Review Article

The usefulness of mathematics in agriculture, for the environment and in contrasting diseases: insights from a wide range of simple models

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Abstract

Mathematics has been applied to physics and engineering in the last few centuries, substantially contributing to the various phases of the industrial revolution. Its application to biology is instead relatively more recent. In this paper we provide an overview of some problems in a few fields mainly related to ecology. The models discussed help in fighting pests in agriculture to improve crop harvesting and to combat the phenomenon of alien species invasions, that due to worldwide trading and climate changes is affecting the temperate regions, threatening the survival of the native species. A pair of examples related to primary oxygen production and fallacies of our linear way of thinking are also presented, to stress the fact that raising temperatures entail huge unforeseen problems. Finally we delve briefly in the vaste field of epidemiology, that would deserve a review on its own, to discuss models for diseases in the environment and one instance related epidemics affecting humans, prompted by the important role of asymptomatics played in them.

Keywords: Agriculture pests; Alien species invasions; Herding; Prey response to attacks; Invading migrants; Profitable use of fungi; Climatic changes; Ecological hysteresis; Disease containment and eradication

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1. Introduction

The basic needs of human beings are shelter and clothing, from which engineering started. However, the very basic one, common to any living organism is food. Hunting has been one of the first ways of dealing with this issue, combined with gathering fruits and roots, easily available from the environment. Later on, agriculture has been discovered and implemented by the early worldwide civilizations. Thus means of producing new harvests from saved and planted seeds in the previous year has become the usual way of providing sustaining for populations. This human activity during the centuries has profoundly changed the environment, especially in Europe and North America, building uniform landscapes that reduce biodiversity, because they favor the emergence of pest insects that harm the harvest of farmers.

To combat these pernicious insects, with the development of chemistry, pesticides have been developed. However, the use of these means in the long run has caused two major problems. The environment has slowly become saturated with them and through the food webs they come on our table and ultimately enter in our body, therefore possibly causing diseases. Secondly, although intended to kill and keep in check the harming populations, these chemicals have negative effects also on other species that are useful for humans, for instance bees. In more recent years, the exploitation of biological controls in agriculture has become an alternative, and both applied and theoretical scientists have invested time and efforts to foster these ways for better harvest production.

Nowadays agriculture is performed with an industrial mentality. It makes sense then to use also scientific approaches to deal with its problems. This implies the development of not only biological means or advanced agrarian techiques involving precision agriculture, but also of mathematical models, which also contribute heavily to improve harvests and contain pests and invasive alien species.

The purpose of this paper is to highlight some of these applications to mathematics, in a field other than industry, where of course they reached very important results. However, it should be kept in mind,

that this has been possible during the industrial revolution and in the following century because mathematics has been applied to physics for about four centuries. On the other hand, the use of mathematical tools in biology and epidemiology dates back only about one hundred years, with the seminal works of Lotka and Volterra, as well as those of Kermack and McKendrick.

The paper is organized as follows. We start to consider various agricultural problems, mainly related to the biological control of pests. In Section 3 the attention is focused on ecology and particularly to contain alien species invasions. Section 4 is devoted to climatic changes and the fallacies of common thinking. Finally in Section 5 we address some issues in epidemiology.

2. Agriculture

2.1. *Very important agricultural pest: Aphids*

Aphids are one of the most relevant pests. Their negative impact on plants comes from their feeding habit of sucking the sap from the plants, thereby reducing their capacity to grow. A way of combating the aphids is by using specialized wasp parasitoids. The latter depose in the aphids bodies their eggs, from which larvae develop and feed on the aphids, ultimately killing them. However, bacterial symbionts possibly present in the aphids' bodies strongly help their survival, because they provide resistance to natural enemies, in particular preventing the wasps' larvae to develop. Thus this biological control is negatively affected by symbionts presence, which affect the aphids in a permanent way. Although symbionts are vertically transmitted from aphid parents to their offsprings, the question remains on how in general these organisms enter the aphids body from the exterior.

The role of modeling could be seen in a twofold way. First it is to describe a well set situation, where the dependent variables and their relationships are known, and the mathematical formulation can more or less easily be set up. On the other hand, models could be constructed in a speculative fashion, formulating hypotheses and through the analysis of the system behavior, giving matter for experimentalist scientists. Devising suitable experiments, data can be obtained that can be compared with the results of the theoretical analysis and finally supporting or not the initial assumption.

In this case, we consider a model to verify a hypotheses about the way for which symbionts penetrate in the aphids bodies, as the coexistence mechanisms of symbiont-infected and uninfected aphids is not yet fully understood.

A minimal model for such an instance can be formed by considering just three basic populations: parasitoid wasps W, uninfected A and bacteria-infected I aphids, [1]. The non-infected aphids reproduce at rate r, experience a natural mortality n, and intraspecific competition at rate g with healthy aphids and at rate $\tilde{g}$ with the infected ones. The assumption that is explicitly made is that at rate β symbionts are transmitted by wasps into the healthy aphids bodies, thereby rendering them infected. An additional mortality rate e is due to the parasitoid wasps, from which new wasps emerge at the same rate. For the infected aphids the rate e is reduced by a factor f. Similar terms for the infected aphids contain possibly different parameters, reproduction rate b, recalling that the symbionts are vertically transmitted, μ as mortality rate, that may be affected by the presence of the symbionts and wasp larvae, intraspecific competition rate c with their similar, and $\tilde{c}$ with healthy aphids and finally the new infected due to the hypothesized wasps as symbionts carriers. Wasps reproduce at rates e and ef respectively from healthy and infected aphids, their natural mortality is m and their intraspecific competition rate is a. All these remarks lead to the system (1), for which a generalization including aphid predators is contained in [2]:

$$(1) \qquad \begin{aligned} \frac{dA}{dt} &= A[r - n - gA - \tilde{g}I - \beta W - eW] \\ \frac{dI}{dt} &= I[-efW + b - \mu - cI - \tilde{c}A] + \beta AW \\ \frac{dW}{dt} &= W[eA + efI - m - aW]. \end{aligned}$$

Possible outcomes include the ecosystem disappearance, the equilibria with just healthy or infected

aphids, the one with both of them, the situation where both wasps and infected aphids thrive, and possibly coexistence. All these points are feasible and stable under particular combinations of the model parameters, and some transcritical bifurcations have been identified that may bring the system from an equilibrium to another one.

In this idealized situation, it is seen that eradication of the aphids is not possible, and, as ecologists know well, in field conditions this result would be even more difficult to achieve. In particular, this study shows that more than one parasitoid is needed to combat these pests in the fields, which forces the use of the so-called integrated pest management.

2.2. *Spiders as biological control of pests: wanderers and web-weavers.*

In Piedmont region (NW Italy), in order to produce wines and hazelnuts, the landscape of the hills of Monferrato and Langhe has been widely reworked by human agricultural activities. In particular, many woods have been logged to leave a kind of monotonous landscape in which these two cultivars are present. In so doing, however, there has been a biodiversity loss, and at the same time this has favored the invasion of insects, harmful for both types of plants. The question thus arises whether to keep small patches of grass and fences in between vineyards may help in preserving spiders populations, that are natural biological controls of insects. Models can be developed to try and answer this question, although naively one could simply say that the classical Lotka-Volterra predator-prey model is sufficient. However, to formulate a model it is imperative to know the whole situation at hand. In particular here it is found that there are two kinds of spiders, wanderers and webweavers, both thriving in bushes, woods and grass patches near the cultivations mentioned above, but exhibiting very different ecological behaviors.

A model for wanderer spiders s must allow them to change environment, freely moving back and forth from grass/woods to the agroecosystem in search for prey. Thus it becomes a one predator-several prey system, where v represent the pest population in the cultivated land, that should be removed or at least kept in check, while f collects all the insect species living in the woods that instead should be preserved to ensure biodiversity, [3].

(2)
$$\frac{df}{dt} = rf\left(1 - \frac{f}{W}\right) - csf \equiv F(t)$$

(3)
$$\frac{ds}{dt} = s\left(-a + \frac{kbv}{H+v} + kcf\right) \equiv S(t)$$

$$\frac{dv}{dt} = ev\left(1 - \frac{v}{P}\right) - \frac{bsv}{H+v} \equiv V(t).$$

On the other hand, web-weaver spiders are mainly nonmigratory but show a peculiar feature, [4]. Namely, once in their lifetime, as young instars, they release a thread, with which normally they make their webs, and let themselves be carried away by the wind, at times covering distances of even tens of kilometers. This phenomenon is called ballooning. In this case, since they are mainly resident, we need to distinguish among those s_w living in the woods and those in the cultivars s_v. To model ballooning, in principle one may think of explicitly introducing space in the model. However, this would entail other problems for setting up the simulation, such as for instance how to treat the boundary conditions. A way out, for which space is accounted for, but not explicitly, consists in introducing in the ordinary differential equations a term allowing part of the population s_w to leave the woods and migrate into the vineyards, thereby increasing the size of s_v, and conversely. As the Monferrato and Langhe region is large, of order 100 kilometers by 100 kilometers, we can neglect what happens at its boundary, or think statistically that the spiders that go out of it in some place are replaced by others coming in in some other location. The problem that remains is how to decide where the ballooning spiders would land. But this is easily solved, observing that the landing area is proportional to the extension of woods versus cultivars, and these extensions, i.e. surface areas, are naturally captured in the model by the respective carrying capacities. Finally, insects are once again partioned among the vineyards pests v and we lump together those in the

woods, w. Thus we obtain the model

$$\frac{dw}{dt} = bw\left(1 - \frac{w}{W}\right) - \ell w s_w$$
$$\frac{dv}{dt} = av\left(1 - \frac{v}{V}\right) - kvs_v$$
$$\frac{ds_w}{dt} = -cs_w + s_w\left[\tilde{\ell}w - \alpha w\tilde{\ell}\frac{V}{V+W}\right] + s_v\alpha v\tilde{k}\frac{W}{V+W}$$

(4)
$$\frac{ds_v}{dt} = -es_v + s_v\left[\tilde{k}v - \alpha v\tilde{k}\frac{W}{V+W}\right] + s_w\alpha w\tilde{\ell}\frac{V}{V+W}.$$

Note also that in this model, since we account for all the insects living in each individual territory, the resident spiders become specialist predators on them, this being expressed by the fact that in the absence of their prey, they die out in view of their respective natural mortalities c and e.

Here, it is mathematically interesting to note that finding the equilibrium at which all populations thrive can be reduced to an intersection of conic sections. This fact is common also to other more complicated models, in which they may often even be skewed. Typically here we have

(5)
$$As_w^2 - 2\tilde{B}s_w - 2Cs_v + Ds_v^2 = 0, \quad Es_w^2 - 2Fs_w - 2\tilde{G}s_v + Hs_v^2 = 0.$$

From these, sufficient conditions for their intersections can be investigated, giving inequalities on the model parameters that ensure the feasibility of the coexistence point.

2.3. Fighting olive tree pests

Another one of the most important cultures in the Mediterranean region, beside vineyards, is represented by olive trees, *Olea europaea* L., in view of the relevant production of olive oil. However, olive trees are subject to several pests, with different causes, which induce sizeable economic losses for the farmers. We focus on the Trás-os-Montes region in Northern Portugal.

The most damaging pest is the olive moth, *Prays oleae* (Bernard) (Lepidoptera: Praydidae), denoted by M in what follows, [5], which, luckily, is subject to the action of parasitoids, the specialist *Ageniaspis fuscicollis* (Dalman) (Hymenoptera: Encyrtidae) A, being the most abundant, and then by the generalists *Elasmus flabellatus* (Fonscolombe) (Hymenoptera: Eulophidae) E and spiders S.

Spiders feed on parasitoids, olive moth, and on other resources, *E. flabellatus*, lives by parasitizing both the other parasitoid A and the moth M, but also finds other food sources on sugary liquids (nectar or honeydews) or parasitizing other insects, and therefore its equation is modeled via a logistic term. *A. fuscicollis* just attacks the moth M, which in turn damages the olive tree, but this action is not explicitly present in the equations, as reducing their population size automatically implies a benefit for the olive tree. In summary:

(6)
$$\frac{dS}{dt} = (uq_E E + vq_A A + wq_M M)S + zS\left(1 - \frac{S}{L}\right) - k_S S,$$
$$\frac{dE}{dt} = eaEA + hbEM + rE\left(1 - \frac{E}{K}\right) - uES - k_E E,$$
$$\frac{dA}{dt} = gcAM - m_A A - fA^2 - aEA - vAS - k_A A,$$
$$\frac{dM}{dt} = -bEM - cAM - wMS + sM\left(1 - \frac{M}{U}\right) - k_M M.$$

Note that the various rates $-k_P P$'s, where P is anyone of the populations in the model, denote possible insecticide spraying effects.

The one-population-only equilibria are easily assessed for feasibility, and ecosystem collapse could indeed occur in particular conditions. For all the remaining points involving two or three nonvanishing populations, some kind of sufficient conditions for feasibility can be ensured. Generally, stability entails the

appropriate use of the Routh-Hurwitz conditions for all these equilibria. Coexistence however, proves to be too complicated for a theoretical analysis and is investigated through simulations. The only forbidden situations are the points in which *P. oleae* is absent, but where *A. fuscicollis* is present, in view of the specialist nature of this parasitoid. Some of the equilibria where the moth thrives can be stably achieved only via insecticide spraying.

As a consequence of the analysis, the natural enemy with most effective pressure over olive moth is the specific parasitoid *A. fuscicollis*, followed by *E. flabellatus* and spiders. This result shows the relevant importance of specific parasitoids, but also hyperparasitoids and generalist predators help keeping in check the pest population. This indicates a further line of investigation for the ecologists, as there appears to be a gap in the biological knowledge of the intermingling of these populations.

The most relevant result of this investigation is that the transcritical bifurcations relating pairs of equilibria can be assessed and studied. A complete graph whose nodes are all the equilibria and whose arcs are the transcritical bifurcation links can be drawn. Thus it is possible to determine how to reach a suitable equilibrium (generally, the moth-free one) starting from any current situation, following a path made of the arcs in the graph. In general, no unique way exists to construct such path and one would like to choose the "best" one, in some sense. Furthermore, to use any arc, the corresponding transcritical bifurcation must be triggered, changing the corresponding bifurcation parameter, so that it crosses the critical threshold. If at all possible, this requires some effort and therefore there is a cost associated with each arc in the path. For instance raising a mortality rate implies the use of traps or insecticide spraying, and these actions must be paid for. To assess the optimal path, i.e. the lowest cost path, techniques from dynamic programming can be used, [6].

Dynamic programming considers the problem as made of several stages: in this case they could be seen as the equilibria containing each the same number of nonvanishing populations. A policy must be determined for passing from the current state to another one belonging to the next stage. It can be determined by the principle of optimality, which essentially says that the optimal sequence of decisions for the remaining stages is not dependent on the policy decisions relative to the previous stages. The optimal current decision is based only the state in which the system is. Examples of this technique are presented in [6].

3. Ecology - Control of invasive animal species

3.1. *Ecological interactions: predators (foxes), native (hares) and invasive (cottontails) prey*

Ecologists distinguish three major competition mechanisms. The first two are are real competitions: interference involves direct interactions among populations; in exploitation of the same resources again the populations interact, with indirect negative effects. Apparent competition is instead mediated by a third species of another trophic level; it concerns species that do not interact directly, do not exploit the same resources, but influence each other via shared enemies.

An example of the latter competition type has been discovered in [7]. It involves the Eastern cottontail (*Sylvilagus floridanus*) S, an invasive lagomorph in Italy, the European hare L, which share different ecological niches, but through the fox *Vulpes vulpes* V, which predates on both of them, they do heavily influence each other. In particular, when the invading population is small, the fox and hare populations are positively correlated. This relationship overturns with increasing number of cottontails, until it is completely reversed for high *Sylvilagus floridanus* densities. To explain this counterintuitive result, that higher number of foxes reduce the native hares, the following model has been built [8].

$$(7) \quad \begin{aligned} \frac{dV}{dt} &= V\left(r - c_{VV}V - m + eaS + ebL\right) \\ \frac{dS}{dt} &= S\left(s - c_{SS}S - n - aV\right) \\ \frac{dL}{dt} &= L\left(u - c_{LL}L - p - bV\right). \end{aligned}$$

It is to be pointed out that in model (7) we distinguish between the reproduction rate and the mortality rate, because in some particular situations field data may indicate that the former is smaller than the latter. The net reproducing rate would then become negative and the logistic model would become meaningless. Furthermore, no direct competition among S and L appears in the equations altogether, because they occupy different ecological niches. Finally we limit ourselves to using the relatively simple Holling type (HT) I response function for modeling the hunting process in view of the fact that the densities of the three populations are either very low, foxes, or do not attain very large numbers, hares and cottontails.

The model simulation results are in agreement with the field data, and can be explained by observing that the invader provides additional food for the foxes, that consequently increase their numbers, and in turn, even if the hunting rate on native hares does not change, the larger predator population ultimately wipes out the autoctonous species.

3.2. *Ecological interactions: native and invasive hares*

In Northern Italy, another kind of invasion is experienced, that threatens the native mountain hare, *Lepus timidus* (Linnaeus, 1758), by the importation, mainly for hunting purposes, of the European hare, *Lepus europaeus* (Pallas, 1778). The competition is experienced primarily for the occupation of the territory, also because the hare's populations are essentially residential. During the years, the autoctonous species has been pushed away from the Piedmontese plains and now occupies the higher territories and the mountains. However, a side phenomenon has arisen, which consists of the interbreeding of these populations where the two respective territories meet, along their perimeter, which is essentially a long stripe separating the two environments. This produces a new hybrid species, capable of reproducing on its own.

A model to investigate this situation has been introduced in [9], in which an idea first presented in [10] has been taken into account. To discuss this idea, let us take a step back into the classical predator-prey model with logistic growth in the prey:

$$\frac{d}{dt}R(t) = r\left(1 - \frac{R(t)}{K}\right)R(t) - aR(t)F(t) \ ,$$

(8)
$$\frac{d}{dt}F(t) = -mF(t) + aeR(t)F(t) \ .$$

Its behavior can be captured by nondimensionalization, which results in a system with the single parameter

$$\Theta = \frac{aeK}{m}.$$

While the origin is unconditionally unstable, the resulting trajectories either tend to the predator-free point $\widehat{P_2} = (K, 0)$, for $\Theta < 1$, while conversely for $\Theta > 1$ predators invade and coexistence is attained,

$$\widehat{P_3} = \left(\frac{m^2}{e^2 a^2}, \frac{rm^3(\rho - 1)}{a^4 K e^3}\right).$$

Figure 1 summarizes these remarks.

The novelty concerns the fact that if the prey gather together and live in a herd, their contacts with external predators occur mainly through the perimeter of the herd. Indeed, large predators hunt alone the herd and attack mainly individuals on the edge of the bunch, that are more easily located. Assuming the prey to be uniformly distributed on the territory, the size of the individuals on the border of the herd is proportional to the square root of the total population, because the perimeter is a one dimensional manifold, while the prey reside on a territory of dimension two. Hence the prey R under attack are $\sqrt{R(t)}$ and the classical model (8) gets replaced by:

$$\frac{d}{dt}R(t) = r\left(1 - \frac{R(t)}{K}\right)R(t) - a\sqrt{R(t)}F(t) \ ,$$

(9)
$$\frac{d}{dt}F(t) = -mF(t) + ae\sqrt{R(t)}F(t) \ .$$
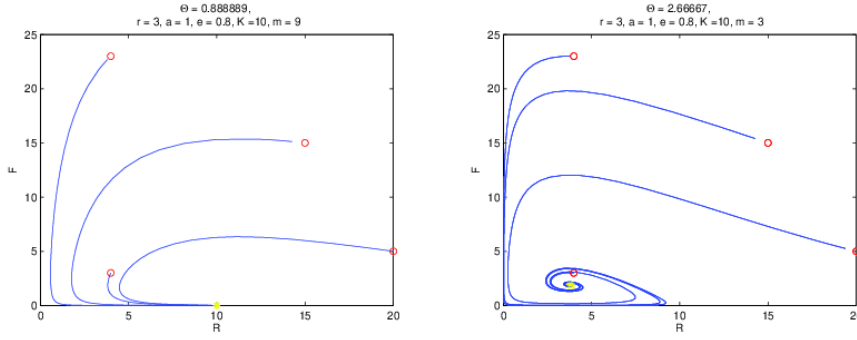
Figure 1. Equilibria: $\widehat{P_2} = (K, 0)$, and coexistence. Left: for $\Theta < 1$ only prey thrive. Right: for $\Theta > 1$ predators invade. Red circles indicate the initial conditions for the trajectories.

Upon reformulation, with $R^2 = P$, in this case, instead of Θ, the important parameter for assessing the ultimate system behavior is

$$(10) \qquad \rho = \frac{Ke^2a^2}{m^2}.$$

The equilibria are $P_1 = (0, 0) = \widehat{P_1}$, again unconditionally unstable, $P_2 = (K, 0) = \widehat{P_2}$, and coexistence:

$$P_3 = \left(\frac{m^2}{e^2a^2}, \frac{rm(a^2e^2K - m^2)}{a^4Ke^3} \right),$$

which turns out to be different from the corresponding one of the classical model (8), $\widehat{P_3}$. Now, for $\rho < 1$ the predator-free environment is obtained, while for $3 > \rho > 1$ the predators invade and coexist with the prey. At the threshold $\rho = 1$ a transcritical bifurcation arises, linking the two above equilibria. Furthermore, for $\rho > 3$ a Hopf bifurcation arises, and the two populations thrive through persistent oscillations. Note that this result distinguishes the new model from the classical one, in that it is well-known that quadratic predator-prey models to not allow limit cycles. On the other hand, the oscillating feature of the solutions is also different from the one obtained say from the Rosenzweig-MacArthur model [11], because here they are originated by prey herding, and therefore constitute a new phenomenon.

On the other hand, model (9) has a drawback. As remarked in [12], the system is not Lipschitz continuous for $R = 0$, and therefore there is a loss of uniqueness for its solutions. Indeed, in some cases, the numerical simulations would tend to an equilibrium where the rescaled prey are negative, $(-1, 0)$. On the other hand, we must take these trajectories as spurious. As soon as they hit the $P = 0$ axis, prey vanish and predators disappearance follows along the predators' axis. Thus the model (9) exhibits another new interesting feature, namely extinction in finite time.

We now have set the background to examine the invasive hares situation. Let E denote the invasive European hare, M the native mountain hare and H the hybrid species, the equations that regulate their interactions are the following ones:

$$(11) \qquad \frac{dE}{dt} = rE\left(1 - \frac{E}{K}\right) - \tilde{a}\sqrt{E}\sqrt{M} - b\sqrt{E}H,$$

$$\frac{dM}{dt} = sM\left(1 - \frac{M}{L}\right) - \tilde{c}\sqrt{E}\sqrt{M} - e\sqrt{M}H,$$

$$\frac{dH}{dt} = qH - nH^2 + \left[q_M\sqrt{M} + q_E\sqrt{E} - \left(g\sqrt{E} + f\sqrt{M}\right)\right]H + \tilde{w}\sqrt{EM}.$$

Note that the last two terms in the first two equations represent direct competition among the invader and the autoctonous species, which occurs on the common boundary of the regions occupied by each one of them, and are therefore modeled via the square root response function, as well as direct competition of

each hare population with the hybrid species. In this case, however, since the hybrid species established itself along the boundary separating the areas occupied by E and M, its territory is rather elongated and therefore "coincides" with its own boundary, so that we do not have to use the root function for this population. The evolution equation for the hybrid species is also interesting. Apart from basic reproduction, allowed because it is a species of its own, and intraspecific competition, there is the specific situation of this species to be taken into account. First of all, it can reproduce, giving rise to hybrid offsprings, with each one of the two other populations, but only with those individuals that are close to the boundary. Hence the occurrence of the terms $q_M\sqrt{M}H$ and $q_E\sqrt{E}H$. On the other hand, the terms $g\sqrt{E}H + f\sqrt{M}H$ denote again interactions in the very same conditions between these populations, but of competition type. Finally, $\widetilde{w}\sqrt{EM}$ accounts for the intermingling of native and invasive hares on their common boundary, which gives rise to new offsprings of hybrid type. Finally, it is to be noted that some of the above coefficients appear with a tilde. At first, they can be taken to have a constant value. However, since they describe direct interactions along the interface of the two main territories occupied by E and M, it should be observed that due to the intermingling of these two species, their direct contacts are reduced as time flows, because in those situations the two main populations get slowly replaced by the hybrid species. Hence H constitutes a barrier that prevents further direct interactions of E and M. A more elaborate version of the model thus replaces these constant values with a more precise description based on a decreasing function of the size of the hybrid population:

$$\widetilde{a} = \frac{a}{1+H}, \quad \widetilde{c} = \frac{c}{1+H}, \quad \widetilde{w} = \frac{w}{1+H}.$$

The investigation reveals that in the current conditions the coexistence of both species and their hybrids is possible at a stable level. The power of the model resides also in the possibility of changing the parameters, hypothesizing higher or lower values of each parameter in correspondence of higher values of the atmospheric temperature. Under climatic changes, however, the survival range for the mountain hare reduces the more, the higher the temperature raises, until their possible final disappearance. Also, the in silico results show that the hybrid species may go extinct in the absence of some competitive advantage with respect to parental species, but in reality this is not yet clear. Overall, in order to maintain the system in equilibrium, the model highlights the relevant role of the competition between European and hybrid hares, that may coexist only in a very narrow region of the parameter space, implying the possible future disappearance of the mountain hare. Above all, the recommendation is to avoid new imports and releases for hunting purposes of the European hares.

3.3. *Extension to Pack behavior*

The the spatial distribution of predators and their hunting behaviors were taken into account implicitly in [13]. However, in [14] these herding ideas are extended to include pack behavior of the predators, that may hunt either individual or herd-gathered prey, as well as to consider symbiotic and competing cases. Again, the restriction is that interactions occur on the border of the packs and the prey herds. Thus models contain square root terms for both interaction terms. Pack hunting giving the most benefit to the predators first to arrive at attacking the prey is perhaps a bit stretched, but in a sense contains the intention of modeling the fact that the strongest predators anyway get the better share of the loot. In a general fashion, these models can be accounted for by the following equations

$$(12) \qquad \frac{dQ}{dt} = r\left(1 - \frac{Q}{K_Q}\right)Q \pm q\sqrt{P}\sqrt{Q}, \quad \frac{dP}{dt} = m\left(1 - \frac{P}{K_P}\right)P \pm p\sqrt{P}\sqrt{Q},$$

where Q and P denote prey and predators respectively, with associated signs $-$ and $+$, or the two interacting populations, where the interactions are of symbiotic or competing nature, again with respective pairs of signs given by $+$ and $+$, and $-$ and $-$.

For pack predation and individualistic prey behavior coexistence is found at the level

$$(13) \qquad E_2^{[pi]} = \left(\frac{rmK}{rm + pqK}, \frac{r^2p^2K^2}{(rm + pqK)^2}\right),$$

which turns out to be globally asymptotically stable, because no limit cycles are allowed. Instead, pack predation combined with prey herd behavior gives the conditionally feasible coexistence equilibrium

$$(14) \qquad E_2^{[ph]} = \left(\frac{rm - pq}{rm} K, \frac{rm - pq}{rm^3} Kp^2 \right),$$

which, if unfeasible, leads to the destruction of the ecosystem, the origin being the final outcome and globally asymptotically stable. A transcritical bifurcation tying together these two points arises when r crosses from below the critical threshold $r^* = pqm^{-1}$. Another critical value of importance is

$$(15) \qquad r = r^\dagger = \frac{3pq - m^2}{2m},$$

beyond which the two populations exhibit persistent limit cycles. Finally, if the initial conditions belong to the set

$$(16) \qquad \Xi = \left\{ (Q, P) : P > 0, 1 \geq Q \geq \exp\left(-\frac{q}{r} \sqrt{P} \right) \right\},$$

the trajectories hit the predator axis, and consequently the prey vanish, in finite time.

For the symbiotic model, the ecosystem attains the coexistence equilibrium independently of the initial populations values and no Hopf bifurcations are allowed. Interestingly, comparing the population values once the system has settled down with the corresponding values of the classical quadratic model for species living in symbiosis, it is found that for the latter, the values are always higher than those attained for the symbiotic system (12). This perhaps counterintuitive result can be explained by observing that with herding/packing, only parts of the populations intermingle and therefore the mutual benefit is not perceived by the whole populations.

The most striking finding however concerns the competition model. For this system, the isoclines are parabolae through the origin, with the second intersection with the coordinate axes also positive. Their axis in one case is horizontal and in the other one vertical. Depending on their slopes at the origin, they may simply touch each other at this point and do not intersect in the first quadrant, or else intersect once or three times, with a situation in between in which one intersection exists and at another point they are tangent to each other. This gives rise to a saddle-node bifurcation. In case of no intersection other than the origin, the system gets extinguished, trajectories hit the coordinate axes and then move along them to the origin. For one feasible intersection, which turns out to be a saddle, the principle of exclusion holds, as in the classical quadratic competition system. Therefore one species wipes out the other one, the outcome being determined just by the location of the initial conditions. Indeed there is a separatrix partitioning the first quadrant in two domains of attraction, one for each one of the possible outcomes, where just the Q population thrives, or alternatively just the P species survives. In case of three intersections instead, the middle one is stable while the other two are again saddles. Hence, the first quadrant is partitioned into three domains of attraction. The extra equilibrium point is an attractor where both species thrive. Thus this model allows for tristability, a new phenomenon unknown for classical quadratic predator-prey systems.

Note that in the classical quadratic populations' competition, the principle of exclusion in particular situations does not hold, and both populations thrive, but of course no tristability arises, as in such case both equilibria with one vanishing population are repellers. Comparing the populations values at coexistence in the classical case and for (12), it is found that the new model allows higher values for both competitors. This seems counterintuitive, but, as for the symbiotic case, it is once again due to the fact that the harming interactions occur only for the individuals occupying the outermost positions in both herds, so that only a subset of the whole populations are negatively affected.

3.4. *Prey response to predators attacks*

Additional considerations can be given to the fact that prey could use herding as a counterstrategy against individual predator's P attacks. If the prey is sizeable and provided of defensive means, e.g. horns,

the predators may indeed renounce to their attacks. Minimal models can be constructed to focus only on the salient features, in that they account just for predator-prey interactions.

To model prey retaliation, a variation of the classical Holling type II function is employed [15]. It consists in scaling the herding term via a linear term in the denominator, so that as the prey size N becomes larger, the function tends to vanish:

$$(17) \qquad \frac{a\sqrt{N}P}{1+bN}.$$

A more complicated variation has been considered in [16], through a Beddington-DeAngelis variation of the above functional response,

$$(18) \qquad \frac{\Phi(N,\alpha)P}{1+bN^{\alpha+q}+cP}, \quad \Phi(N,\alpha) = \frac{N}{1+N^{1-\alpha}}.$$

The function Φ used here is a way to avoid the problems arising in the singularities of the Jacobian because, respectively for small and large N, it behaves as follows

$$(19) \qquad \Phi(N,\alpha) \approx N, \qquad \Phi(N,\alpha) \approx \sqrt{N}.$$

The exponent $\alpha \in [0.5, 1)$ accounts for irregular or higher dimensional domains, for instance to model fish schools or bird flocks. The parameter $q \in \{0,1\}$ is instead a shorthand to capture prey counterattacks, $q = 1$, or not, $q = 0$.

A detailed comparison for a number of classical and more recent models is given in both references [15,16]. As expected, in all these situations, the prey are much better off than in the classical predator-prey models, and also with respect to the earlier models involving herding.

3.5. *A possible mechanisms of invasion for migrating species*

A novel idea for trying and understanding invasion mechanisms for migrating species has been introduced and discussed in [17] and with marginal contacts, in [18]. The basic idea consists in forcing a periodic behavior in time,

$$(20) \qquad \frac{d^2 A}{dt^2} + \omega^2(A - A_0) = 0,$$

this mimicking the migrating species A, and then coupling it with an underlying predator H-prey P system residing in the environment crossed by the migrants. At first A is assumed just to disrupt the living conditions of the resident ecosystem that it crosses, given by the system

$$(21) \qquad \begin{aligned} \frac{dP}{dt} &= sP - aPH, \\ \frac{dH}{dt} &= rH\left(1 - \frac{H}{k}\right) + \alpha PH. \end{aligned}$$

Introducing the derivative Y of A in (20) a pair of first order equations is obtained. Combining with (21) leads to the following formulation

$$(22) \qquad \begin{aligned} \frac{dP}{dt} &= sP - aPH - bPA, \\ \frac{dH}{dt} &= rH\left(1 - \frac{H}{k}\right) + \alpha PH - \beta HA, \\ \frac{dA}{dt} &= Y, \\ \frac{dY}{dt} &= -\omega^2(A - A_0), \end{aligned}$$

where the migrants do not get any gain from this action, but the resident populations are negatively affected by the migrants.

The only possible system's equilibria are

$$E_0 = (0, 0, A_0, 0), \quad A_0 = \frac{s}{b}, \quad E_1 = (0, H_1, A_0, 0), \quad H_1 = \frac{k}{r}(r - \beta A_0)$$

and

$$E_* = (P_*, H_*, A_0, 0), \quad H_* = \frac{s - bA_0}{a}, \quad P_* = \frac{1}{\alpha}\left(\frac{rH_*}{k} + \beta A_0 - r\right).$$

Note that in the $A - Y$ two dimensional subspace E_0 is constructed so as to be a center.

Consequently, we can distinguish the following situations as the prey and predators reproduction rates s and r vary. When $s < bA_0$ the system approaches persistent oscillations around the non-zero components either of E_0, when $r < \beta A_0$, or E_1, when $r \geq \beta A_0$. Instead for $bA_0 \leq s < bA_0 + ak$ the outcome consists of persistent fluctuations around the non-zero equilibrium components of E_1, when $r > r^\dagger := \beta A_0 ak[bA_0 + ak - s]^{-1}$, or of E_*, when $r \leq r^\dagger$, Lastly, for $s \geq bA_0 + ak$ the system exhibits periodic oscillations around the three nonvanishing components of E_*. Let us recall and stress that these oscillations are always of neutral type, they never converge to the equilibrium point.

As a general consequence, when the migrants do not get benefits from the crossed territory, they continue their migrations back and forth.

In the second situation, A is assumed to be a superpredator. Mathematically, this implies that demographics must be added to the migrants equation.

$$(23) \qquad \frac{dA}{dt} = \gamma A(P + H) - mA.$$

After differentiation of (23) we get a second order equation, that is reduced to a pair of first order equations introducing the derivative Y of A as before. Combining with (20) and (21) we finally obtain the model with superpredators
(24)
$$\frac{dP}{dt} = sP - aPH - bPA,$$
$$\frac{dH}{dt} = rH\left(1 - \frac{H}{k}\right) + \alpha PH - \beta HA,$$
$$\frac{dA}{dt} = Y,$$
$$\frac{dY}{dt} = \gamma Y(P + H) - mY - \omega^2(A - A_0) + \gamma A\left[sP - aPH - bPA + rH\left(1 - \frac{H}{k}\right) + \alpha PH - \beta HA\right].$$

The equilibria of this model are exactly the same as those of (22). However, their stability conditions differ. This implies that they are no longer centers, but attractors, so that the oscillations damp and the trajectories tend to these equilibrium points. Therefore the migrants, finding food in the environment, cease to migrate and settle down in it. This phenomenon could be considered as the trigger for an alien species invasion mechanism.

A variant of this migration setting is explored in [18]. Here is it assumed that the contacts of the migrants with the crossed environment are scant, in the sense that they occur on the margin of this territory. Futhermore, a more general boundary is accounted for, adequately represented by the parameter α appearing in the function Φ, recall (19).

The final outcome is similar. Just this scant contact with a favorable environment makes the migrant to settle down in it, therefore becoming once again an invasive population.

3.6. *A serendipity case: a particular kind of predator, the herbivores*

Debarking is a phenomenon that occurs both among domestic and wild herbivores. It consists in removing part of the bark from a tree, looking for nutriment, especially when grass is scarcely available.

The main difference is that sheeps peel off all around the trunk causing trees death because they interrupt completely the flow of nutrients from the roots to the leaves; deer instead peel off only vertical stripes so that the damage is milder.

The model formulation accounts for feeding saturation by the herbivores H, that are "predators" of both grass G and trees T:

$$
(25) \qquad
\begin{aligned}
\dot{H} &= -\mu H + e\frac{HG}{c + H + \alpha G} + f\frac{HT}{g + H + \beta T + \alpha G} \\
\dot{G} &= r_1 G\left(1 - \frac{G}{K_1}\right) - \frac{HG}{c + H + \alpha G} \\
\dot{T} &= r_2 T\left(1 - \frac{T}{K_2}\right) - \frac{HT}{g + H + \beta T + \alpha G}
\end{aligned}
$$

Indeed, as $G \to \infty$, the second term in the first equation tends to $e\alpha^{-1}H$, while the third one vanishes. Only if grass is little available, herbivores switch to debarking with a maximum given by $f\beta^{-1}H$. The investigation of this model in a concrete situation, using parameter values that come from parks in Italy, shows that instead of the forests, more at risk are the herbivores themselves, because studying the situation in the (μ, e, α) parameter space, there is a surface separating the basins of attraction of the coexistence equilibrium of the three populations from the one of the herbivore-free equilibrium [19,20]. The actual situation indicates that the current equilibrium allows the thriving of all populations, but it is very close to this separatrix, so that even small parameter perturbations due to climatic changes may push it into the other basin of attraction, for which herbivores extinction follows [21].

Preservation strategies based on this result can be suggested, whose implementation may or may not be rather difficult. To move away from the separatrix in the $\mu - e - \alpha$ parameter space one could think to decrease μ and α, or increasing e, hence the benefit for herbivores H. Specifically, this could be obtained by building safety niches so as to decrease of the herbivores mortality rate μ in the winter season. Grass more rich in nutrients could also be planted, increasing α^{-1}, for which herbivores have a more rich diet.

4. Environment: a glimpse on climatic changes and pollution

4.1. *Primary oxygen producers*

Life on Earth is possible because of the continous production of oxygen by vegetation as a consequence of the action of chlorophyll and sunlight. Plants as all living organisms breath, but the oxygen release is higher than carbon dioxide during the day. At night of course, CO_2 emission is the result of respiration. What may be less known is the fact that about three quarters of the Earth surface is covered by waters, and in them phytoplankton plays the same role as plants on the ground. In view of the larger proportion of these aquatic microorganims over terrestrial plants, the amount of oxygen present in the atmosphere is kept constant mainly by its release from the oceans. This stresses the importance of phytoplankton for life on Earth.

However, in particular bad circumstances, mainly due to the use of chemicals as fertilizers in agriculture, which ultimately are washed down into rivers and consequently dumped into the seas, together with other organic materials, the onset of red, or brown, tides, is favored. These tides are triggered by the outgrowth of plankton cells followed by dissolved oxygen depletion. This causes at first their own and afterwards the death and decomposition of fish. In turn this entails problems for fisheries and tourism. Investigating the causes of these situations is therefore important. For instance harmful algal blooms have been considered in [22].

In another investigation, [23], the following model has been introduced to study possible regime shifts induced by climate, using as basic variables the phytoplankton and zooplankton densities u and v as well

as the oxygen concentration c:

$$(26) \qquad \frac{dc}{dt} = A\frac{c_0 u}{c + c_0} - \frac{\delta uc}{c + c_2} - \frac{\nu cv}{c + c_3} - mc,$$

$$(27) \qquad \frac{du}{dt} = \left(B\frac{c}{c + c_1} - \gamma u \right) u - \frac{\beta uv}{u + h} - \sigma u,$$

$$(28) \qquad \frac{dv}{dt} = \frac{\eta c^2}{c^2 + c_4{}^2} \frac{\beta uv}{u + h} - \mu v.$$

The analysis shows that there is a tongue in the A-B parameter space where life is sustainable. In Figure 2 the current situation is somewhere in the bottom right corner of the tongue. Now the situation under climatic changes may lead to a movement of this point. If the shift is in the direction of the green arrow, i.e. with increasing temperature the phytoplankton growth rate B increases and oxygen production A decreases, the conditions are safe, we remain within the safety region. On the other hand if the shift in the opposite direction, yellow arrow, the outcome depends on the extent of this shift. If it is small enough, again the situation does not escape from the safety region, otherwise for a larger shift, the region where life is impossible will be attained. A similar situation will occur in the case of orange and red arrows, but with a difference between the two. For the orange arrow, if the increment is small enough, the safety region is not abandoned and life is still possible; in any case in this situation a regime of bifurcations leading to spatiotemporal oscillations will arise as early warning signals. For the red arrow instead, even a small change will suddenly lead outside the safety tongue and this will occur without any signs that indicate its occurrence. In such case the oxygen depletion will occur, with a consequent disappearance of life on the planet. However, there is a fundamental question that remains open. Nothing is known on the influence of raising water temperatures on the phytoplankton reproduction B and on the oxygen production rate A. The model also fails to account for possible adaptation of phytoplankton to the new environmental conditions. Therefore at the moment no sure inferences can be taken, although these studies should be given an adequate attention.
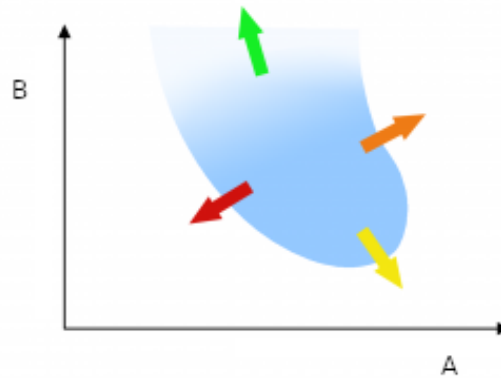

Figure 2. Blue: the safe region in the A-B parameter space, phytoplankton growth rate B versus oxygen production A. The arrows denote changes due to raising water temperature. Green is safe, Yellow may be safe if change is small, Orange and Red are unsafe, Orange gives early warning signals, while Red does not.

4.2. Ecological hysteresis

We discuss now the situation of a continuous change in environmental conditions, leading to a sudden dramatic transition of the ecosystem from a state to another very different one, with risk of collapse. It is an example of fallacy is our thinking that generally is linear. Namely, after a regime shift due to some parameters crossing some critical threshold, [24,25], we in a naive way assume that to push back the system to return to the previous state it is enough a small change of the environmental conditions in

the opposite direction, [26]. This is illustrated in Figure 3, where the height of the ice cap in Greenland is expressed as function of temperature. Time is explicitly absent in the diagram, but in reality we have to understand that any point in the first quadrant represents a transient situation, for which the system will quickly approach the attracting steady states, represented by the red solid curve or the blue dashed one. The black curve acts as a separatrix. In the green region, the system movement is downward, while in the yellow one, it is upward.

Hence any point in the first quadrant represents a given thickness of the ice cap for a given temperature, but will approach the red line from below or from above, depending on the color of the region in which it lies. We can thus assume that the current situation is at steady state somewhere on the red curve, to the left of the point at which the curve drops suddenly. With increasing temperature this point will move toward the right on the red curve, entailing a small decrease in the height of the ice cap. With a steady increase in the temperature, the shift toward the right will continue, until the vertical drop occurs, and suddenly the ice cap disappears. At this point the naive interpretation would suggest that it is enough to decrease the temperature below the critical threshold to restore the previous condition. But the system has reached a situation in which no ice is present and a decrease of the temperature past the critical threshold would leave the system in the green area, so that the trajectories are pushed down, toward the blue dashed line. Hence, there is no restoration of the previous conditions. This will continue to hold even for larger temperature decrease, until the second critical threshold, with lower temperature, is attained. A further decrease leads the system to jump in the yellow area and therefore it is pushed upwards to the red curve, now restoring the original conditions. However, this shift, if at all possible, may take dozens of years or even centuries. Therefore it makes sense to say that crossing the first threshold, the one with a larger temperature, a permanent shift to novel conditions occurs, with no way of coming back in a reasonable amount of time. In a different context, an example of such situation has occurred in Bengal in India, where before "green revolution" of the seventies more than about ten thousand varieties of rice were present, but nowadays they are reduced to about a few hundred [27].

A second and very important consequence is that the melting of more than 3 Km of ice over a vast region such as Greenland produces a huge amount of freshwater, that is suddenly dumped into the ocean. Physically, this entails a huge wave, a soliton, that may harm the coastal lands and waters, similar to a tsunami. Biologically instead, the release of freshwater alters the salinity of the nearby ocean waters threatening the ocean ecosystems. Furthermore it may change the course of a very important current, the American Meridional Overturning Circulation (AMOC), with a severe impact on the climate of the coastal regions in the North Atlantic, leading to far lower temperatures and harsher living conditions than are nowadays experienced.
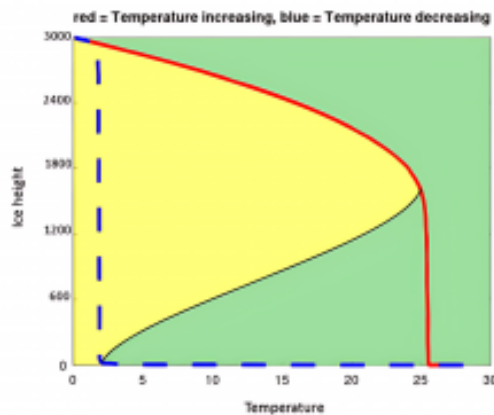

Figure 3. Hysteresis. Ice height (vertical axis) versus temperature (horizontal axis). Red, equilibria for increasing temperatures; Blue, equilibria for decreasing temperatures.

4.3. *Fungi model for water purification*

Climatic changes are triggered by the release of gases in the atmosphere, that contribute to the greenhouse effect on a planetary scale. Another cause is represented by dumping pollutants in freshwaters and then in the ocean, triggering harmful algal blooms threatening phytoplankton survival as we have seen above in Subsection 4.1.

We now discuss a model for a biological wastewater remediation. For this purpose, fungi can be employed to eliminate pollutants from industrial wastewaters. In a small scale experiment, which would be a prelude to the construction and installation of tanks to treat these waters, the *Trametes pubescens* has been used to remove Remazol Brilliant Blue Reactive dye in a solution, in a closed system where inputs and outputs are absent. A model of this process can be set up by defining the following dependent variables: the organic pollutant concentration, P, the biomass of the *Trametes pubescens* fungus, F, and the nutrients, essentially glucose, C, [28].

(29)
$$\frac{dP}{dt} = -a_1 \frac{P}{h_P + P} F - a_P \frac{C}{h_C + C} \frac{P}{h_P + P} F$$
$$\frac{dF}{dt} = e a_1 \frac{P}{h_P + P} F + e a_P \frac{C}{h_C + C} \frac{P}{h_P + P} F + f k_C \frac{C}{h_C + C} F$$
$$\frac{dC}{dt} = -k_C \frac{C}{h_C + C} F + (a_C - 1) a_1 \frac{P}{h_P + P} F + (a_C - 1) a_P \frac{C}{h_C + C} \frac{P}{h_P + P} F.$$

The model appears rather complicated, because the Holling type II response function is used to mimick the fact that with time elapsing, the action of the fungi may reach an upper bound. The model has been tested against the experiment results. However, the experiment lasted about a week, and less than two dozens of values were collected for each one of the dependent variables. This made the direct assessment of the parameter values rather ill conditioned. In spite of the fact that the tank is shared among all the laboratory scientists and therefore its use is not available at all times, a renewed line of experiments was set up, to reduce the number of parameters to be assessed in each case. Namely, three cultural lines with comparable F and P were considered, with differences only for the nutrient content: (A) glucose absence; (B) pollutant absence; (C) both pollutant and glucose present. In this way the smaller size experiments contained less parameters, and their determination was easier.

The good results of line (A) are first that the pollutant does not harm the fungus, that thrives, but the growth is scant during the week's experiment. Secondly, there is degradation of the pollutant, which is a source of nourishment for the fungus. From this reduced size experiment, some parameters can be directly estimated, in particular $a_1 = 664(ls)^{-1}$, $h_P = 100g/l$ and others indirectly. Indeed, at the end of the experiment the system settles to $(0, F(\infty))$, the final value of the fungus being obtained by the data; observing that $eP + F = eP(0) + F(0) = eP(\infty) + F(\infty) = 0 + F(\infty)$, the conversion factor e is determined as a consequence,

(30)
$$e = \frac{F(\infty) - F(0)}{P(0)} = 0.022.$$

Line (B) allows evaluating the role of glucose in the fungus growth and in a similar way, as a side result, allows the determination of other model parameters.

All the information gathered on the parameters in lines (A) and (B) is then used in line (C), which still contains some unknown parameters, but in a reduced amount. Their determination is obtained directly from the experiment results. It is observed that high and fast degradation of P by F is attained, favored by helping the fungus metabolism via glucose as food source in the same amount used in line (B).

The results of lines (A) and (C) are similar for the degradation of the pollutant, but feeding the fungus, line (C), allows to achieve the final outcome with a much faster reduction rate and therefore this practice should be recommended.

5. Epidemiology in the environment, the farms and among humans

5.1. *Profitable use of resources: fungi and phyllosphere microorganims*

We consider at first two more situations involving the olive tree, in which fungi have a relevant role. However, in the first case their action is beneficial, while in the second one it is pathogenic. As a common result, the findings in both models indicate that human action has a relevant role in keeping in check the diseases. It is represented mainly by pruning of the infected parts of the tree, represented by the terms $-gI$ in the systems (31) and (32) below. Nevertheless, we describe in detail the construction of these models to illustrate their similarities, but also their discrepancy, that arises from the difference in the ecological situations in consideration.

5.2. *Beneficial fungi*

The olive tree may be affected by galls, a result of the "olive knot" disease. The latter is caused by the *Pseudomonas savastanoi* pv. *savastanoi (Psv)* bacteria. It can be contrasted by the endophytic fungus *Epicoccum nigrum*. For the investigation of this situation [29], let S denote the healthy branches and I the bacteria-infected branches of the olive tree, B the pathogenic bacterium *Psv* infecting the olive branches and N the endophytic fungi *E. nigrum* that remove the *Psv* bacterium B. In so doing, *E. nigrum* gets more space in the branches and more nutrients from the plant. Conversely, N also produce a positive effect on the healthy parts of the plant.

(31)
$$\frac{dS}{dt} = s\left(1 - \frac{S+I}{K}\right)S - \lambda SB + bNS$$
$$\frac{dI}{dt} = -s\frac{S+I}{K}I + \lambda SB - qIB - gI$$
$$\frac{dB}{dt} = hqIB - aNB - mB - rB^2$$
$$\frac{dN}{dt} = ebNS + uaNB - nN - pN^2.$$

Note that in this model all kinds of possible population interactions are present, demographic for the growth of the branches, e.g. the first two terms in the equations for S and I. Predator-prey interactions exist among the bacteria and the infected branches from which they take nourishment, as well as from the removal action of *E. nigrum* over the bacteria. Symbiosis, as explained above, occurs among N and S. Since the bacteria are pathogenic, the epidemological parts are represented by the terms involving the bacteria transmission in the branches, with infection coefficient λ. Note finally that the removal of the bacteria by N does not change the branches status, in that the infected branches may not harbor the disease, but remain on the tree.

5.3. *Phyllosphere microorganisms*

In the second instance, the fungus is pathogenic, but it can be contrasted by phyllosphere microorganims [30]. They control plant diseases by removing pathogens from the tree's canopy. In addition they represent bioprotectants, with a direct positive action on the tree. In turn they benefit from the plant, feeding on it.

To set up the model, the following dependent variables are defined: S denoting the healthy and I the pathogenic fungi-infected leaves of the olive tree, F the filamentous fungi infecting leaves through a pathogenic action, G the phyllosphere microorganisms. They are important also because "artificial" antagonistic molecules could be extracted from them and then produced in a larger scale in the laboratory, so that they can be used on the cultures as a prevention against pathogens.

$$(32) \quad \frac{dS}{dt} = s\left(1 - \frac{S+I}{K}\right)S - \lambda SF + bGS$$

$$\frac{dI}{dt} = -s\frac{S+I}{K}I + \lambda SF - gI - qIF$$

$$\frac{dF}{dt} = hqIF - aGF - mF - rF^2 - s\frac{S+I}{K}IF_{av} - gIF_{av},$$

$$\frac{dG}{dt} = ebGS + uaGF - nG - pG^2 - gIG_{av} - s\frac{S+I}{K}(S+I)G_{av},$$

$$(33) \quad F_{av} = \frac{F}{I}, \quad G_{av} = \frac{G}{S+I}.$$

As for (31), this model contains demographic terms and interactions of predator-prey, symbiotic and intraspecific competition types.

There is however a basic relevant feature that the model has to capture during its set-up. It is represented by the remark that dead leaves fall from the tree, in contrast to what happens to dead branches in (31). In so doing, they carry all the fungi content they have away with them, and the equations must take this phenomenon into account. This is expressed by the terms F_{av} and G_{av} which give the average amount of pathogenic fungi and phyllosphere antagonists present in each leaf. Each term causing mortality of an infected leaf carries with it this amount of the latter two populations. Only $-qIF$ does not, because this represents the feeding of F on the infected branches and not a real mortality of the latter. Once again this remark stresses the fact that to properly formulate a model, the understanding of the whole picture of the situation is of paramount importance.

5.4. *An epidemiological situation in goat farms*

A disease affecting goats, similar to HIV for AIDS for humans, has been discovered in the seventies of the past century. It is caused by a virus named lentivirus, because it develops symptoms in a very slow fashion, about 10 years, which is also the goat lifetime. Apart from other negative effects, from which its name, Caprine Arthritis Encephalitis Virus (CAEV), it causes a reduced milk production and thus it is not economic for the farmers. No vaccine is known. There are several strains worldwide of this virus, but two are the main ones: genotype E which is not pathogenic and can only be vertically transmitted, i.e. from mothers to offsprings. It is also called Roccaverano strain, from the Piedmontese town where farms are located when it was discovered. Genotype B instead is pathogenic, and can be transmitted vertically and horizontally by direct contact.

Farmers try to contain the disease by removing newborns of infected mothers and raising them by healthy goats; after weaning they rejoin the flock, but could still get infected horizontally.

The alternative of "test-and-slaughter" is very expensive because the veterinarian has to take blood samples, which need to be analysed in the laboratory and therefore it is impractical and not used on large scale.

A basic demographic model for an 'ideal breeding' with no disease has been proposed in [31]. Keeping in mind that the farmer's perspective is to have it at maximum capacity, it is possible to deduct a formula telling how many newborns per year need to be kept in the farm and raised, to maintain it economically viable. Every farmer has an intuition for such a number, the replacement rate α_{farm}, but the model quantifies the answer in terms of goat mortality μ and reproduction rate r, namely

$$(34) \quad \alpha_{farm} = \frac{\mu}{r}.$$

In Italy there are three main races in the farms, the Sardinian, the Saanen and the Roccaverano. Each one of them has different values for the above parameters, from which it follows

$$(35) \quad \alpha_{sard} > \alpha_{saanen} > \alpha_{rocc}.$$

Hence the farmer is better off raising goats of the Roccaverano race.

In case of a genotype-B-lentivirus-affected breeding, intuition indicates that more offsprings should be kept, to compensate for additional disease-related mortality. Again, the model validates the intuition, [32] providing the value of the replacement rate in pathogenic conditions α_{path} as follows

$$(36) \qquad\qquad \alpha_{path} > \alpha_{farm}.$$

In this case the disease remains endemic, because the model shows that eradication would entail to reduce the size of the breeding so much so as to make it not economically sustainable.

For genotype E-affected breedings, because this strain is not pathogenic, the replacement rate obtained from a suitable model for this situation is the same as for a disease-free farm:

$$(37) \qquad\qquad \alpha_E = \frac{\mu}{r} = \alpha_{farm}.$$

The sanitary strategy [33] of removing newborns and raising them by healthy goats simply boosts the speed at which the disease-free equilibrium is attained, a fact that will anyway occur. We denote by γ the rate of newborns that are not removed from the breeding; for $\gamma = 0$ all newborns are removed while for $\gamma = 1$ all newborns are kept in the breeding.

In a farm in which both genotypes B and E are present, a more general model including both types of infection, but no coinfection, can be built, [34] and the replacement rate is seen to behave like the one just for genotype B, (36). In general the farmers' strategy to contain the disease consists in two actions: full newborns removal, $\gamma = 0$, and preventing goats intermingling, expressed by another parameter, $0 \le \beta \le 1$, with $\beta = 0$ denoting animal segregation. In such case the model predicts disease eradication, but at the cost of reducing to very small numbers the size of the breeding, as seen above, and it is not economic. A deeper investigation however shows that the number of genotype B-infected goats is drastically reduced, with genotype E replacing the pathogenic genotype B acting as a kind of natural vaccine. However this entails a complete reversal of the farmers' policy, namely for $\gamma = 1$ and $\beta = 1$, imposing no newborns removal and complete mixing of the goats.

The model therefore leads to a conclusion that at first sight is quite counterintuitive and suggests the introduction in each breeding of a few genotype E-infected goats, an action that will trigger the eradication mechanism.

5.5. Disease introduction in herding

An interesting variation of the ideas exposed in the previous subsections 3.2 and 3.3, consists in considering an ecoepidemic system. Again focusing only on herding prey and individualistic predators, introducing a disease in the former population, the infected prey could be assumed either to leave, or being left behind, the herd [35] or alternatively remain in the herd, [36]. Focusing on the last case, let S denote the healthy prey population, I be the infected prey and P the predators, the model can be written as

$$(38) \qquad \begin{aligned} \frac{dS}{dt} &= rS\left(1 - \frac{S+I}{K}\right) - \sigma\frac{SI}{S+I} - qP\frac{S}{S+I}\sqrt{S+I}, \\ \frac{dI}{dt} &= \sigma\frac{SI}{S+I} - wP\frac{I}{S+I}\sqrt{S+I} - \mu I, \\ \frac{dP}{dt} &= -mP + gP\frac{S}{S+I}\sqrt{S+I} + fP\frac{I}{S+I}\sqrt{S+I}. \end{aligned}$$

In the first equation, apart from the logistic term and the disease transmission at rate σ, the last term expresses the hunting at rate q of predators on the prey on the boundary. The total prey population is $S + I$, of which we take the root to account for those on the perimeter. Since the first equation is for susceptible prey, their fraction in the total population is represented by $S(S + I)^{-1}$ and the one on the boundary multiplies this fraction by the total boundary population $\sqrt{S + I}$. A similar explanation holds

for the last term in the second equation as well as for the gain that the predators get from catching the prey in the last equation.

Through a chain of changes of variables, in order to eliminate the singularities that would appear in the Jacobian, we are finally led to the system

(39) $\quad \dfrac{dA}{dt} = (\sigma - r - \mu) A^2 + \dfrac{r}{K} A^2 T^2 + (q - w) A^2 U + (r + \mu - \sigma) A - \dfrac{r}{K} AT^2 + (w - q) AU,$

$\quad \dfrac{dT}{dt} = -\dfrac{r}{2K} AT^3 - \dfrac{\mu}{2} T + \left(\dfrac{r}{2} + \dfrac{\mu}{2}\right) AT - \dfrac{w}{2} UT + \left(\dfrac{w}{2} - \dfrac{q}{2}\right) AUT,$

$\quad \dfrac{dU}{dt} = \dfrac{w}{2} U^2 + \dfrac{q - w}{2} AU^2 + \left(\dfrac{\mu}{2} - m\right) U + (g - f) AUT - \dfrac{r + \mu}{2} AU + fUT + \dfrac{r}{2K} AUT^2.$

The new variables introduced in this way can be expressed via back substitution in terms of the original model variables, as follows

$$A = \frac{V}{T} = \frac{S}{T^2} = \frac{S}{S + I} \leq 1, \quad T = \sqrt{S + I}, \quad U = \frac{P}{T} = \frac{P}{\sqrt{S + I}}.$$

It is interesting to note that all of them have an interpretation in terms of the original variables, namely: A represents the fraction of healthy prey over total prey, T is the total prey population on the edge of the herd, U denotes the ratio of predators over the total prey population on the edge, i.e. the ratio of predators over the total prey available for their hunting.

5.6. Disease by invasive carriers: grey squirrels

The Eastern grey squirrel (*Sciurus carolinensis* Gmelin, 1788) originates in the United States, thriving in forests, but is able to live also in many other different habitats. In Great Britain it was imported and released at the end of the nineteenth century. In Italy at the end of WW2, a pair coming from the US accidentally escaped and started to reproduce in the wild. The result in both cases is that it slowly started to replace the autoctonous Eurasian red squirrel (*Sciurus vulgaris* Linnaeus, 1758) in view of the fact that it is bigger and it can be sustained by more resources than the native one. In particular nowadays in the UK the red squirrel survives only in small patches in an environment almost uniformly occupied by the grey invader [37,38] Some other models exploring this situation and trying to explain its origin have appeared in the literature, [39,40].

In order to see if the invasive process can be contained, it is important to consider the predators of the squirrels. In particular the pine marten plays a special role, since it hunts the squirrels following them even on the trees. However, the bigger size of the grey squirrel now becomes a hindrance, because in order to escape from the attack of the marten, it flees on the tip of the branches which eventually break under its weight, while they do not with the lighter red one. Thus the attacks of the marten are more effective on the invaders than on the native species.

In addition in UK there is the squirrel poxvirus (SQPV), which is lethal for the native species, and for which the grey squirrels are asymptomatic carriers, [37,38]. To model this situation, in [41] four populations have been considered. Let G denote the grey squirrels harboring the SQPV, R and I be susceptibles and infected red squirrels, M the pine martens, the predators. We have

(40) $\qquad \dfrac{dG}{dt} = G(d - rG - fR - zI - uM)$

$\qquad \dfrac{dR}{dt} = R[a - bR - cG - wI - \lambda I - \beta G - sM]$

$\qquad \dfrac{dI}{dt} = I(\lambda R - \mu - vM) + \beta RG$

$\qquad \dfrac{dM}{dt} = M[g - hM + e(sR + uG + vI)].$

In spite being formulated with four equations, the model is conceptually relatively simple, accounting for reproduction of each species, but for the infected native squirrels, which would rapidly die of the virus

before being able to generate offsprings. There is then intraspecific competition, pine marten predation on the three squirrel populations. The virus is transmitted from the grey or from the infected red squirrels at rates β and λ respectively and produces new individuals belonging to class I. The marten thrives on other resources, but gets benefit also from hunting the populations appearing explicitly in the model.

We aim at preserving the native population and possibly at eradicating the invaders, hence R must not vanish and possibly $G \to 0$. Only four attainable equilibria exist in this model, other than possibly coexistence. the point at which only the marten survives, $E_1 = (0, 0, 0, M_1,)$, $M_1 = gh^{-1}$, which is unconditionally feasible and whose stability conditions are known. Also, pine marten can thrive together with the invader population, i.e. $E_2 = (G_2, 0, 0, M_2)$; in this case both feasibility and stability are conditional, with known inequalities to be satisfied by the system parameters. However in both these equilibria the native population is extinguished, and therefore they must be avoided. This means that some of the above conditions must be violated, in order to ensure that these points are unstable, or, for E_2, unfeasible. The desirable system outcomes are instead represented by the grey squirrel-and-disease-free point, the most desirable one: $E_3 = (0, R_3, 0, M_3)$. Again both feasibility and stability are conditional and known. Alternatively, also the equilibrium with the disease could be allowed, conditionally feasible and stable, but of course it is less appealing: $E_4 = (0, R_4, I_4, M_4)$. For both these equilibria feasibility and stability should instead be satisfied, in order to achieve the desired result. In case they are not, an intervention from outside, if at all possible, should concentrate in changing the system parameter values so that the relevant inequalities are satisfied, [41].

5.7. *Human response to diseases*

We finally consider a situation involving diseases spreading among human populations. Epidemiology has become a very important field of research in applied mathematics, because it is important to fight existing diseases, and try to prevent other diseases that are endemic in the tropical areas. Nowadays they spread toward more temperate areas, carried mainly by invasive insect vectors. We do not want even to give a few ideas in this very important research field, but consider a problem that is related to some topics previously discussed.

Using the same ideas in another context, we may consider the following simple situation in epidemiology. The first important paper accounting for human behavior against a communicable infection is [42]. Later on, other investigators included the perception that people may have against vaccination [43–45]. Considering [42], the fundamental idea is that if an epidemics is known to spread among humans, people will tend to reduce their contacts in order not to be infected. The weight of the epidemics that pushes people to react is given by the number of infected. However, in the recent Covid-19 epidemics, the role of asymptomatics in the spread of the infection has become more clear, as well as their avoidance being of paramount interest in curbing the disease incidence. The problem is that asymptomatics are not recognizable, and therefore preventive measures cannot be taken by the individuals, other than those based on the number of the recognized infected. This remark prompted the formulation of a model that differs from [42] in the response function. We consider the following specific instance of the susceptibles-infected-recovered (S-I-R) model [42]

(41)
$$\frac{dS}{dt} = -\frac{\alpha SI}{1 + \beta I^2},$$
$$\frac{dI}{dt} = \frac{\alpha SI}{1 + \beta I^2} - \gamma I,$$
$$\frac{dR}{dt} = \gamma I$$

and the counterpart introduced in [46], with similar notation, A denoting asymptomatic individuals, and

deprived from any demographic terms present in [46], so that a fair comparison can be made:

$$
(42) \quad
\begin{aligned}
\frac{dS}{dt} &= -\frac{\alpha SA}{1 + \beta I}, \\
\frac{dA}{dt} &= \frac{\alpha SA}{1 + \beta I} - \pi A, \\
\frac{dI}{dt} &= -(m + \mu)I + \pi A.
\end{aligned}
$$

It is immediate to see that in this variant with asymptomatics, no quadratic term in the denominator is necessary to obtain the desired result. Indeed as $I \to \infty$, the transmission tends to zero, because no I is present in the numerator.

Two main conclusions can be drawn from the analysis. At first the comparison of the two models behavior indicates that splitting infected among asymptomatic and symptomatic, preserves more susceptibles from getting the infection, should the progression rate from asymptomatic to symptomatic π be larger than the disease contact rate,

$$
\frac{\alpha I}{1 + \beta I} < \pi.
$$

This is contrary to what happens in the classical SI model. Indeed, in this situation the asymptomatic compartment becomes quickly empty, and consequently the transmission rate drops considerably.

Secondly, it is also possible to calculate the minimal weight that the individuals must give to the information about the symptomatics,

$$
\beta^{\dagger} = \frac{\alpha}{\pi} - \frac{1}{I}
$$

from which it follows the importance that authorities should give in providing reliable estimates of these rates to allow people to adequately respond to the infection propagation.

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