e,

$$\frac{dV}{dt} = rV \left(\frac{V}{a} - 1 \right) \left(1 - \frac{V}{k} \right), \quad (2.1)$$

where $r > 0$ is the reproduction rate, k the voles carrying capacity and a the critical Allee threshold, with $0 < a < k$. Now, we want to model the fact that voles are heavily disturbed by agricultural practices, such as plowing the soil (see [17]). In the scenario where no work is done on the soil we want the carrying capacity of the voles to settle at k . When the soil is being completely cleared, instead we want the carrying capacity to get as small as the critical point a . As a measure of the amount of work performed on the orchard, we use the ratio of dead trees with respect to the total amount of trees in the orchard, i.e.,

$$m \frac{T_o + (1 + \epsilon_{oy})D_o}{w}.$$

This is due to the fact that every tree that dies is immediately uprooted and a new one is planted to replace it. We consider this operation to be the most influential one on the soil to disturb the voles. This is consistent with the available biological information in the literature. Indeed, population models suggest that changes in survival rates are more influential than reproductive output in determining vole population cycles [21, 29]. Moreover, it has further been established that the type of cultivation, field management around the orchard, and agricultural practices can significantly impact the population size of Savi's pine voles [1]. Specifically, the management of ground vegetation and the irrigation system may exert a strong influence [1, 4].

The resulting equation for the vole population is then

$$\frac{dV}{dt} = rV \left(\frac{V}{a} - 1 \right) \left(1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy})D_o}{w} \right) \right).$$

Here, the additional term with respect to (2.1) can be interpreted as a spreading panic among the population of voles that forces them to leave the orchard.

In the end, the system of differential equations associated to this model is the following:

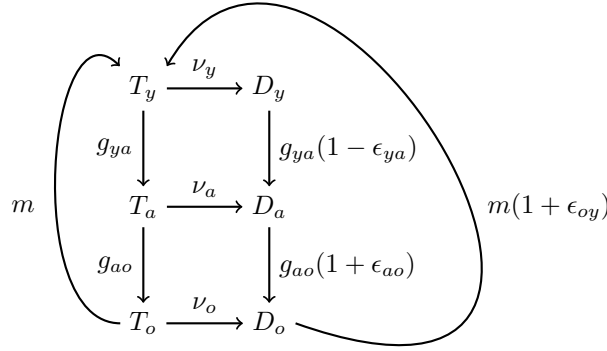
$$\begin{aligned} \frac{dT_y}{dt} &= mT_o + m(1 + \epsilon_{oy})D_o - (g_{ya} + \nu_y V) T_y, \\ \frac{dD_y}{dt} &= \nu_y V T_y - g_{ya}(1 - \epsilon_{ya})D_y, \\ \frac{dT_a}{dt} &= g_{ya}T_y - (g_{ao} + \nu_a V) T_a, \\ \frac{dD_a}{dt} &= \nu_a V T_a + g_{ya}(1 - \epsilon_{ya})D_y - g_{ao}(1 + \epsilon_{ao})D_a, \\ \frac{dT_o}{dt} &= g_{ao}T_a - (m + \nu_o V) T_o, \\ \frac{dD_o}{dt} &= \nu_o V T_o + g_{ao}(1 + \epsilon_{ao})D_a - m(1 + \epsilon_{oy})D_o, \\ \frac{dV}{dt} &= rV \left(\frac{V}{a} - 1 \right) \left(1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy})D_o}{w} \right) \right), \end{aligned} \quad (2.2)$$

where w represents the trees carrying capacity in the orchard, namely

$$T_y + D_y + T_a + D_a + T_o + D_o = w. \quad (2.3)$$

Remark 2.2. In (2.2) the bilinear form for the interaction terms has been chosen to model the damage suffered by the trees. Therefore it is not subjected to the “saturation effect” that is expressed by other more sophisticated functional responses, such as the Holling type II form. In an orchard, since the ground is frequently managed by farmers, tunnels are constantly destroyed and new are opened, hence we can expect the interaction not to change in behavior with respect to the number of individuals of the populations involved. Moreover, trees are assumed to be distributed uniformly and the interaction between them and the voles occurs underground. Therefore, without explicitly introducing a spatial model, it is natural to consider all possible interactions between individuals of the vole population and trees as viable. Therefore, from this perspective, the bilinear form adequately represents the actual situation.

We then have the following flow chart for the trees subpopulations:



In order to simplify the model, we can exploit (2.3) to reduce the number of populations by one and so the number of equations of (2.2) by one. Since, D_y is the subpopulation that has the least amount of interaction with the other ones, we can eliminate it using (2.3) and get the reduced system

$$\frac{dT_y}{dt} = mT_o + m(1 + \epsilon_{oy})D_o - (g_{ya} + \nu_y V)T_y, \quad (2.4)$$

$$\frac{dT_a}{dt} = g_{ya}T_y - (g_{ao} + \nu_a V)T_a, \quad (2.5)$$

$$\frac{dD_a}{dt} = g_{ya}(1 - \epsilon_{ya})(w - T_y - T_a - D_a - T_o - D_o) + \nu_a VT_a - g_{ao}(1 + \epsilon_{ao})D_a, \quad (2.6)$$

$$\frac{dT_o}{dt} = g_{ao}T_a - (m + \nu_o V)T_o, \quad (2.7)$$

$$\frac{dD_o}{dt} = \nu_o VT_o + g_{ao}(1 + \epsilon_{ao})D_a - m(1 + \epsilon_{oy})D_o, \quad (2.8)$$

$$\frac{dV}{dt} = rV \left(\frac{V}{a} - 1 \right) \left(1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy})D_o}{w} \right) \right). \quad (2.9)$$

Before proceeding with the analysis of the system (2.4)–(2.9), it is worth considering two simpler models based on the same ideas but with less classes for the age stratification of the plant population.

2.1. The bare bones model

We begin at first by considering only two major classes of trees, namely healthy T and damaged D , in addition to the voles population. The resulting system of differential equations associated to this model is the following:

$$\begin{aligned}\frac{dT}{dt} &= mT + m(1 + \epsilon)D - \nu VT - mT, \\ \frac{dD}{dt} &= \nu VT - m(1 + \epsilon)D, \\ \frac{dV}{dt} &= rV \left[\frac{V}{a} - 1 \right] \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \frac{mT + m(1 + \epsilon)D}{w} \right) \right],\end{aligned}\tag{2.10}$$

under the assumption that the total tree population does not vanish and remains at a constant level, $w > 0$, namely

$$T + D = w.\tag{2.11}$$

Moreover, the Allee effect prescribes that

$$a < k.\tag{2.12}$$

Eliminating D from (2.11) we obtain

$$\begin{aligned}\frac{dT}{dt} &= m(1 + \epsilon)(w - T) - \nu VT, \\ \frac{dV}{dt} &= rV \left(\frac{V}{a} - 1 \right) \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \frac{mT + m(1 + \epsilon)(w - T)}{w} \right) \right].\end{aligned}\tag{2.13}$$

Note also that

$$0 \leq mT + m(1 + \epsilon)D = mT + m(1 + \epsilon)(w - T) = m[(1 + \epsilon)w - \epsilon T]\tag{2.14}$$

2.1.1. Feasible equilibria

System (2.10) allows only two feasible equilibria, namely the damaged trees-free one, $E_T = (w, 0)$ and the coexistence one $E_e = (T_e, V_e)$. To assess the latter, note that from the first equilibrium equation of (2.13) we obtain the first nullcline

$$V = \phi(T) = m(1 + \epsilon) \frac{w - T}{\nu T},\tag{2.15}$$

while annihilating the second equation of (2.13), we obtain either $V_{e1} = a$ or

$$V = \psi(T) = \frac{1}{\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \left[m(1 + \epsilon) - \frac{m}{w} \epsilon T \right]}.\tag{2.16}$$

In the former case, the coexistence equilibrium is

$$E_{e1} = (T_{e1}, V_{e1}) = (\phi^{-1}(a), a), \quad T_{e1} = \phi^{-1}(a) = \frac{mw(1 + \epsilon)}{a\nu + m(1 + \epsilon)} < w.$$

For the second case (2.16), note that

$$\psi(0) = \frac{1}{\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m(1 + \epsilon)} \leq \frac{1}{1/k} = k, \quad T_\infty = w \frac{\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) [m(1 + \epsilon)]}{\left(\frac{1}{a} - \frac{1}{k} \right) \epsilon m},\tag{2.17}$$

T_∞ establishing the location of the vertical asymptote of $\psi(T)$. Note also that combining (2.12) and (2.17) we have

$$\psi(0) > a, \quad \psi'(T) = \frac{m}{w} \epsilon \left\{ \frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \left[m(1 + \epsilon) - \frac{m}{w} \epsilon T \right] \right\}^{-2} > 0. \quad (2.18)$$

Hence $\psi(T)$ is an increasing convex hyperbola rising up from $(0, \psi(0))$ to infinity at T_∞ and negative for $T > T_\infty$, having as horizontal asymptote the T axis. The function $\phi(T)$ is instead a decreasing convex hyperbola with a vertical asymptote at the origin, coming down and intersecting the axis $V = 0$ at $T = w$ and ultimately approaching the horizontal asymptote $V = -m(1 + \epsilon)\nu^{-1} < 0$. On the other hand, we can rewrite T_∞ and obtain the estimate

$$T_\infty = w \left[1 + \frac{\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m}{\left(\frac{1}{a} - \frac{1}{k} \right) \epsilon m} \right] > w.$$

These two curves must intersect, by continuity, in the interval $(0, w)$. This point gives the second coexistence equilibrium E_{e2} . In view of the above discussion, there is also a second unfeasible intersection with a negative value for V , $V_{e3} < 0$ and the corresponding abscissa $T_{e3} > w$, which will not be considered any further.

We can also analytically specify the intersection point, as upon substitution, the nullclines system leads to the following quadratic equation:

$$a_2 T^2 - a_1 T + a_0 = 0,$$

where, recalling (2.12)

$$a_2 = \left(\frac{1}{a} - \frac{1}{k} \right) \epsilon \frac{m}{w} > 0, \quad a_0 = \frac{w}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m(1 + \epsilon)w > 0,$$

$$a_1 = \left[\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m(1 + 2\epsilon) + \frac{\nu}{m(1 + \epsilon)} \right] > 0.$$

In view of these and the above considerations, by Descartes' rule, two real non-negative solutions are always ensured, of which the smaller one is the only one of interest, namely

$$T_{e2} = \frac{a_1 - \sqrt{a_1^2 - 4a_2 a_0}}{2a_2}, \quad V_{e2} = \psi(T_{e2}) = \phi(T_{e2}) > 0.$$

2.1.2. Local stability

The Jacobian of (2.13) is

$$J = \begin{pmatrix} -m(1 + \epsilon) - \nu V & -\nu T \\ rV^2 \left(\frac{V}{a} - 1 \right) \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon & J_{22} \end{pmatrix}$$

with

$$J_{22} = r \left(\frac{V}{a} - 1 \right) \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \frac{mT + m(1 + \epsilon)(w - T)}{w} \right) \right] \quad (2.19)$$

$$+ V \frac{r}{a} \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \frac{mT + m(1 + \epsilon)(w - T)}{w} \right) \right]$$

$$- rV \left(\frac{V}{a} - 1 \right) \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \frac{mT + m(1 + \epsilon)(w - T)}{w} \right).$$

More synthetically,

$$J_{22} = \left(2r \frac{V}{a} - 1 \right) \left[1 - \frac{V}{\psi(T)} \right] - rV \left(\frac{V}{a} - 1 \right) \frac{1}{\psi(T)}.$$

Now, at $E_T = (w, 0)$ the Jacobian reduces to an upper triangular matrix from which we easily find the eigenvalues $-m(1 + \epsilon) < 0$ and $-r < 0$. Hence this point is unconditionally stable.

At $E_{e1} = (\phi^{-1}(a), a)$, we also obtain an upper triangular Jacobian with eigenvalues

$$-m(1 + \epsilon) - \nu a < 0, \quad r \left(1 - \frac{a}{\psi(T_{e1})} \right), \quad (2.20)$$

from which stability is ensured by

$$\psi(T_{e1}) < a, \quad (2.21)$$

an implicit condition because $\psi(T_{e1})$ depends on a as well. But geometrically this condition states that the coexistence equilibrium with fixed value of the voles a is stable if and only if it lies in the portion of the first quadrant above the isocline $\psi(T)$.

For the coexistence case, the full Jacobian must be evaluated at E_{e2} and stability is ensured by the corresponding Routh-Hurwitz conditions. Using the two equilibrium equations, we can rewrite the relevant diagonal elements of the Jacobian as

$$J_{11}(E_{e2}) = -\frac{mw(1 + \epsilon)}{T_{e2}}, \quad J_{22}(E_{e2}) = -rV_{e2} \left(\frac{V_{e2}}{a} - 1 \right) \frac{1}{V_{e2}} = -r \left(\frac{V_{e2}}{a} - 1 \right).$$

Indeed, the first and second terms in the sum (2.19) vanish because the coexistence equilibrium point lies on the isocline, so that $V \neq 0$, $V \neq a$ and therefore the bracket must be annihilated, namely giving

$$\frac{1}{V_{e2}} = \frac{1}{\psi(T_{e2})}.$$

The trace condition gives

$$-\text{tr}(J(E_{e2})) = \frac{mw(1 + \epsilon)}{T_{e2}} + r \left(\frac{V_{e2}}{a} - 1 \right) > 0$$

and is therefore satisfied if

$$V_{e2} > a. \quad (2.22)$$

For the determinant, suitably collecting terms, we find

$$\det(J(E_{e2})) = rm \left(\frac{V_{e2}}{a} - 1 \right) \left[\frac{w(1 + \epsilon)}{T_{e2}} + \nu T_{e2} r V_{e2}^2 \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon \right] > 0$$

if and only if (2.22) holds.

In summary, coexistence E_{e2} is stable if and only if its height V_{e2} lies above the horizontal line $V = a$, while the other coexistence point E_{e1} , in view of (2.21), is stable if and only if its height lies below the same horizontal line. In other words, the three equilibria can be arranged in a linear order corresponding to the increasing order of their abscissae, in two alternative ways corresponding to the two alternative conditions mentioned below:

$$(2.22) : \quad E_{e2}, E_{e1}, E_1; \quad (2.21) : \quad E_{e1}, E_{e2}, E_1$$

with the extremal ones always stable and the middle one being a saddle.

Two important inferences can therefore be made from these considerations. When E_{e1} and E_{e2} cross each other, they exchange their stability, through a transcritical bifurcation, occurring at $\psi(T_{e1}) = a = V_{e2}$. Secondly, there is a regime of bistability, in which the separatrix goes through the saddle point, either E_{e1} or E_{e2} , as discussed above.

2.1.3. Analytic determination of the transcritical bifurcation

We consider the point $E_{e1} = (\phi^{-1}(a), a)$ for the bifurcation and choose a as bifurcation parameter. From (2.20) we can possibly annihilate only the second eigenvalue by setting $a = \psi(T_{e1})$. Since $\psi(T)$ depends on a itself, we first find the critical value by expanding the above inequality

$$\frac{1}{a} = \frac{1}{\psi(T_{e1})} = \frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k}\right) \left[m(1 + \epsilon) - \frac{m}{w} \epsilon T \right].$$

Simplifying,

$$\left(\frac{1}{a} - \frac{1}{k}\right) \left[m(1 + \epsilon) - \frac{m}{w} \epsilon T - 1 \right] = 0.$$

to finally obtain

$$a^\dagger = k. \tag{2.23}$$

Now we use Sotomayor's theorem, [30]. The left w and right v eigenvalues of the Jacobian evaluated at E_{e1} for $a = k$ are easily found:

$$w^T = (0, 1), \quad v^T = (\nu T_{e1}, -m(1 + \epsilon) - \nu k).$$

Let us begin by differentiating the right hand side F of (2.13) with respect to the bifurcation parameter a :

$$F_a = \frac{dF}{da} = \left[\begin{array}{c} 0 \\ -\frac{rV^2}{a^2} \left[1 - \frac{V}{\psi(T)} \right] + rV \left(\frac{V}{a} - 1 \right) \frac{V}{a^2} \frac{mT + m(1 + \epsilon)(w - T)}{w} \end{array} \right].$$

It follows

$$\begin{aligned} \left. \frac{dF}{da} \right|_{E_{e1}, a=k} &= \left[\begin{array}{c} 0 \\ -r \left(1 - \frac{a^\dagger}{\psi(T)|_{E_{e1}, a=k}} \right) \end{array} \right] \\ &= \left[\begin{array}{c} 0 \\ -r \left(1 - k \left\{ \frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) \left[m(1 + \epsilon) - \frac{m}{w} \epsilon T \right] \right\} \right) \Big|_{E_{e1}, a=k} \end{array} \right] = \left[\begin{array}{c} 0 \\ 0 \end{array} \right] \end{aligned}$$

and consequently

$$w^T \left. \frac{dF}{da} \right|_{E_{e1}, a=k} = 0 \tag{2.24}$$

which prevents the occurrence of a saddle-node bifurcation [30].

To further investigate the matter, we calculate the Jacobian DF_a

$$DF_a = \left[\begin{array}{cc} 0 & 0 \\ \frac{\partial DF_a}{\partial V} & \frac{\partial DF_a}{\partial T} \end{array} \right]$$

where

$$\begin{aligned} \frac{\partial DF_a}{\partial V} &= -\frac{2rV}{a^2} \left[1 - \frac{V}{\psi(T)} \right] + \frac{rV^2}{a^2} \frac{1}{\psi(T)} \\ &\quad + \frac{2rV}{a^2} \left(\frac{V}{a} - 1 \right) \frac{mT + m(1 + \epsilon)(w - T)}{w} + \frac{rV^2}{a^2} \frac{1}{a} \frac{mT + m(1 + \epsilon)(w - T)}{w} \end{aligned}$$

and

$$\frac{\partial DF_a}{\partial T} = \frac{2V^3}{a^2} \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon - \frac{rV^2}{a^2} \left(\frac{V}{a} - 1 \right) \frac{m}{w} \epsilon.$$

Hence, since $\psi(E_{e1})|_{a=k} = k^{-1}$,

$$DF_a|_{E_{e1}, a=k} = \begin{bmatrix} 0 & 0 \\ -\frac{2r}{k}(1-k^2) + rk + \frac{r m T_{E_{e1}} + m(1+\epsilon)(w - T_{E_{e1}})}{w} & 0 \end{bmatrix}.$$

It follows

$$w^T DF_a|_{E_{e1}, a=k} v = \nu T_{e1} \left[\frac{2r}{k}(k^2 - 1) + rk + \frac{r m T_{E_{e1}} + m(1+\epsilon)(w - T_{E_{e1}})}{w} \right]$$

and consequently, in view of (2.14) and if we assume that the carrying capacity is large enough, $k > 1$, we find that this scalar does not vanish,

$$w^T DF_a|_{E_{e1}, a=k} v > 0. \quad (2.25)$$

We then proceed to evaluate the higher derivatives of F , D^2F . In view of the entries of the eigenvalue w we need only to differentiate the second component F_2 of F . Note that being linear in T , the second derivative of F with respect to T vanishes. Hence we find

$$w^T D^2Fv = \left[\frac{\partial^2 F_2}{\partial V^2} v_1 + 2 \frac{\partial^2 F_2}{\partial V \partial T} v_2 \right] v_1$$

From (2.19), differentiating further with respect to V we have

$$\frac{\partial^2 F_2}{\partial V^2} = \frac{2r}{a} + r \left(1 - \frac{6V}{a} \right) \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T + (1+\epsilon)(w - T)}{w} \right)$$

and with respect to T

$$\begin{aligned} \frac{\partial^2 F_2}{\partial V \partial T} &= r \left(\frac{V}{a} - 1 \right) V \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon + V^2 \frac{r}{a} \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon - rV \left(\frac{V}{a} - 1 \right) \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon \\ &= V^2 \frac{r}{a} \left(\frac{1}{a} - \frac{1}{k} \right) \frac{m}{w} \epsilon. \end{aligned}$$

so that

$$\frac{\partial^2 F_2}{\partial V^2} \Big|_{E_{e1}, a=k} = -2 \frac{r}{k}, \quad \frac{\partial^2 F_2}{\partial V \partial T} \Big|_{E_{e1}, a=k} = 0.$$

Therefore

$$w^T D^2Fv|_{E_{e1}, a=k} = -2 \frac{r}{k} v_1^2 < 0. \quad (2.26)$$

Combining (2.24), (2.25) and (2.26), Sotomayor's theorem ensures the occurrence of a transcritical bifurcation between E_{e1} and E_{e2} when the parameter a crosses from below the critical threshold $a^\dagger = k$.

Remark 2.3. *Although we have assumed that $a < k$, so that technically speaking this transcritical bifurcation could not possibly arise, nevertheless the result indicates that if the two relevant points, the critical Allee threshold $V = a$ and the voles carrying capacity $V = k$, exchange their positions, in such case the nature of the larger one after the exchange, $V = a$, would retain its stability, and conversely the smaller one, $V = k$, its instability. Mathematically, this is due to the fact that this exchange of its roots does produce any change in the shape of the cubic polynomial in the right hand side of the voles equation. Assessing its sign near the origin, it was negative, for $V < a < k$, before the exchange, and it remains so after the exchange, for $V < k < a$.*

2.2. The intermediate model

To make a step towards the full model, we consider here four classes of trees, T_y , T_a , D_y and D_a and the voles population. The tree classes are the same as in the full model, but the classes of old trees T_o and D_o , healthy and damaged, have been clustered together with the corresponding adult ones, T_a and D_a . Here we therefore have $w = T_y + D_y + T_a + D_a$. Exploiting this fact, $D_y = w - (T_y + T_a + D_a)$, so that we obtain the reduced system in which the equation for D_y is absent:

$$\begin{aligned}\frac{dT_y}{dt} &= r_T T_a + g_{ay}(1 + \epsilon_{ay})D_a - (g_{ya} + \nu_y V)T_y, \\ \frac{dT_a}{dt} &= g_{ya}T_y - (g_{ay} + \nu_a V)T_a, \\ \frac{dD_a}{dt} &= g_{ya}(1 - \epsilon_{ya})D_y + \nu_a V T_a - g_{ay}(1 + \epsilon_{ay})D_a, \\ \frac{dV}{dt} &= rV \left[\frac{V}{a} - 1 \right] \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) g_{ay} \frac{T_a + (1 + \epsilon_{ay})D_a}{w} \right) \right],\end{aligned}\tag{2.27}$$

in which we now take $r_T = g_{ay} = m$, the latter being again the trees mortality:

$$\begin{aligned}\frac{dT_y}{dt} &= mT_a + m(1 + \epsilon_{ay})D_a - (g_{ya} + \nu_y V)T_y, \\ \frac{dT_a}{dt} &= g_{ya}T_y - (m + \nu_a V)T_a, \\ \frac{dD_a}{dt} &= g_{ya}(1 - \epsilon_{ya})[w - (T_y + T_a + D_a)] + \nu_a V T_a - m(1 + \epsilon_{ay})D_a, \\ \frac{dV}{dt} &= rV \left[\frac{V}{a} - 1 \right] \left[1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_a + (1 + \epsilon_{ay})D_a}{w} \right) \right],\end{aligned}\tag{2.28}$$

Excluding the populations combinations that lead immediately to equilibrium equations that cannot be satisfied, there are only three possible equilibria candidates in addition to coexistence. The latter will not be analytically investigated, as we will perform this task for the larger model (2.4)-(2.9).

2.2.1. E_T

First of all, the healthy-trees-only point. The first and second equilibrium equations are the same, relating the two trees classes; the third one gives a constraint on their sum, so that we have

$$T_y = \frac{m}{g_{ya}} T_a, \quad T_y + T_a = w$$

from which it follows

$$E_T = (T_{y,T}, T_{a,T}, 0, 0) = \left(\frac{mw}{g_{ya} + m}, \frac{wg_{ya}}{g_{ya} + m}, 0, 0 \right),$$

always feasible.

2.2.2. E_1

Next, the point with no damaged adult trees, but in which the voles are present

$$E_1 = (T_{y,1}, T_{a,1}, 0, V_1).$$

Summing the first two equilibrium equations we find

$$-(\nu_y T_y + \nu_a T_a)V = 0.$$

In view of the fact that here we seek $V \neq 0$ and all parameters and populations must be positive, this equation is inconsistent and therefore this equilibrium does not exist.

2.2.3. E_2

Finally, we examine the equilibrium with damaged trees and no voles,

$$E_2 = (T_{y,2}, T_{a,2}, D_{a,2}, 0).$$

Again, summing the first two equilibrium equations, we obtain

$$m(1 + \epsilon_{ay})D_a = 0$$

which is inconsistent, as all parameters are positive and we seek $D_a \neq 0$. Hence also E_2 does not exist.

2.2.4. Stability

The Jacobian of (2.28) is

$$J = \begin{pmatrix} -(g_{ya} + \nu_y V) & m & m(1 + \epsilon_{ay}) & -\nu_y T_y \\ g_{ya} & -(m + \nu_a V) & 0 & -\nu_a T_a \\ -g_{ya}(1 - \epsilon_{ya}) & -g_{ya}(1 - \epsilon_{ya}) + \nu_a V & J_{33} & \nu_a T_a \\ 0 & J_{42} & J_{43} & J_{44} \end{pmatrix}$$

where

$$\begin{aligned} J_{33} &= -g_{ya}(1 - \epsilon_{ya}) - m(1 + \epsilon_{ay}) \\ J_{42} &= -rV^2 \left(\frac{V}{a} - 1 \right) \frac{m}{w} \left(\frac{1}{a} - \frac{1}{k} \right) \\ J_{43} &= -(1 + \epsilon_{ay})rV^2 \left(\frac{V}{a} - 1 \right) \frac{m}{w} \left(\frac{1}{a} - \frac{1}{k} \right) \\ J_{44} &= r \left(\frac{2V}{a} - 1 \right) - rV \left(\frac{3V}{a} - 2 \right) \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_a + (1 + \epsilon_{ay})D_a}{w} \right) \end{aligned} \quad (2.29)$$

Evaluating the Jacobian at the equilibrium E_T , we observe that $J(E_T)$ has one negative eigenvalue, $-r < 0$ from the last row. The remaining 3×3 submatrix $J^{(3)}(E_T)$ has negative trace,

$$\text{tr}(J^{(3)}(E_T)) = -g_{ya} - m - g_{ya}(1 - \epsilon_{ya}) - m(1 + \epsilon_{ay}),$$

the sum of the minors of order two reduces to

$$\Sigma^{(3)}(J^{(3)}(E_T)) = g_{ya}[g_{ya}(1 - \epsilon_{ya}) + m(1 + \epsilon_{ay})] + g_{ya}(1 - \epsilon_{ya})m(1 + \epsilon_{ay}) + m[g_{ya}(1 - \epsilon_{ya}) + m(1 + \epsilon_{ay})],$$

and the determinant is

$$\det(J^{(3)}(E_T)) = -g_{ya}^2(1 - \epsilon_{ya})m(1 + \epsilon_{ay}) - m^2g_{ya}(1 - \epsilon_{ya})(1 + \epsilon_{ay}) < 0.$$

Hence the stability condition is provided by the Routh-Hurwitz condition

$$\text{tr}(J^{(3)}(E_T))\Sigma^{(3)}(J^{(3)}(E_T)) < \det(J^{(3)}(E_T)). \quad (2.30)$$

Explicitly, from (2.30) we obtain

$$-g_{ya}^2m(1 - \epsilon_{ya}) - g_{ya}m^2(1 + \epsilon_{ay}) - m^2g_{ya}^2(1 - \epsilon_{ya}) - m^3g_{ya}(1 + \epsilon_{ay}) < 0, \quad (2.31)$$

which is unconditionally satisfied so that E_T is always stable.

	non-zero populations	feasible	equilibria	stability
Case I	T_y, T_a, T_o	always	E_T	either a stable node or focus
Case II	T_y, T_a, D_a, T_o, D_o	never	–	–
Case III	$T_y, T_a, D_a, T_o, D_o, V$	always	E_a plus either 1 or 3 more	E_a is not stable

Table 1: Summary of the cases and equilibria for the system (2.4)–(2.9)

2.3. Analysis of the full model

We are now ready to discuss the full model. Searching for the equilibria of the system (2.4)–(2.9), we need to consider only the 3 possible cases summarized in Table 1. Moreover, the Jacobian matrix of this full system is:

$$J = \begin{bmatrix} -g_{ya} - \nu_y V & 0 & 0 & m & m(1 + \epsilon_{oy}) & -\nu_y T_y \\ g_{ya} & -g_{ao} - \nu_a V & 0 & 0 & 0 & -\nu_a T_a \\ -g_{ya}(1 - \epsilon_{ya}) & -g_{ya}(1 - \epsilon_{ya}) + \nu_a V & \tau_0 & -g_{ya}(1 - \epsilon_{ya}) & -g_{ya}(1 - \epsilon_{ya}) & \nu_a T_a \\ 0 & g_{ao} & 0 & -m - \nu_o V & 0 & -\nu_o T_o \\ 0 & 0 & g_{ao}(1 + \epsilon_{ao}) & \nu_o V & -m(1 + \epsilon_{oy}) & \nu_o T_o \\ 0 & 0 & 0 & \tau_1 & \tau_2 & \tau_3 \end{bmatrix}, \quad (2.32)$$

where

$$\begin{aligned} \tau_0 &= -g_{ya}(1 - \epsilon_{ya}) - g_{ao}(1 + \epsilon_{ao}), \\ \tau_1 &= -rV^2 \left(\frac{V}{a} - 1 \right) \frac{m}{w} \left(\frac{1}{a} - \frac{1}{k} \right), \quad \tau_2 = -rV^2 \left(\frac{V}{a} - 1 \right) \frac{m(\epsilon_{oy} + 1)}{w} \left(\frac{1}{a} - \frac{1}{k} \right), \\ \tau_3 &= r \left(\frac{2V}{a} - 1 \right) + rV \left(2 - \frac{3V}{a} \right) \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy})D_o}{w} \right). \end{aligned}$$

Case I: The first case corresponds to the absence of voles and damaged trees from the orchards. With $D_a = D_o = V = 0$ the system (2.4)–(2.9) reduces to

$$\begin{aligned} \frac{dT_y}{dt} &= mT_o - g_{ya}T_y, \\ \frac{dT_a}{dt} &= g_{ya}T_y - g_{ao}T_a, \\ \frac{dT_o}{dt} &= g_{ao}T_a - mT_o, \end{aligned} \quad (2.33)$$

with

$$T_y + T_a + T_o = w,$$

which is needed for D_a having a vanishing time derivative. Searching for the stationary points of (2.33) leads to a unique equilibrium:

$$E_T = C [g_{ao}m, mg_{ya}, 0, g_{ao}g_{ya}, 0, 0] \quad C = \frac{w}{g_{ao}m + mg_{ya} + g_{ao}g_{ya}}.$$

The Jacobian matrix evaluated at this point is

$$J(E_T) = \begin{bmatrix} -g_{ya} & 0 & 0 & m & m(\epsilon_{oy} + 1) & -Cg_{ao}m\nu_y \\ g_{ya} & -g_{ao} & 0 & 0 & 0 & -Cmg_{ya}\nu_a \\ -g_{ya}(1 - \epsilon_{ya}) & -g_{ya}(1 - \epsilon_{ya}) & \tau_0 & -g_{ya}(1 - \epsilon_{ya}) & -g_{ya}(1 - \epsilon_{ya}) & Cmg_{ya}\nu_a \\ 0 & g_{ao} & 0 & -m & 0 & -Cg_{ao}g_{ya}\nu_o \\ 0 & 0 & g_{ao}(\epsilon_{ao} + 1) & 0 & -m(\epsilon_{oy} + 1) & Cg_{ao}g_{ya}\nu_o \\ 0 & 0 & 0 & 0 & 0 & -r \end{bmatrix},$$

and its spectrum is

$$\sigma_{J(E_T)} = \left\{ -g_{ya}(1 - \epsilon_{ya}), -g_{ao}(1 + \epsilon_{ao}), -m(1 + \epsilon_{oy}), -\frac{g_{ya} + g_{ao} + m \pm \sqrt{S}}{2}, -r \right\},$$

with

$$\begin{aligned} S &= g_{ya}^2 + g_{ao}^2 + m^2 - 2g_{ya}g_{ao} - 2g_{ao}m - 2mg_{ya} \\ &= [g_{ya} \quad g_{ao} \quad m] \begin{bmatrix} 1 & -1 & -1 \\ -1 & 1 & -1 \\ -1 & -1 & 1 \end{bmatrix} \begin{bmatrix} g_{ya} \\ g_{ao} \\ m \end{bmatrix}. \end{aligned}$$

When $S \geq 0$,

$$-\frac{g_{ya} + g_{ao} + m - \sqrt{S}}{2} < 0,$$

and so E_T is a stable node. Instead, when $S < 0$, we have two complex conjugate eigenvalues with negative real part. Therefore, in this case, E_T becomes a stable focus.

Remark 2.4. *The vole-free equilibrium E_T , where only the healthy tree populations survives, turns out to be locally asymptotically stable for all models: the bare-bones, the intermediate and the full one. This is due to two factors, namely the orchard constrain (2.3) and the Allee effect for the voles population. The first one prevents the healthy trees from dying out, while the second one guarantees the existence of a neighbor of E_T where the population of voles dies out. This is enough to ensure local asymptotic stability. The only slightly different behavior is the nature of E_T that can change from a stable node to a stable focus, depending on the choices of the parameters related to the type of plants present in the orchard. In other words, changing the type of cultivated trees can change the nature of E_T but not its stability.*

Case II: Here we do not have voles, but both populations of damaged trees do not vanish. The system then reduces to the following one:

$$\begin{aligned} \frac{dT_y}{dt} &= mT_o + m(1 + \epsilon_{oy})D_o - g_{ya}T_y, \\ \frac{dT_a}{dt} &= g_{ya}T_y - g_{ao}T_a, \\ \frac{dD_a}{dt} &= g_{ya}(1 - \epsilon_{ya})(w - T_y - T_a - D_a - T_o - D_o) - g_{ao}(1 + \epsilon_{ao})D_a, \\ \frac{dT_o}{dt} &= g_{ao}T_a - mT_o, \\ \frac{dD_o}{dt} &= g_{ao}(1 + \epsilon_{ao})D_a - m(1 + \epsilon_{oy})D_o. \end{aligned} \tag{2.34}$$

Searching for equilibria, one can show that this scenario never occurs. For example, obtaining T_y and T_o from the second and the fourth equations and substituting them in the first one gives $D_o = 0$ which contradicts the assumptions of this case.

Case III: In this scenario, all populations coexist. From (2.9), we need to study when either

$$\frac{V}{a} - 1 = 0 \quad \text{or} \quad 1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy})D_o}{w} \right) = 0.$$

If $V = a$, then we obtain

$$E_a = \begin{bmatrix} \frac{g_{ao} + \nu_a a}{g_{ya}} E_a(2) \\ E_a(2) \\ \frac{m(1 + \epsilon_{oy})E_a(5) - \nu_o a E_a(4)}{g_{ao}(1 + \epsilon_{ao})} \\ \frac{g_{ao}}{m + \nu_o a} E_a(2) \\ \frac{(g_{ya} + \nu_y a)E_a(1) - mE_a(4)}{m(1 + \epsilon_{oy})} \\ a \end{bmatrix}$$

with

$$E_a(2) = \frac{w}{\frac{\nu_y a(g_{ao} + \nu_a a)}{g_{ya}^2(1 - \epsilon_{ya})} + \frac{g_{ao}}{m + \nu_o a} + \frac{g_{ao} + \nu_a a}{g_{ya}} + \frac{(g_{ya} + \nu_y a)(g_{ao} + \nu_a a)(m + \nu_o a) - g_{ya} g_{ao} m}{g_{ya} m(1 + \epsilon_{oy})(m + \nu_o a)} + \frac{a(g_{ao} \nu_y + g_{ya} \nu_a + \nu_a \nu_y a)}{g_{ao} g_{ya} (1 + \epsilon_{ao})} + 1}$$

Looking at (2.32), it is easy to see that the last row of $J(E_a)$ has a unique non-zero element, the diagonal one, namely

$$\tau_3 = r - ra \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{E_a(4) + (1 + \epsilon_{oy}) E_a(5)}{w} \right) \in r \left(0, 1 - \frac{a}{k} \right).$$

Thus $J(E_a)$ has a real positive eigenvalue and E_2 cannot be a stable equilibrium. If we consider instead

$$1 - V \left(\frac{1}{k} + \left(\frac{1}{a} - \frac{1}{k} \right) m \frac{T_o + (1 + \epsilon_{oy}) D_o}{w} \right) = 0,$$

annihilating also equations (2.4), (2.5), (2.7) and (2.8), we can express all the tree populations with respect to the vole population as follows:

$$\begin{aligned} T_y &= \frac{wa(k - V)}{V(k - a)(g_{ya} + \nu_y V)}, \\ T_a &= \frac{g_{ya} wa(k - V)}{V(k - a)(g_{ya} + \nu_y V)(g_{ao} + \nu_a V)}, \\ D_a &= \frac{wa(k - V)}{V(k - a)g_{ao}(1 + \epsilon_{ao})} \left[1 - \frac{g_{ya} g_{ao}}{(g_{ya} + \nu_y V)(g_{ao} + \nu_a V)} \right], \\ T_o &= \frac{g_{ya} g_{ao} wa(k - V)}{V(k - a)(g_{ya} + \nu_y V)(g_{ao} + \nu_a V)(m + \nu_o V)}, \\ D_o &= \frac{wa(k - V)}{V(k - a)m(1 + \epsilon_{oy})} \left[1 - \frac{g_{ya} g_{ao} m}{(g_{ya} + \nu_y V)(g_{ao} + \nu_a V)(m + \nu_o V)} \right]. \end{aligned} \tag{2.35}$$

In doing so, from (2.6), we are left with finding the roots of a fourth degree polynomial in V . In particular,

$$\sum_{j=0}^4 C_j V^j = 0, \tag{2.36}$$

with

$$\begin{aligned}
C_0 &= -akg_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy})(g_{ya}g_{ao} + g_{ya}m + g_{ao}m) < 0, \\
C_1 &= -akm(1 + \epsilon_{oy}) \left(\frac{g_{ao}(1 + \epsilon_{ao})}{g_{ya}(1 - \epsilon_{ya})} + 1 \right) (g_{ao}m\nu_y + g_{ya}m\nu_a) \\
&\quad - akg_{ao}(1 + \epsilon_{ao})(g_{ao}m\nu_y + g_{ya}m\nu_a + g_{ya}g_{ao}\nu_o) \\
&\quad + g_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy}) \left(a \left(g_{ya}g_{ao} + g_{ya}m + g_{ao}m \right. \right. \\
&\quad \left. \left. - k \left(g_{ya}\nu_o + g_{ao}\nu_o - \frac{\epsilon_{ya}m\nu_a}{1 - \epsilon_{ya}} \right) \right) + (k - a)g_{ya}g_{ao}m \right), \\
C_2 &= ((k - a)m(1 + \epsilon_{oy}) + a)g_{ao}(1 + \epsilon_{ao})(g_{ao}m\nu_y + g_{ya}m\nu_a + g_{ya}g_{ao}\nu_o) \\
&\quad + am^2(1 + \epsilon_{oy}) \left(\frac{g_{ao}(1 + \epsilon_{ao})}{g_{ya}(1 - \epsilon_{ya})} + 1 \right) (g_{ao}\nu_y + g_{ya}\nu_a) \\
&\quad - \alpha ak(m\nu_y\nu_a + g_{ao}\nu_y\nu_o + g_{ya}\nu_a\nu_o) \\
&\quad + ag_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy}) \left(g_{ya}\nu_o + g_{ao}\nu_o + \frac{\epsilon_{ya}(k\nu_a\nu_o - m\nu_a)}{1 - \epsilon_{ya}} \right), \\
C_3 &= (k - a)g_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy})(g_{ya}\nu_a\nu_o + g_{ao}\nu_y\nu_o + m\nu_y\nu_a) \\
&\quad + \alpha(g_{ya}\nu_a\nu_o + g_{ao}\nu_y\nu_o + m\nu_y\nu_a - k\nu_y\nu_a\nu_o) \\
&\quad - ag_{ao}m \frac{\epsilon_{ya}(1 + \epsilon_{ao})(1 + \epsilon_{oy})}{1 - \epsilon_{ya}} \nu_a\nu_o, \\
C_4 &= ((k - a)g_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy}) + \alpha) \nu_y\nu_a\nu_o > 0,
\end{aligned}$$

where

$$\alpha = a \left(g_{ao}(1 + \epsilon_{ao}) + m(1 + \epsilon_{oy}) \left(\frac{g_{ao}(1 + \epsilon_{ao})}{g_{ya}(1 - \epsilon_{ya})} + 1 \right) \right) > 0.$$

Since $C_0 < 0$ and $C_4 > 0$, the existence of a positive solution for (2.36) is always guaranteed. Moreover, we either have one or three positive solutions for (2.36) and thus one or three coexistence equilibria in addition to E_a . Unfortunately, this is all we can say analytically about this case and thus we proceed studying a specific scenario numerically.

Remark 2.5. *The coefficients of (2.36) and the expression in (2.35) do not depend on the parameter r . This is curious but not surprising since the starting point for voles' equation is a logistic equation with Allee effect for which the three roots do not depend on r .*

3. Simulations on a peach orchard

Due to the lack of data about voles in orchards, in order to use data of [11], we consider the case of an ideal one-hectare peach orchard. The chosen time unit is the year. For the parameters regarding the tree populations we refer to [26, 27]. There, the optimal number of trees for a one-hectare orchard is $w = 1000$. Peach trees have an average life span of 20 years and can be partitioned into three classes as follows: young up to 6 year old, adult from 6 to 15 year old, old from 15 to 20 years old. Therefore, we can choose

$$g_{ya} = \frac{1}{6}, \quad g_{ao} = \frac{1}{9}, \quad m = \frac{1}{5}.$$

Hence, the vole-free equilibrium in this case is the following:

$$E_T = [300, 450, 0, 250, 0, 0].$$

For the voles, on one hand, we choose $a \in \{1, 2, 3\}$: $a = 1$ is the lowest possible threshold from a biological point of view (a single vole is necessary to have a positive net increase of the population either via recruitment or via childbirth, if female and already pregnant), while 2 and 3 are chosen to show how a impacts on the equilibria of the system. On the other hand, we set the reproduction rate at

$$r = \frac{2.5 \times 4.5}{2} - \frac{1}{2} = 5.125,$$

since females (which we assume to be roughly half of the total population), give birth to 2.5 voles, on average 4.5 times a year, while having a life expectancy of 2 years [5].

Remark 3.1. *While 2.5 voles per litter has been found to be true both in the wild and in laboratory, the data concerning the average number of litters per year reported in [5], 11.8, is true only in a controlled environment. We then decided to use here a more realistic number for a cultivated environment, i.e., 4.5. The equilibria of the system are not affected by this change due to Remark 2.5.*

For the carrying capacity, we actually consider the maximum available data in a generic one-hectare territory not subjected to human intervention (see [10]) namely $k \approx 1000$. This value is very different from the one assessed for peach orchards in [11], where the average number of voles per hectare is estimated at a value about 18.5. In order to further simplify the sensitivity analysis, we add two constrains. Since the voles damage the trees primarily by creating tunnels in the orchard, which are around the same depth as the root of young peach trees, we can assume that they damage in the same way all tree populations, i.e. there exists a unique $\nu > 0$ such that

$$\nu_y = \nu_a = \nu_o = \nu.$$

Moreover, since there is no evidence of an increase mortality of trees due to the presence of voles, we can assume the same expected average lifespan for a hypothetical tree that is born already damaged, i.e.,

$$\frac{1}{g_{ya}} + \frac{1}{g_{ao}} + \frac{1}{m} = \frac{1}{g_{ya}(1 - \epsilon_{ya})} + \frac{1}{g_{ao}(1 + \epsilon_{ao})} + \frac{1}{m(1 + \epsilon_{oy})},$$

which leads to

$$\begin{aligned} \epsilon_{ya} &= g_{ya} \frac{g_{ao}\epsilon_{oy}(1 + \epsilon_{ao}) + m\epsilon_{ao}(1 + \epsilon_{oy})}{g_{ao}m(1 + \epsilon_{ao})(1 + \epsilon_{oy}) + g_{ya}m\epsilon_{ao}(1 + \epsilon_{oy}) + g_{ya}g_{ao}\epsilon_{oy}(1 + \epsilon_{ao})} \\ &= \frac{14\epsilon_{ao}\epsilon_{oy} + 9\epsilon_{ao} + 5\epsilon_{oy}}{20\epsilon_{ao}\epsilon_{oy} + 15\epsilon_{ao} + 11\epsilon_{oy} + 6} \in [0, 1). \end{aligned}$$

We are then left with three parameters, namely ν , ϵ_{ao} , ϵ_{oy} . For ν , from the negative term of (2.4), (2.5) and (2.7), we can expect

$$0 \leq \nu \leq \min \left\{ \frac{1 - g_{ya}}{V}, \frac{1 - g_{ao}}{V}, \frac{1 - m}{V} \right\} \leq \frac{1 - \max\{g_{ya}, g_{ao}, m\}}{a} = \frac{2}{5} = 0.4.$$

In our numerical tests, we then consider $\nu = 10^{-j}$ for $j \in \{-5, \dots, 0\}$. For ϵ_{ao} and ϵ_{oy} , we take 100 equally spaced values in $[0, 1]$: the upper bound of 1 corresponds to doubling the exit rate of damaged trees from the adult/old class with respect to the non-damaged ones. In all considered cases, the polynomial equation (2.36) has a unique positive root, whose corresponding Jacobian matrix is negative definite, meaning that there are two basins of attraction: one leads to the vole-free equilibrium, while the other one leads to the unique stable equilibrium of coexistence. The results of these simulations are presented in Figure 1-6, where

the amount of voles at equilibrium (i.e., the unique positive root of (2.36)) and the percentage of adult trees with respect to the total number of trees at equilibrium, i.e.,

$$\lim_{t \rightarrow \infty} \frac{T_a(t) + D_a(t)}{w},$$

are shown. We observe that, counterintuitively, raising the critical point a has the effect of raising the population of voles at the equilibrium, since the latter must always belong to $[a, k]$.

4. Discussion

In this paper we have presented three models of various complexity. However, all share the same properties, namely they possess an unconditionally feasible and stable equilibrium in which the voles disappear. This represents the optimal state of the orchard. However, due to the assumption that the voles experience the Allee effect, bistability is produced by the presence of the Allee threshold. Indeed, in the bare bones model, coexistence is found to be unconditionally stable. We have not investigated the coexistence equilibrium in the intermediate model, but reserved this task for the most complex one. In it, although a full analytic investigation is not possible, multiple coexistence points are found to possibly arise, thereby making a sizeable difference with the simplest situation. In addition, the incorporation of a stratified tree population by age groups in the most complex model allows more refined simulations that contribute to give some insights that might help in the fight against these agricultural nuisances. The numerical simulations indeed show that at least one of them is feasible and stable. Further, they also allow to assess the sensitivity of its population values with respect to some relevant model parameters.

5. Conclusions

We have presented a rather refined model, together with two simpler ones, for the description and understanding of the underground interactions between cultivated trees in orchards and voles. The model takes into account the fact that the voles are responsible for damages of root trees, ultimately leading to a reduced fruit production and a noticeable loss for the farmer profits.

First of all, from the simulations results of the age-stratified model, we see that, independently from the choice of the parameters, the vole population has an equilibrium of a few dozen individuals in the orchard in contrast to the thousand found in an uncultivated territory. This is coherent with the observation of [5, 11]. Therefore (2.2) can be a good starting point for modeling the human activities-induced disturbance to voles and similar rodents in a field. More precisely, the scenario with $a = 1$ and $\nu \approx 10^{-1}$ is the one that is closest to the average of 18.5 for the vole population found in [11].

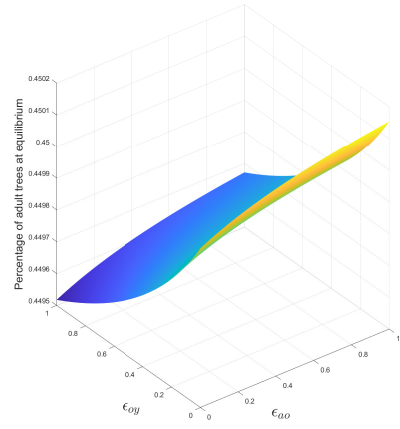
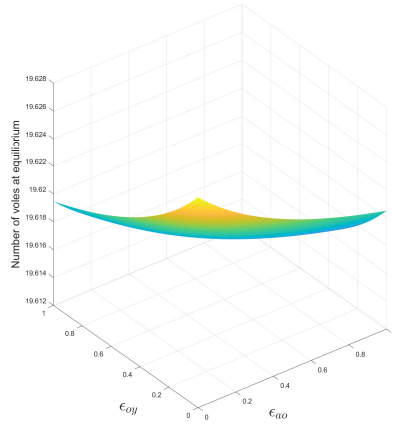
Second and most notably, we see that the peak for the vole population, which always appears at $\epsilon_{ao} = \epsilon_{oy} = 0$, does not correspond to the highest damage to the fruit production, which occurs for $\epsilon_{ao} = 0$ and $\epsilon_{oy} = 1$.

The model hopefully gives insights into the dynamics of *Microtus* populations in orchards, the level of damage they could produce and could ultimately turn out to be useful for their control. Savi's pine vole populations exhibit less significant numerical fluctuations and low-density values than other *Microtus* species [1, 4]. In orchards, Savi's pine vole densities are notably lower than in more natural environments [32]. While this implies the presence of damage in orchards, it is generally not as severe as with other vole species. As a result, economic damage has often not justified substantial investments in vole control measures. Consequently, there has been limited research into potential management interventions, such as chemical or physical control of voles in their burrows, periodic soil flooding, or selecting resistant rootstock trees, which could help limit vole populations and mitigate damage [1].

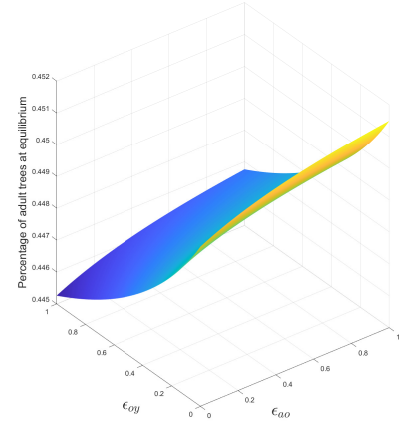
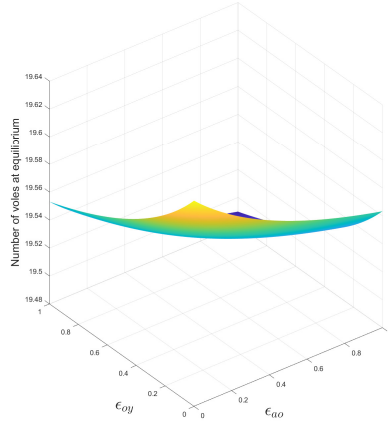
The findings of our models, which indicate the presence of equilibrium points, support the idea that without specific interventions, Savi's pine vole populations may persist in orchards over an extended period, resulting in limited annual damage. However, this damage could accumulate and become significant in the long term. The damage may become apparent in voles-affected plants: they die, requiring these plants to be

$$a = 1$$

$$\nu = 0.00001$$



$$\nu = 0.0001$$



$$\nu = 0.001$$

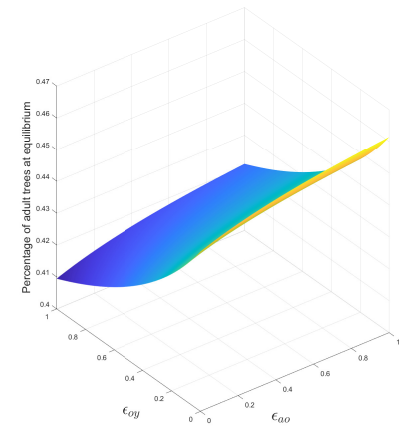
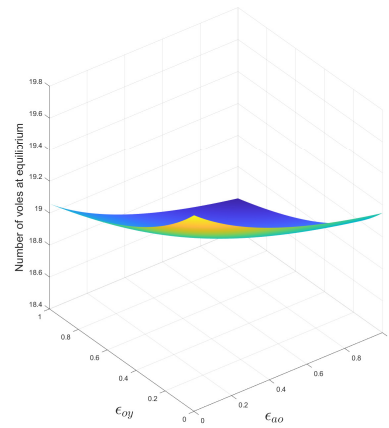


Figure 1: The results of the simulations described in Section 3 for $a = 1$ and $\nu \in \{0.00001, 0.0001, 0.001\}$ (row-wise). The two columns show, respectively, the number of voles at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{ao}, \epsilon_{oy} \in [0, 1]$.

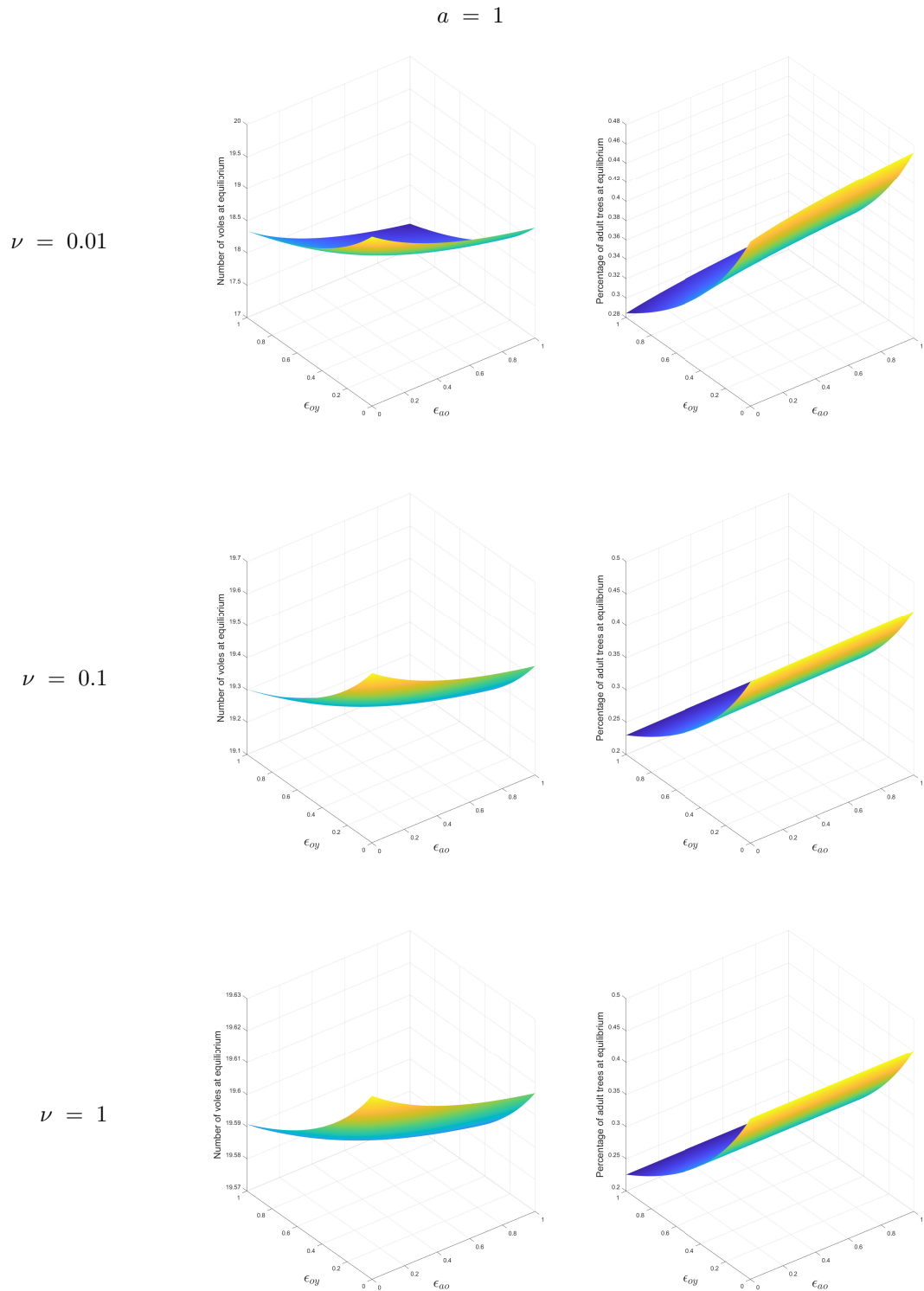
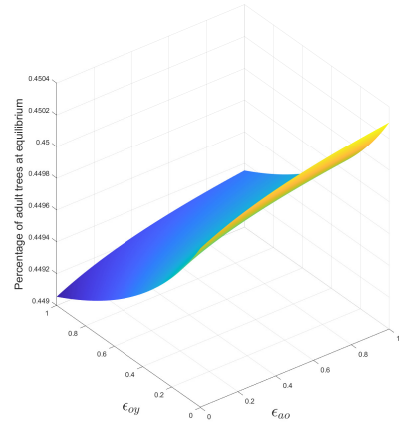
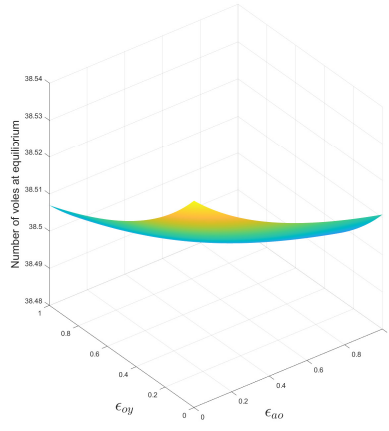


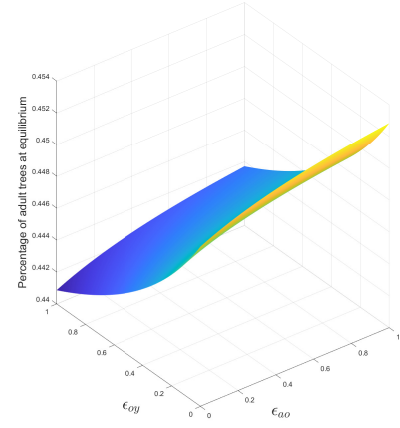
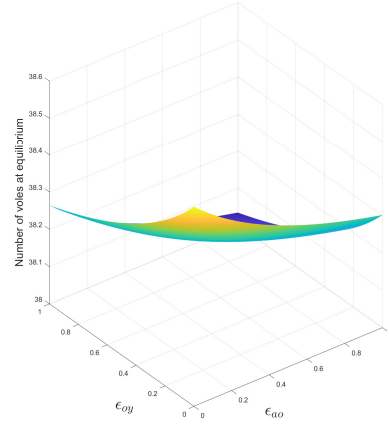
Figure 2: The results of the simulations described in Section 3 for $a = 1$ and $\nu \in \{0.01, 0.1, 1\}$ (row-wise). The two columns show, respectively, the number of voles at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{a0}, \epsilon_{oy} \in [0, 1]$.

$$a = 2$$

$$\nu = 0.00001$$



$$\nu = 0.0001$$



$$\nu = 0.001$$

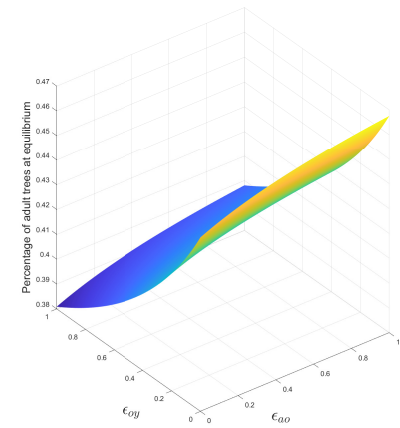
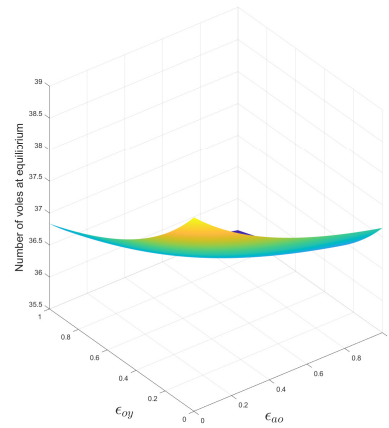
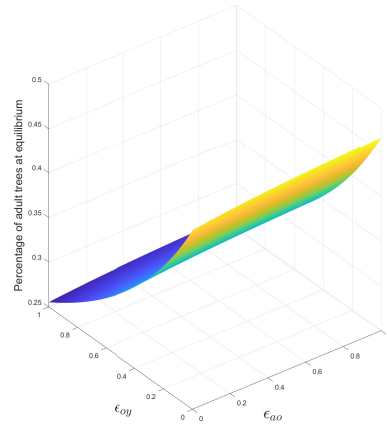
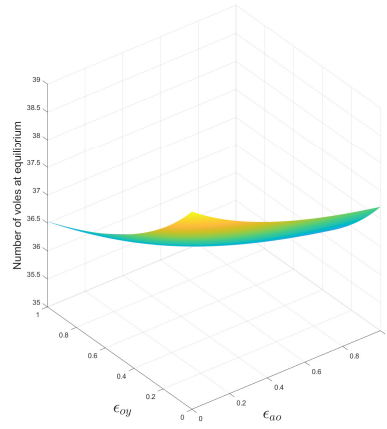


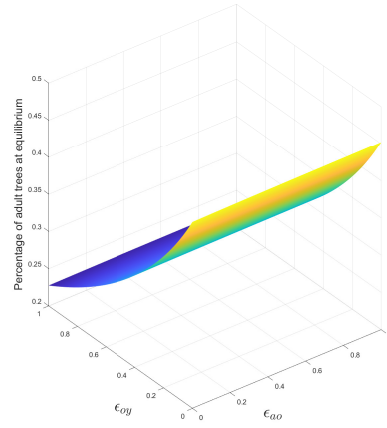
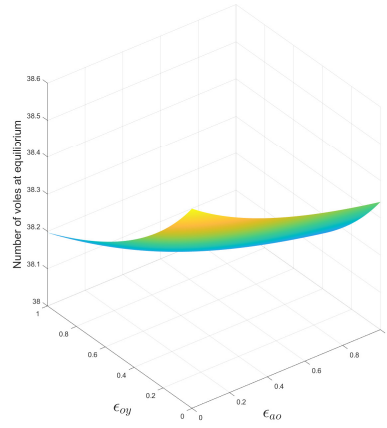
Figure 3: The results of the simulations described in Section 3 for $a = 2$ and $\nu \in \{0.00001, 0.0001, 0.001\}$ (row-wise). The two columns show, respectively, the number of voles at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{ao}, \epsilon_{oy} \in [0, 1]$.

$$a = 2$$

$$\nu = 0.01$$



$$\nu = 0.1$$



$$\nu = 1$$

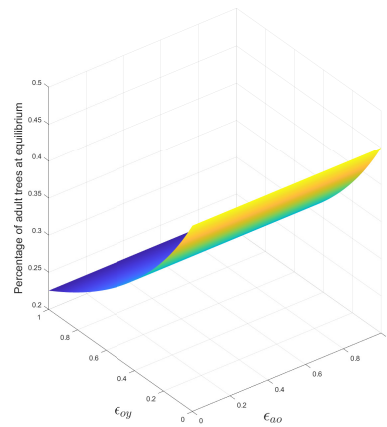
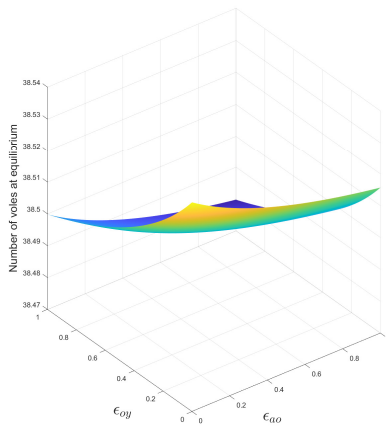
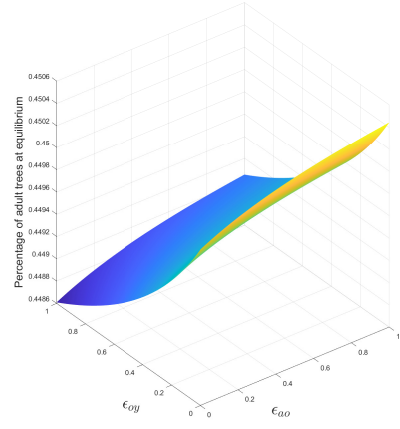
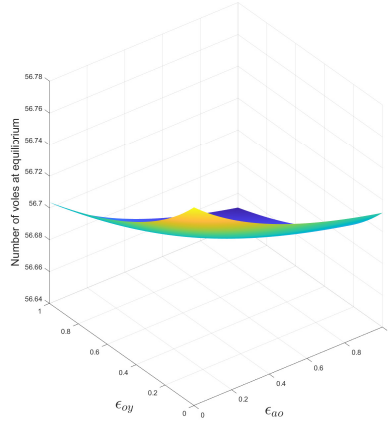


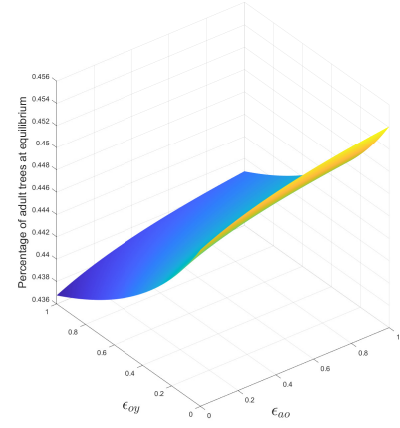
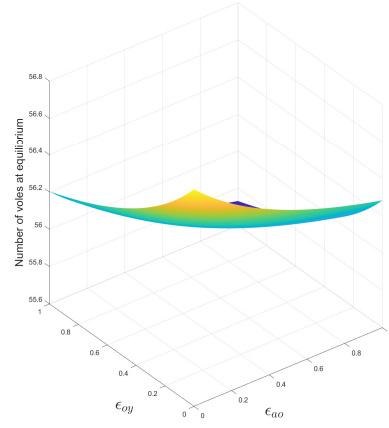
Figure 4: The results of the simulations described in Section 3 for $a = 2$ and $\nu \in \{0.01, 0.1, 1\}$ (row-wise). The two columns show, respectively, the number of voles at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{ao}, \epsilon_{oy} \in [0, 1]$.

$$a = 3$$

$$\nu = 0.00001$$



$$\nu = 0.0001$$



$$\nu = 0.001$$

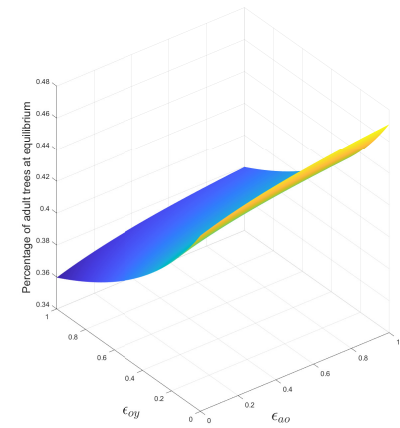
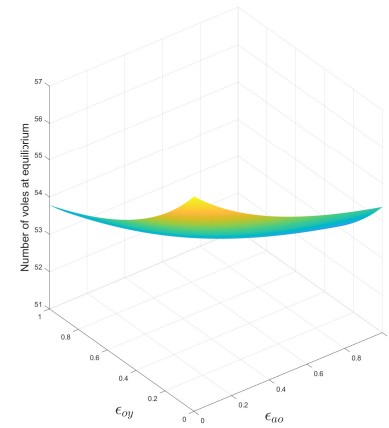


Figure 5: The results of the simulations described in Section 3 for $a = 3$ and $\nu \in \{0.00001, 0.0001, 0.001\}$ (row-wise). The two columns show, respectively, the number of votes at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{ao}, \epsilon_{oy} \in [0, 1]$.

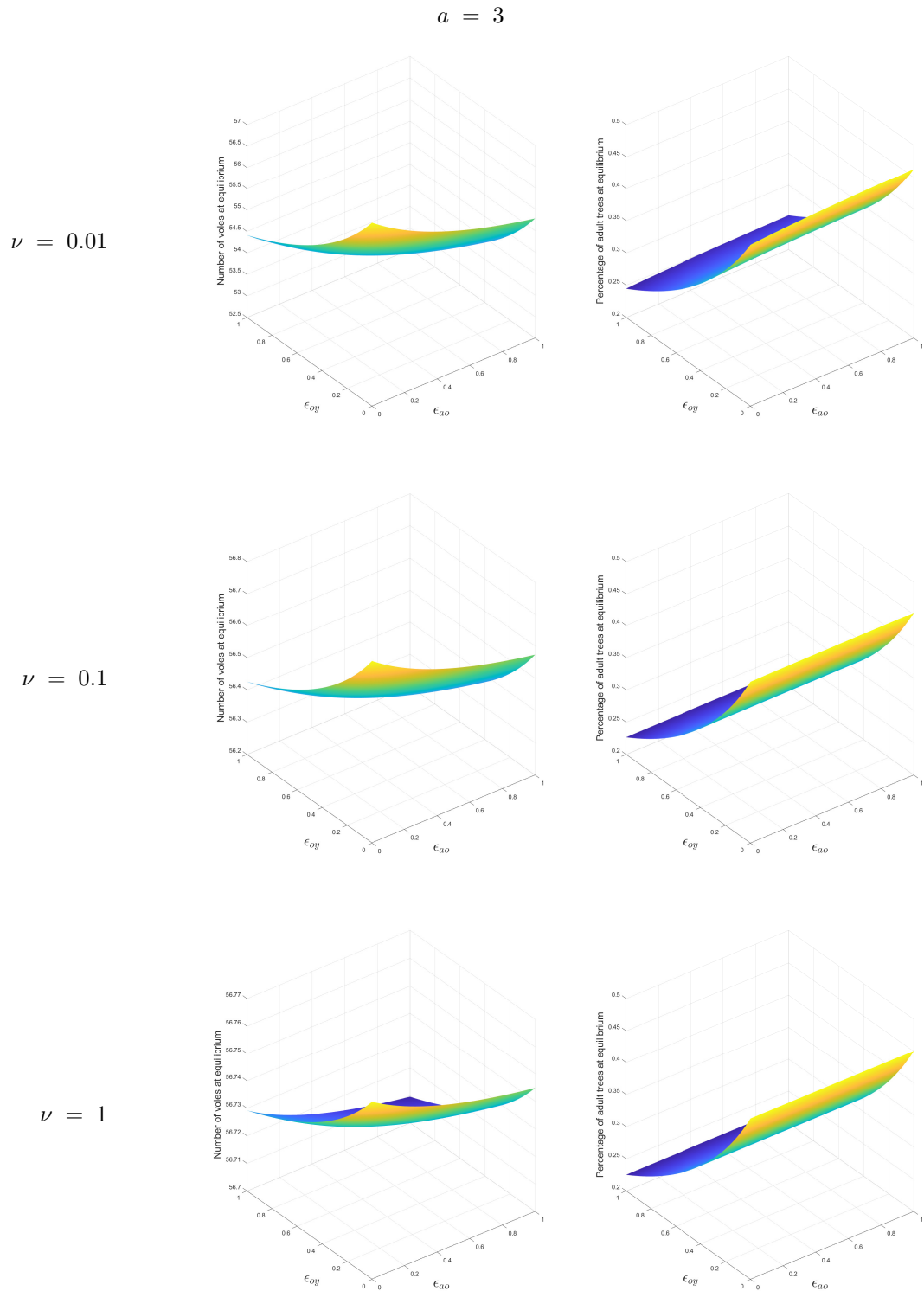


Figure 6: The results of the simulations described in Section 3 for $a = 3$ and $\nu \in \{0.01, 0.1, 1\}$ (row-wise). The two columns show, respectively, the number of voles at equilibrium and the percentage of adult trees at equilibrium, varying $\epsilon_{ao}, \epsilon_{oy} \in [0, 1]$.

replaced. Additionally, there may be reduced production in plants affected by voles, as some branches may wither without causing the entire plant to die. Research on the extent of damage and the loss of production due to the presence of voles is currently lacking for Savi's pine vole, and it should become a priority.

In addition, note that the three models with enriching age structure allow more refined considerations. For the coexistence of all the populations these can only be inferred by the numerical simulations. However, the results for the intermediate, 4 populations in the reduced form, and for the full model indicate that the equilibria in which either the voles only, or the damaged trees classes vanish cannot exist. This shows that neither the tree damages can occur without a cause, nor the voles thrive without damaging the trees. This conclusion is much less apparent in the bare-bones model. Further, the enlarged models allow to describe more and more precisely the trees age groups compositions. When the voles are absent and therefore trees are not damaged, while their level is just w in the bare-bones model, it becomes

$$T_y = \frac{mw}{g_{ya} + m}, \quad T_a = \frac{g_{ya}w}{g_{ya} + m}$$

in the intermediate one, and

$$T_y = \frac{g_{ao}w}{g_{ao}m + g_{ya}m + g_{ao}g_{ya}}, \quad T_a = \frac{g_{ya}w}{g_{ao}m + g_{ya}m + g_{ao}g_{ya}}, \quad T_o = \frac{g_{ao}g_{ya}}{g_{ao}m + g_{ya}m + g_{ao}g_{ya}}$$

in the full model. This is relevant, as fruit production of trees in different ages is different, being low for young not fully developed trees, and reduced for older trees. Being able to tune the parameters so as to maximize production, favoring the adult class, would allow better profits for the farmer. However, in case of the voles' presence, this task must be performed numerically.

Acknowledgments

The authors thank the referee for his constructive remarks that helped to considerably improve the paper. E. Venturino and A. Viscardi are members of RITA (Research ITALian network on Approximation) and of the INdAM research group GNCS. The authors are also very much indebted to Dr. Lucio Martino and Paola Gradoni of the "Società Agricola Cascina Rosa s.s. (Caraglio, CN - NW Italy)" for introducing them to the problem, for their support and for the fruitful feedback provided.

References

- [1] S. BERTOLINO, L. ASTEGGIANO, M. A. SALADINI, L. GIORDANI, G. VITTONI, AND A. ALMA, *Environmental factors and agronomic practices associated with Savi's pine vole abundance in Italian apple orchards*, Journal of Pest Science, 88 (2015), pp. 135–142.
- [2] S. BHATTACHARYYA AND D. K. BHATTACHARYA, *Pest control through viral disease: mathematical modeling and analysis*, J. Theoret. Biol., 238 (2006), pp. 177–197.
- [3] D. CAPIZZI, S. BERTOLINO, AND A. MORTELLITI, *Rating the rat: global patterns and research priorities in impacts and management of rodent pests*, Mammal Review, 44 (2014), pp. 148–162.
- [4] D. CAPIZZI AND L. SANTINI, *I Roditori Italiani: Ecologia, Impatto sulle Attività Umane e Sugli Ecosistemi*, Gestione delle Popolazioni, Antonio Delfino Editore, 2007.
- [5] L. CAROLI, D. CAPIZZI, AND L. LUISELLI, *Reproductive strategies and life-history traits of the savi's pine vole*, Microtus savii, Zoological Science, 17 (2000), pp. 209–216.
- [6] R. CASTIGLIA, G. ALOISE, G. AMORI, F. ANNESI, S. BERTOLINO, D. CAPIZZI, E. EMILIANO MORI, AND P. COLANGELO, *The italian peninsula hosts a divergent mtDNA lineage of the water vole, arvicola amphibius s.l., including fossorial and aquatic ecotypes*, Hystrix, 27 (2016), pp. 99–103.
- [7] S. CHATTERJEE, K. DAS, AND J. CHATTOPADHYAY, *Time delay factor can be used as a key factor for preventing the outbreak of a disease—results drawn from a mathematical study of a one season eco-epidemiological model*, Nonlinear Anal. Real World Appl., 8 (2007), pp. 1472–1493.
- [8] J. CHATTOPADHYAY, R. SARKAR, AND S. MANDAL, *Toxin-producing plankton may act as a biological control for planktonic blooms—field study and mathematical modelling*, J. Theor. Biol., 215 (2002), pp. 333–344.
- [9] J. CHATTOPADHYAY, R. SARKAR, AND S. PAL, *Dynamics of nutrient-phytoplankton interaction in the presence of viral infection*, Biosyst., 68 (2003), pp. 5–17.
- [10] L. CONTOLI, *Fauna d'Italia Vol. XLIV - Mammalia II - Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia, Caratteri generali dei Microtus (Terricola) del 'gruppo savii'*, Edizioni Calderini, 2008.

- [11] F. DELL'AGNELLO, R. BARFKNECHT, S. BERTOLINO, D. CAPIZZI, M. MARTINI, V. MAZZA, F. RIGA, AND M. ZACCARONI, *Consistent demographic trends in Savi's pine vole between two distant areas in central Italy*, *Folia Zoologica*, 67 (2018), pp. 35–42.
- [12] F. DELL'AGNELLO, M. MARTINI, E. MORI, G. MAZZA, V. MAZZA, AND M. ZACCARONI, *Winter activity rhythms of a rodent pest species in agricultural habitats*, *Mammal Research*, 65.
- [13] F. DELL'AGNELLO, C. NATALI, S. BERTOLINO, L. FATTORINI, E. FEDELE, B. FOGGI, M. MARTINI, C. PISANI, F. RIGA, A. SGARLATA, C. CIOFI, AND M. ZACCARONI, *Assessment of seasonal variation of diet composition in rodents using DNA barcoding and real-time PCR*, *Scientific Reports*, 9 (2019), pp. 1–11.
- [14] J. Z. FARKAS AND A. Y. MOROZOV, *Modelling effects of rapid evolution on persistence and stability in structured predator-prey systems*, *Math. Model. Nat. Phenom.*, 9 (2014), pp. 26–46.
- [15] K. P. HADELER AND H. I. FREEDMAN, *Predator-prey populations with parasitic infection*, *J. Math. Biol.*, 27 (1989), pp. 609–631.
- [16] F. M. HILKER, *Population collapse to extinction: the catastrophic combination of parasitism and Allee effect*, *J. Biol. Dyn.*, 4 (2010), pp. 86–101.
- [17] J. JACOB, *Short-term effects of farming practices on populations of common voles*, *Agriculture, Ecosystems and Environment*, 95 (2003), pp. 321–325.
- [18] J. JACOB, P. MANSON, R. BARFKNECHT, AND T. FREDRICKS, *Common vole (Microtus arvalis) ecology and management: implications for risk assessment of plant protection products*, *Pest Management Science*, 70 (2014), pp. 869–878.
- [19] A. KACHA, M. H. HBID, AND R. BRAVO DE LA PARRA, *Mathematical study of a bacteria–fish model with level of infection structure*, *Nonlinear Anal. Real World Appl.*, 10 (2009), pp. 1662–1678.
- [20] Q. J. A. KHAN, E. BALAKRISHNAN, AND G. C. WAKE, *Analysis of a predator-prey system with predator switching*, *Bull. Math. Biol.*, 66 (2004), pp. 109–123.
- [21] E. KORPIMÄKI, P. R. BROWN, J. JACOB, AND R. P. PECH, *The puzzles of population cycles and outbreaks of small mammals solved*, *BioScience*, 54 (2004), pp. 1071–1079.
- [22] X. LAMBIN, V. BRETAGNOLLE, AND N. G. YOCOZ, *Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern?*, *Journal of Animal Ecology*, 75 (2006), pp. 340–349.
- [23] A. LOY, G. ALOISE, L. ANCILLOTTO, F. M. ANGELICI, S. BERTOLINO, D. CAPIZZI, R. CASTIGLIA, P. COLANGELO, L. CONTOLI, B. COZZI, D. FONTANETO, L. LAPINI, N. MAIO, A. MONACO, E. MORI, A. NAPPI, M. PODESTÀ, D. RUSSO, M. SARÀ, M. SCANDURA, AND G. AMORI, *Mammals of Italy: an annotated checklist*, *Hystrix, the Italian Journal of Mammalogy*, 30 (2019), pp. 87–106.
- [24] J. J. LUQUE-LARENA, F. MOUGEOT, J. VINUELA, D. JARENO, L. ARROYO, X. LAMBIN, AND B. ARROYO, *Recent large-scale range expansion and outbreaks of the common vole (Microtus arvalis) in NW Spain*, *Basic and Applied Ecology*, 14 (2013), pp. 432–441.
- [25] H. MALCHOW, S. V. PETROVSKII, AND E. VENTURINO, *Spatiotemporal patterns in ecology and epidemiology*, Chapman & Hall/CRC Mathematical and Computational Biology Series.
- [26] R. P. MARINI, *Pruning peach trees*, Virginia Cooperative Extension, (2020), pp. 1–11.
- [27] R. P. MARINI AND L. CORELLI-GRAPPADELLI, *Horticultural Reviews*, vol. 32, John Wiley & Sons, Inc., Hoboken, New Jersey, 2006, ch. Peach Orchard Systems, pp. 63–110.
- [28] A. MYLLYMÄKI, *Outbreaks and damage by the field vole, Microtus agrestis (L.), since World War II in Europe 1*, *EPPO Bulletin*, 7 (1977), pp. 177–207.
- [29] K. NORRDAHL AND E. KORPIMÄKI, *Changes in population structure and reproduction during a 3-yr population cycle of voles*, *Oikos*, 96 (2002), pp. 331–345.
- [30] L. PERKO, *Differential equations and dynamical systems*, vol. 7 of Texts in Applied Mathematics, Springer-Verlag, New York, second ed., 1996.
- [31] M. RAFIKOV AND J. SILVEIRA, *On dynamical behavior of the sugarcane borer – parasitoid agroecosystem*, *Ecol. Complex.*, 18 (2014), pp. 67–73.
- [32] E. RANCHELLI, R. BARFKNECHT, D. CAPIZZI, F. RIGA, V. MAZZA, F. DELL'AGNELLO, AND M. ZACCARONI, *From biology to management of savi's pine vole (Microtus savii)*, *Pest Management Science*, 72 (2016), pp. 857–863.
- [33] M. SALVIONI, *Home range and social behavior of three species of european pitymys (mammalia, rodentia)*, *Behavioral Ecology and Sociobiology*, 22 (1988), pp. 203–210.
- [34] M. TANSKY, *Switching effect in prey-predator system*, *J. Theoret. Biol.*, 70 (1978), pp. 263–271.
- [35] P. WALTMAN, *Competition models in population biology*, vol. 45 of CBMS-NSF Regional Conference Series in Applied Mathematics, Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, 1983.
- [36] Y. WANG AND J. WANG, *Influence of prey refuge on predator-prey dynamics*, *Nonlinear Dynam.*, 67 (2012), pp. 191–201.