Dynamical scenarios from a two-patch predator–prey system with human control – Implications for the conservation of the wolf in the Alta Murgia National Park

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ABSTRACT

We evaluate a mathematical model of the predator–prey population dynamics in a fragmented habitat where both migration processes between habitat patches and prey control policies are taken into account. The considered system is examined by applying the aggregation method and different dynamical scenarios are generated. The resulting implications are then discussed, their primary aim being the conservation of the wolf population in the Alta Murgia National Park, a protected area situated in the Apulian Foreland and also part of the Natura 2000 network. The Italian wolf is an endangered species and the challenge for the regional authorities is how to formulate conservation policies which enable the maintenance of the said wolf population while at the same time curbing that of the local wild boars and its negative impact on agriculture. We show that our model provides constructive suggestions in how to combine wild boar abatement programs a while maintaining suitable ecological corridors which ensure wolf migration, thus preserving wolves from extinction.

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1. Introduction and research motivations

The establishment of management policies for protected areas has to face the issue of crop damages originating from wildlife. These damages have the negative effect of increasing the intolerance toward the wildlife and of diverting a substantial part of the usually scarce resources allocated to nature conservation toward compensation actions (Ficetola et al., 2014). Wild boars, which in Italy represent the most widespread species throughout the country, are deemed responsible for the largest amount of damages by wildlife. However, their heavy impact on agriculture practices may be partially compensated by their positive action on the native biotic communities of the ecosystem they are embedded in. For instance, it is known that wild boars can favor the regeneration of woods, at least when the population density is kept low enough. To reduce the size of the wild boar population and its ensuing impact on agriculture, while at the same time retaining the advantages of their presence in protected areas, culling activities need to be carefully planned by the managing authorities. A further relevant issue in such a planning task is that, although wild boar is not at risk of extinction itself, it plays a significant role in the trophic chain of another species which is currently red listed, i.e. the wolf. Wild boars represent in fact the favorite prey of the Italian wolf, especially in areas where other preys such as wild ungulates, are absent. Wolves, as well as other large carnivores, e.g. coyotes and dingoes, are considered keystone species, as their impact on their embedding ecosystems is disproportionally large with respect to their abundance. In Soulé et al. (2003) the authors describe the ecological effectiveness of the role of top predators for communities and ecosystems. Their extinction can cause a cascade of secondary extinctions. For that reason, they are a focus of interest in a number of large-scale re-wilding projects such as the North America Wildlands Network1 which is aimed at building large reconnected areas of land at continental scale to ensure the viability and sustainability of big wild animal populations (Soulé and Terborgh, 1999). In several European countries wolves are protected by national laws that try to conserve and increment the number of such predators. The legal status of wolves in the European Union countries

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is directly specified in the Habitats Directive (92/43/EEC)\(^2\) which is also responsible for the establishment of the Natura 2000 network of protected areas. The Directive requires strict protection, prohibiting any destruction or damage to the wolf population (Kaczynski and Chapron, 2013).

The present paper actually focuses on the Alta Murgia National Park in Italy, a node of the Natura 2000 network. In this area a small sample of wolves recently showed up and their presence is being constantly monitored even if the area extension and vegetation type appears to be unsuited for hosting a viable and stable population of predators. Instead, the wild boar population – initially brought to the site in small bunches for hunting purposes – exploded in recent years, especially because hunting activities in the area were strictly banned after the inclusion in the Natura 2000 network. The specific issues related to the presence of wolves in the Alta Murgia site have been under study within a European funded project (BIO-SOS) aiming at building an Earth observation monitoring system for assisting the reporting obligations of managing authorities. It is known that wolves reached Alta Murgia from a nearby protected area, Monti Dauni, through ecological corridors. Wolves are socially organized in packs, normally with only two reproductive animals. Wolf packs are territorial and, in Italy, are small in size but can travel long distances and have very large home ranges. They expand their range via dispersal and typically settle into unoccupied territories or assimilate into established packs within 50–100 km of their natal pack (Gese and Mechi, 1991). Presently, it is not known if the area of the Alta Murgia site can host a whole pack. Nevertheless national legal obligations bind the managing authorities to set up conservation policies even for such a limited number of individuals. The challenge for the regional authorities is to plan actions capable of maintaining the small population of wolves while at the same time limiting the presence of wild boars. A recent act by the management authority of the Alta Murgia Park (PGC, 2012), addresses the issue of the minimum number of wild boars capable of maintaining favorable conservation conditions for wolves without providing any guideline to quantify such an amount. The crucial point is: to what extent could one control wild boars without affecting the wolves’ survival? Mathematical modeling can suggest answers for the solution of this problem. Mathematical models are in fact exploratory tools that can be very useful in conservation ecology since they allow the building of hypothetical scenarios and provide management indications (and warnings) in planning control programs as well as in exploring the benefits of different control options (Diele et al., 2014; Garvie and Golinski, 2014; Gobattoni et al., 2014; Lacitignola et al., 2007, 2010; Schmolke et al., 2010; Vincent et al., 2011).

For this purpose, we recast the wild boars and wolves problem through a predator–prey model in a two-patch environment and use the modeling approach to evaluate how the interplay between wolf migration processes between patches and human control policies on wild boars can affect both populations dynamics as well as the wolf survival in the Alta Murgia Park. The model includes two time scales, a fast one associated to wolves movements between the two patches and a slow one corresponding to demographic events of the wolf and wild boar populations. The presence of these two different time scales enable us to use the general theoretical approach known as aggregation method which is quite effective when used in population dynamics (Auger et al., 2007; Auger and Bravo de la Parra, 2000; Auger and Poggiale, 1998; Auger and Roussarie, 1995). This allows for the reduction of the dimension of a multi-patch model into a reduced system which describes the dynamics of a small number of global variables. The reduced model is nevertheless capable of providing useful analytical insights into complex multi-patch systems. We refer to Auger et al. (2007) for an extensive review of the underlying philosophy behind the aggregation method as well as for a wide number of applications.

The paper is structured as follows: in Section 2 the two-patch model is presented together with the assumptions made and the model parameters are selected. In Section 3 some preliminary numerical test about the model behavior are presented, and the reduced model is obtained by applying the aggregation method. The results of the theoretical analysis of different kinds of equilibria, also in terms of their stability properties, are shown. By using field data, possible scenarios are discussed for the dynamics of the wolf and wild boar populations in the Alta Murgia National Park. Implications for the wolf conservation are also discussed as a function of the interplay between human control on the wild boar population and wolf migration processes between patches. In Section 4, concluding remarks are drawn.

2. Materials and methods

2.1. The two-patch model

The starting point of our analysis was a classical population dynamics approach redesigned to describe the predator–prey population dynamics in a fragmented habitat, where patches are connected via ecological corridors, as depicted in Fig. 1. Under the assumptions related to the specific case study we derived a two-patch model for the wild boar and wolf population dynamics. We considered the site of Alta Murgia Park as patch1 and the Dauni Mountains site as patch2. Consequently, we indicated as \( p_1 \) and \( p_2 \) the density of the wolf population in Alta Murgia Park and in the Dauni Mountains site respectively. We also indicated as \( n \) the density of the wild boar population in the Alta Murgia Park. In fact, experimental field data indicated that the wild boar population was present in the Dauni Mountains at very low densities and no movements between patches was observed for wild boars, so we considered their presence in patch2 as negligible for the aims of the present study. In the following, we list our assumptions on (a) the migration processes and (b) the local dynamics within the patches:

(a) Migration between patches

1. Wild boars (preys) are sedentary inside their living patch so that no migration was assumed from one patch to the other and vice versa.

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2. Regarding the wolves (predators), we assumed that they moved from patch1 (Alta Murgia) to patch2 (Dauni Mountains) at a constant rate $d_1$ and from patch2 (Dauni Mountains) to patch1 (Alta Murgia) at a constant rate $d_2$. Since the ‘attractiveness’ in terms of habitat suitability of the two patches was different, we expected the migration rate not to be the same in both directions, i.e. $d_1 \neq d_2$.

3. We assumed that migration between patches occurred at a faster time scale than the local predator–prey dynamics.

(b) Local dynamics within the patches

1. Field data showed that wild boar colonization of the Alta Murgia Park occurred more slowly in the first stages of a restocking program, applied in the years 2000, 2001 and 2002. The animals were released in two different areas of the Park, i.e. Gravina di Puglia (Bosco Difesa grande) and Spinazzola (Canale S. Lucia) and the releases were staggered over three years. The repopulation started in 2000 with 20 individuals, then 47 in 2001 and finally additional 105 animals were introduced in 2002, for an overall number of 172. In the initial stages of the reintroduction program the population growth was slower, probably due to stress factors related to the transportation as well as to the disruption of the social organization of animals removed from the wild. Therefore, wild boars spread faster and the population growth was fostered by the hunting ban introduction in 2004 (PGC, 2012). This characteristic appeared to be strongly similar to the spread of wild pigs in California where the occupation at first sporadic and then permanent of some areas has suggested the occurrence of a natural range expansion (Waithman et al., 1999). The same pattern was observed with other invasive organisms where range expansion is initially slow and then rapidly accelerates (Lodge, 1993). For example, although house finches benefited from human introductions when invading North America, they expanded rapidly only after populations reached some threshold size (Veit and Lewis, 1996). On the basis of the above considerations, we assumed an Allee growth for prey population in patch1, where $r$ is the intrinsic growth rate, $k$ is the carrying capacity and $A$ is the Allee threshold, with $A < k$.

2. For the predator population we assumed the same natural per capita mortality rate $\mu$ both in patch1 and in patch2.

3. We assumed a linear Lotka–Volterra functional response with $a_1$ and $b_1$ as predation coefficients in patch1 for prey and predator populations, respectively. We also supposed $b_1 = e_1 a_1$ where $e$ is a positive parameter which indicates the conversion of prey into predator biomass.

4. We assumed a control policy of the wild boar population which corresponds to a harvesting density dependent term in the prey dynamics.

5. We also assumed that such a control policy had the effect of increasing the mortality rate of the wolf population in the Alta Murgia Park by the rate $qE$ where $q$ is the catchability (vulnerability) coefficient and $E$ is a parameter which represents the effort and hence the strength of the control policy.

Taking into account the above assumptions, the full model reads:

$$\frac{dn}{dt} = \epsilon \left( mn - \frac{n}{k} \right) - a_1 np_1 - qEn,$$

$$\frac{dp_1}{dt} = d_2p_2 - d_1p_1 + \epsilon [-\mu p_1 + e_1 a_1 np_1],$$

$$\frac{dp_2}{dt} = d_1p_1 - d_2p_2 + \epsilon [-\mu p_2],$$

where all the involved parameters are assumed positive constants; $\epsilon$ is a small positive parameter, i.e. $\epsilon \ll 1$, $\tau$ is the fast time scale and $\tau = \tau_1$ is the slow time scale. Model (1) clearly shows that the fast part of the model only describes the displacement of wolves between the two patches whereas, at slow time scale, the evolution of the wild boar and wolf populations is described by a classical predator–prey system including (i) a logistic growth of the prey with Allee effect; (ii) a linear functional response for predation and (iii) a harvesting density dependent term for the human control on the wild boar population. We stress that the control on wild boars has also the effect of increasing the mortality rate of the wolf population in patch1 by the rate $qE$. Moreover, it was assumed that in patch2 – where no wild boars are present – mortality was the prominent process (with respect to other demographic processes that are here considered as negligible) and also that it occurred at a slow time scale. In this regard, one can obviously ask what interest the wolves that inhabit patch1 would have in moving back to patch2. The most probable reason is likely to be the specific habitat features of Dauni Mountains that, in spite of the absence of prey, would justify the presence of wolves in this site. It is well known that wolves are habitat generalists and, in addition to prey abundance, secluded sites and relatively low levels of human activity are general habitat requirements for wolves (Fish and Service, 1987). A study by Mladenoff et al. (1995) in the northern Great Lakes Region (USA) showed for example that low densities of roads and low fractal dimension of vegetation patches were the most important predictors of wolf colonization in logistic regression models. Moreover, wolf pack territories were shown to be negatively correlated with amounts of agricultural land, road density, human population density and positively correlated with coniferous forest cover and county-managed forest lands (Mladenoff et al., 1999).

In the framework of the present model, a further point that deserves a deeper explanation is the meaning that we attach to the word migration. Migration can in fact take a number of forms and has been described by ecologists in many different ways. We stress that the word migration refers here to a form of individual movement. Movements can generally occur either within the animal home range or can take the individual beyond it (Dingle, 1996). The behavior known as ‘station keeping’ (Kennedy, 1985), belongs to the formers kind of movements: it is mainly concerned with finding and appropriating resources, (e.g. food, mate, etc.) and typically occurs on short timescales and small spatial scales. Its extended form – known as ‘commuting’ – regards longer to-and-fro journeys that are made regularly (often daily) to spatially separated resource patches, roost sites and other localities, within the home range, where specific activities occur (Dingle and Drake, 2007; Dingle, 1996). In the present model, we denote the latter type of movements with the term migration. Moreover, given the dispersal distances of 30–60 km traveled by a wolf at constant rate of 6–10 km/h per day (Tardio, 2011), and since the minimum distance between the two patches is less than 30km, the wolf migration between Alta Murgia and Dauni Mountains can be reasonably considered as a daily one.

2.2. Parameters selection

The model parameters have been selected as follows:

- $A$: Allee threshold. From a preliminary analysis of the literature we found that the evaluation of the minimum viable self-sustaining wild boar population size produces somehow inconsistent results. However, some empirical assessments were done on the specific case. From available data, a reasonable minimum size was 68, i.e. the minimum of the two animal amounts released in Gravina and Spinazzola, respectively. This size was consistent with the numbers given in Leaper et al. (1999), where

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the authors estimated a minimum size in the range 25–50, and the minimum of 75 animals provided by Howells and Edward-Jones (1997) in their model without inbreeding depression. Since the woodland occupies 110 km² of the total area of Alta Murgia Park, in terms of density we have $A = 68/110 = 0.6182$ individuals per km².

- $k$: carrying capacity. In PGC (2012), the number of individuals counted in each sample area of the park is reported. The maximum density registered therein was 120 individuals per km² (Masserie Nuove site) and it was assumed as the carrying capacity for the site.

- $a_1$: predation coefficient. By supposing that the intake of biomass was entirely provided by wild boars, a wolf was estimated to consume 13.3 wild boars annually (Noreis et al., 2008). By supposing that this predation corresponds to the prey carrying capacity, from the relation $a_1 = 13.3$ we obtained an estimated value of $a_1 = 0.1108$ km²/year per individual.

- $r$: wild boar growth rate. During the years of the restocking program, the wild boar dynamics in the Alta Murgia Park was supposed to be described by the simplified equation

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{A}\right) \left(\frac{n}{A} - 1\right).$$

The initial wild boar density in early 2000 corresponds to the first introduction of 20 individuals into the area. We set $n(2000) = 20/110$ and we simulated the dynamics until early 2001 when additional 47 individuals were introduced. Hence, by starting with density set to $n(2001) = 47/110$ we followed the dynamics through the years. In order to take into account the last introduction of 105 individuals carried out in 2002, the model (2) was used with an initial wild boar density set to $n(2002) = 105/110$. Since 2004, when the first tracks of the wolves were discovered, a different simplified model

$$\frac{dn}{dt} = rn \left(1 - \frac{n}{A}\right) \left(\frac{n}{A} - 1\right) - a_1 np_1,$$

was considered where a constant wolf presence with density equal to $p_1 = 4/110$ was supposed. In so doing, we were able to estimate $r$ by minimizing the norm of the error among the predicted values in 2010, 2011 and 2012 and the estimated values deduced by the census made by the Park Authority in the same years. The result provided an optimized value of $r = 0.0484$ year⁻¹. In Fig. 2 we illustrate the simulation of the wild boar population growth starting from the first introduction in 2000 until 2012 in correspondence with this optimized value. All the above data can be found in PGC (2012).

- $\mu$: wolf death rate. We supposed the value of $\mu$ to be 0.12 year⁻¹ (Knickerbocker, 2013).

- $e$: the conversion coefficient. We assumed $e = 0.028$ (Knickerbocker, 2013), by supposing that the conversion coefficient related to wild boars was five times greater than the value related to elks. To justify this last assumption, we observe that the conversion of prey into predator biomass is related to a number of different factors which include the average size of the wolf packs, the size of the prey and its social behavior. When the predation is done by a large pack, added members of the wolf pack eat portions of prey that would be lost to scavengers if pack size were reduced to a single individual. So the rate of conversion into predator biomass of one big prey, is different whether the predator acts in a pack or not. The common situation in Alta Murgia was currently a predation done by a single wolf. Given that premise, we remind that wild boars usually live in groups with one or more adult females and numerous puppies, and that the average size of a wild boar in such groups is about five times smaller than the average elk size. It was then reasonable to assume that the food intake and the biomass conversion of wild boars, resulting from predation in the case at hand, was about 5 times the one for elks (Mech and Boitani, 2006).

All the parameters with their numerical values have been summarized in Table 1 where we reported also the related sources.

### 3. Results and discussion

In the following we illustrate a preliminary numerical investigation performed on the full model (1). That in order to set a term of reference for the behavior of the reduced system obtained by means of the aggregation method. Thereafter, we describe the aggregated model and qualitative scenarios which were built on it. Potential implications for the wolf conservation policies are the subject of the next section.

#### 3.1. A preliminary numerical investigation of the full model behavior

Numerical investigations on the full model (1) were performed in Matlab by using the built-in function ode15s with absolute and relative tolerances set to $10^{-15}$ and $10^{-13}$, respectively. This choice was motivated by the necessity to tackle stiffness in differential equations due to the presence of two different time scales.

We started by setting the fast time scale migration dynamics in day units and the slow evolution in year units, corresponding to $e = 1/365$. We also assumed that the initial value for wild boar population in the Alta Murgia patch was the estimated density value provided by the census in 2012 that is $n(2012) = 1540/110 = 14$ (PGC, 2012). The densities of wolves population in the Alta Murgia and the Monti Dauni sites in 2012 are $p_1(2012) = 4/110 = 0.0363$ (PGC, 2012), and $p_2(2012) = 25/1247 = 0.02$ respectively (Pennacchioni, 2010), where 25 is the number of wolves (5 packs with an estimated value of 5 wolves per pack) at the Monti Dauni site (Pennacchioni, 2010), whose extension corresponds to 1247 km² (PPTR, 2013). Therefore, we considered these values as our realistic initial conditions for the preliminary investigation of the long-term behaviors of system (1). The model variables, their initial values and their related qualitative description have been summarized in Table 2.

The numerical simulations presented in Figs. 3 and 4 yield the following results. The wolf population survival through coexistence was attained by a stable equilibrium as shown in Fig. 4(a) or, as in
Table 1
Parameter values used in simulations and the related sources.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Units</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_1$</td>
<td>Predation coefficient</td>
<td>0.1108</td>
<td>km$^2$ year$^{-1}$ N$^{-1}$</td>
<td>Nores et al. (2008)</td>
</tr>
<tr>
<td>$r$</td>
<td>Wild boar growth rate</td>
<td>0.0484</td>
<td>year$^{-1}$</td>
<td>Census data</td>
</tr>
<tr>
<td>$e$</td>
<td>Conversion coefficient</td>
<td>0.0280</td>
<td>Dimensionless</td>
<td>Knickerbocker (2013)</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Wolf death rate</td>
<td>0.12</td>
<td>year$^{-1}$</td>
<td>Knickerbocker (2013)</td>
</tr>
<tr>
<td>$k$</td>
<td>Carrying capacity</td>
<td>120</td>
<td>N km$^{-2}$</td>
<td>Leaper et al. (1999)</td>
</tr>
<tr>
<td>$A$</td>
<td>Allee threshold</td>
<td>0.6182</td>
<td>N km$^{-2}$</td>
<td>Leaper et al. (1999)</td>
</tr>
<tr>
<td>$q$</td>
<td>Catchability coefficient</td>
<td>1</td>
<td>year$^{-1}$</td>
<td>Assumed</td>
</tr>
</tbody>
</table>

Table 2
Variables of the models with initial values and related sources.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Initial value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$p_1$</td>
<td>Wolf density in the Alta Murgia Park (patch1)</td>
<td>0.0363</td>
<td>PGC (2012)</td>
</tr>
<tr>
<td>$p_2$</td>
<td>Wolf density in the Dauni Mountains site (patch2)</td>
<td>0.02</td>
<td>Pennacchioni (2010)</td>
</tr>
<tr>
<td>$n$</td>
<td>Wild boar density in the Alta Murgia Park</td>
<td>14</td>
<td>PGC (2012)</td>
</tr>
<tr>
<td>$p$</td>
<td>Total number of wolves</td>
<td>0.0563</td>
<td>Pennacchioni (2010)</td>
</tr>
</tbody>
</table>

Fig. 4(b) and (c), by small stable periodic oscillations. In the long-term behavior, extinction for both the species was found in Fig. 3(a) and in Fig. 4(d), whereas in Fig. 3(b), only wild boar population survival was observed.

3.2. The aggregated model

As previously stated, the presence of two different time scales (years/day) gave the chance to benefit from the general theoretical approach known as aggregation method (Auger et al., 2007). This allowed for the reduction of the dimension of the two-patch model (1) through a reduced one-patch system describing the dynamics of a smaller number of global variables.

We defined $p = p_1 + p_2$ as the total amount of wolves and $v_1 = p_1 / p$ and $v_2 = p_2 / p$ as the fraction of wolves in patch1 and patch2, respectively. Model (1) was rewritten as:

$$
\frac{dn}{dt} = e n [r \left(1 - \frac{n}{k}\right) \left(\frac{n}{A} - 1\right) - a_1 v_1 p - q E],
$$

$$
\frac{dv_1}{dt} = d_2 - v_1 (d_1 + d_2) + e v_1 (1 - v_1)(e a_1 n - q E),
$$

$$
\frac{dp}{dt} = ep[-\mu + ea_1 v_1 n - q E v_1].
$$

The first step was to consider the equilibrium value of the fast variable $v_1$, i.e. the so-called fast equilibrium. This was obtained by neglecting the slow dynamics in system (4). Then the fast equilibrium was given by $v_1^* = d_2 / (d_1 + d_2)$. By substituting $v_1^*$ in the first and the third equation of system (4), we obtained the following two-dimensional system which approximately describes the dynamics of the total population densities $n$ and $p$:

$$
\frac{dn}{dt} = n \left[ r \left(1 - \frac{n}{k}\right) \left(\frac{n}{A} - 1\right) - a_1 dp - q E \right],
$$

$$
\frac{dp}{dt} = p[-\mu + ea_1 dp - q Ed],
$$

where the positive parameter $d$ is given by

$$
d = \frac{d_2}{d_1 + d_2},
$$

and represents the stable fraction of predators in patch1 (Alta Murgia Park), attained at the fast time scale. We observe that such a parameter $d$ can be interpreted as the relative migration rate from patch2 (Dauni Mountains site) to patch1 (i.e. the ratio between the migration rate $d_2$ and the total migration rate $d_1 + d_2$) and can hence be thought as an interesting ecological indicator since it can be indirectly related to the existence of ecological corridors between patches. The description of parameters $E$, $d_1$, $d_2$ and $d$ has been summarized and reported in Table 3.

3.3. Qualitative scenarios from the aggregated model

We recall that if system (5) is structurally stable and the parameter $e$ is small enough, the dynamics of the aggregated model is a good approximation of the dynamics of the global variables in the full system (1).

Theoretical investigations on the aggregated model (5) have been presented in Appendix A. We considered as bifurcation parameters both the parameter $d$, which is related to the wolf migration processes between patches, and the parameter $E$ which represents the effort of the human control on the wild boar population. It turned out that, according to the specific choice for the bifurcation parameters, three kinds of equilibria are possible: the predator–prey extinction equilibrium $P_0 = (0, 0)$; the predator’s extinction equilibria $P_1 = (n_1, 0)$ and $P_2 = (n_2, 0)$; the coexistence equilibrium $P^* = (n^*, p^*)$.

The predator–prey extinction equilibrium $P_0$ is stable for every parameter values whereas the predator’s extinction equilibria $P_1$ and the coexistence equilibrium $P^*$ can be stable or unstable according to the specific choice of the parameter values. In this regard, a remarkable feature is that – under certain conditions – the coexistence equilibrium can lose its stability by the means of an Hopf bifurcation when the control parameter $E$ reaches the threshold value $E_{th}$. The importance of this kind of bifurcation is well known in the ecological literature since – when supercritical – it produces the occurrence of self-sustained oscillations in the system dynamics (Kot, 2001). With reference to the present case study, the supercritical nature of the Hopf bifurcation occurring at $E = E_{th}$ has been established by the means of numerical investigations which have revealed the occurrence of stable small amplitude oscillations surrounding the unstable equilibrium $P^*$ in the neighborhood of the Hopf threshold.

The relevant $d$ and $E$ thresholds, derived in Appendix A and related to the existence and stability properties of the equilibria, have been summarized in Table 4.
Fig. 3. Long-term behaviors of the full model (1) with different parameter sets. (a) \( E = 2.4 \) and \( d_1 = 4, d_2 = 1 \). (b) \( E = 0.2 \) and \( d_1 = 1.5, d_2 = 1 \). The other parameter values are fixed as in Table 1. For the reasons detailed in the text, the chosen initial conditions are: \( n(0) = 14, p_1(0) = 0.0363 \) and \( p_2(0) = 0.02 \). In (a) it is shown that, following a brief transient, the wild boar population \( n(t) \) and the wolf population become extinct in both the patches \( p_1(t) \) and \( p_2(t) \). In (b) it is shown that, after a rather long transient, the wolf population become extinct in both the patches \( p_1(t) \) and \( p_2(t) \), whereas the wild boar population \( n(t) \) tends to its carrying capacity.

Fig. 4. Long-term behaviors of the full model (1) with different parameter sets. (a) \( E = 0.1 \) and \( d_1 = 0.667, d_2 = 1 \); (b) \( E = 0.0537 \) and \( d_1 = 0.111, d_2 = 1 \); and \( E = 0.05 \). The other parameter values are fixed as in Table 1. For the reasons detailed in the text, the chosen initial conditions are: \( n(0) = 14, p_1(0) = 0.0363 \) and \( p_2(0) = 0.02 \). In (a) it is shown that wild boar population \( n(t) \) and the wolf population in both the patches, \( p_1(t) \) and \( p_2(t) \), tend to a stable coexistence equilibrium. The asymptotic behavior is achieved after a rather long transient. In (b) it is shown that, after a relatively brief transient, coexistence among wild boars and wolves is obtained through stable small amplitude periodic oscillations. In (c) the simulation, carried out for very long times, shows in details that the coexistence is obtained via a persistent oscillatory dynamics. In (d) it is shown that, after a relatively brief transient, the wild boar population \( n(t) \) and the wolf populations \( p_1(t) \) and \( p_2(t) \) become extinct.

Table 3
Control parameters of the models with the related description.

<table>
<thead>
<tr>
<th>Control parameter</th>
<th>Description</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>( d_1 )</td>
<td>Wolf migration rate from patch1 to patch2</td>
<td>year(^{-1})</td>
</tr>
<tr>
<td>( d_2 )</td>
<td>Wolf migration rate from patch2 to patch1</td>
<td>year(^{-1})</td>
</tr>
<tr>
<td>( E )</td>
<td>Effort of the control</td>
<td>year(^{-1})</td>
</tr>
<tr>
<td>( d )</td>
<td>Relative migration from patch2 to patch1 ((d = d_2/(d_1 + d_2)))</td>
<td>Dimensionless</td>
</tr>
</tbody>
</table>
Table 4  
d and E bifurcation thresholds with the related qualitative and mathematical descriptions.

<table>
<thead>
<tr>
<th>d and E thresholds</th>
<th>Description</th>
<th>Math. description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\delta_{\text{low}}$</td>
<td>Existence threshold for $P'$</td>
<td>Formula (A.10)</td>
</tr>
<tr>
<td>$\delta_{\text{stab}}$</td>
<td>Stability threshold for $P'$</td>
<td>Formula (A.11)</td>
</tr>
<tr>
<td>$E_{\text{cr}}$</td>
<td>Existence threshold for $P_1$ and $P_2$</td>
<td>Formula (A.8)</td>
</tr>
<tr>
<td>$E_{\text{crit}}$</td>
<td>Hopf threshold for $P'$</td>
<td>Formula (A.11)</td>
</tr>
</tbody>
</table>

![Figure 5](image.png)  
Fig. 5. Dynamical scenarios of the aggregated model (5) as function of the wolf migration processes between patches (i.e. parameter $d$) and of the effort of the human control on the wild boar population (i.e. parameter $E$). The other parameter values are fixed as in Table 1. The different dynamical scenarios of the system are represented through the two-parameter bifurcation diagram in the plane $(d, E)$ with $0 < d < 1$. For the chosen parameter values, the $d$ thresholds assume the following values: $d_{\text{low}} = 0.3223$, $d_{\text{stab}} = 0.6413$. The bifurcation curves $E = E_{\text{crit}}(d)$ are transition curves between different scenarios and divide the $(d, E)$ plane in four regions: (i) Region 0 in which both the wolf and the wild boar population will be extinct; (ii) Region I in which wolf population will be extinct in any case; (ii) Region II in which, according to the initial conditions, either wolf extinction or wolf survival via a stable coexistence equilibrium is expected; (iii) Region III in which, according to the initial conditions, (a) wolf extinction or (b) wolf survival through small amplitude periodic oscillations in the strict neighborhood of the Hopf bifurcation line $E = E_{\text{crit}}(d)$ are expected.

With parameters in model (5) chosen as in Table 1, the above $d$ thresholds become: $d_{\text{low}} = 0.3223$, $d_{\text{stab}} = 0.6413$. Recalling (6), it also follows that $0 < d < 1$ and hence we considered $d = 1$ as the maximum feasible value for the parameter $d$. As far as the $E$ thresholds are concerned, we observe that $E_{\text{stab}}$ does not depend on the parameter $d$ and is such that $E_{\text{stab}} = 2.32$. On the contrary, $E_1$ and $E_2$ are both functions of $d$ and are such that, when $d > d_{\text{low}}$, $E_1 = E_1(d) < 0$ and $E_2 = E_2(d) > 0$. The Hopf threshold $E_{\text{crit}}$ also depends on $d$ and turns out to be strictly positive if and only if $d > d_{\text{crit}}$.

The bifurcation curves $E = E_{\text{crit}}$, $E = E_2(d)$ and $E = E_{\text{crit}}(d)$ divide the $(d, E)$ plane in four regions. As a consequence, the existence of four dynamical scenarios can be proved, as depicted in Fig. 5 where the different dynamics of the aggregated model (5) are shown as functions of the two bifurcation parameters $d$ and $E$.

In Fig. 5, the regions in the $d - E$ parameter space where wolf population survival can be ensured were labeled as Region II and Region III. Inside these regions, wolf population survival can occur in two different ways since system dynamics can approach a stable coexistence equilibrium (Region II) or a stable coexistence limit cycle for $d$ and $E$ in the strict neighborhood of the Hopf bifurcation line $E = E_{\text{crit}}(d)$ (Region III). However both Region II and III also have wolf extinction as a possible output: in fact, whether the wolf population will survive or will be extinct depends on the chosen initial conditions. On the other hand, in Region 0 or in Region I, there is no chance of survival for the wolf population.

In particular, in Region 0 which corresponds to very high values of the control parameter $E$ - both the wolf and the wild boar population will be extinct independently of the value of the parameter $d$. Moreover, as showed in Fig. 6, the wolf extinction equilibrium $P_1$, whatever existing and ecologically meaningful (namely in Regions I, II, III), is always unstable. On the contrary, the wolf extinction equilibrium $P_2$ is stable in Region I and unstable in Regions II and III.

In Table 5 we have summarized the existence and stability properties of the equilibria of the aggregated model (5) in the four regions of the two-parameter bifurcation diagram in Fig. 5.

In conclusion, the bifurcation diagram in Fig. 5 indicates that (i) too high values of the control parameter $E$, i.e. $E > E_{\text{stab}}$, lead both the species toward extinction independently of the value of the parameter $d$ (Region 0); (ii) too low values of the parameter $d$, i.e. $d < d_{\text{low}}$, can lead either to only wolves extinction (Region I) or to both wild boar and wolf populations extinction (Region 0), according to the specific value of the control parameter $E$; (iii) wolves
survival is possible only in Region II in which coexistence between wolf and wild boar populations can be ensured through a stable coexistence equilibrium or in Region III where, in the strict neighboring of the Hopf bifurcation line, coexistence can be obtained via a stable small amplitude limit cycle. Away from the Hopf line, the amplitude of oscillations tends to increase and this portion of Region III is hence not a good one. In fact large amplitude oscillations should be prevented since environmental fluctuations could lead to the extinction of the wolf population.

The numerical simulations presented in Figs. 3 and 4 show a complete qualitative match between the theoretical scenarios obtained through the aggregated model (5) and the dynamics of the full model (1). In fact, recalling the definition of d provided in (6), population coexistence has been attained through a stable equilibrium in Fig. 4(a) where the parameters $E = 0.1$ and $d = 0.6$ lie in Region II. Coexistence has been achieved through small stable periodic oscillations in Fig. 4(b) and (c) where the parameters $E = 0.0537$ and $d = 0.9$ have been set in Region III, in the strict neighboring of the Hopf bifurcation line. Extinction for both the species has been found in both Fig. 3(a) and Fig. 4(d), where the parameters $E$ and $d$ have been chosen in Region $0 (E = 2.4, d = 0.2)$ and in Region III ($E = 0.05, d = 0.9$) far from the Hopf bifurcation line, respectively. Instead, in Fig. 3(b) only wild boar population survival is expected in the long-term behavior, since the parameters $E = 0.2$ and $d = 0.4$ lie in Region I. Because of the qualitative matching outlined above, we are allowed to use the bifurcation diagram of the aggregated system (5) depicted in Fig. 5, to discuss the dynamical scenarios of the full model (1).

A closer look at the dynamics of system (5) (and, hence of model (1)) suggests that – from the point of view of the control strategies – Region II can be further divided in two different sub regions: a Security Region and a Risky Region, Fig. 7.

The Security Region is characterized by sufficiently low $E$ values and intermediate $d$ values, i.e. $d_{low} < d < d_{stag}$ and $0 < E < E_2$. It represents the perfect region since it allows a monitoring of the control strategies. In fact, for a fixed value of $d$ in the Security Region, coexistence can be ensured by keeping the value of $E$ below $E_2$. For $E$ tending toward $E_2$, the wolf population level progressively decreases until it approaches zero entering Region I. In this case, a careful monitoring of the control policy can avoid wolf extinction by lowering $E$ below the $E_2$ threshold.

Coexistence can be ensured via a stable equilibrium also in the Risky Region. However such a region could be associated to a more dangerous situation in terms of control perspectives. In fact, for a fixed $d$ value in the Risky Region, specific changes into the $E$ level can lead to the sudden collapse of both the wild boar and wolf population. To better elucidate this point, suppose an ecological situation belonging to the Risky Region and labeled with the point A in Fig. 7. If a higher removal level is decided by the authorities for the wild boar population, then system dynamics can be brought progressively toward wolf extinction (point $D$, in Region I). However, also in this case, a careful planning of the control policy can avoid wolf extinction by lowering $E$ below the $E_2$ threshold. But what happens if the control level is set too low? Going well into Region III, you can suddenly pass from coexistence to extinction for both the species, (point $B$, in Region III) and, in this case, wolf survival is not necessarily guaranteed. As a consequence, although the Risky Region could ensure coexistence between wild boar and wolf populations, it would be wiser to avoid such a situation, preferring the safer Security Region. This can be obtained by properly reducing the value of the parameter $d$, for example reaching the point $C$ in Fig. 7.

We refer to Section 3.4 for discussions on the practical implications of this choice.

Such reasoning was insightfully expressed in terms of the basins of attraction of the involved system attractors. We recall that the basin of attraction of a given attractor (i.e. a stable equilibrium, a stable limit cycle) is the set of initial conditions which leads to the long-time behavior that approaches that attractor (Guckenheimer and Holmes, 1997). This means that the qualitative long-time behavior of a given system can be significantly different according to which domain of attraction the considered initial condition lies.

Fig. 8 shows that if we are in the Risky zone of Region II (point A in Fig. 7) we clearly have a bistability situation with two different basins of attraction. The smaller one (the green region) is related to the coexistence equilibrium $P^*$ and the other one (the red region) is related to the two species extinction equilibrium $P_0$. By suitably reducing the value of the parameter $d$, we can move into the Security zone of Region II (point C in Fig. 7) and – although the two system’s attractors remain the same – we can note a difference in terms of the related basins of attraction since the basin of attraction of the coexistence equilibrium $P^*$ considerably enlarges in the Security Region, thus suggesting a situation of higher ecological resilience (van Nes and Scheffer, 2007). Interestingly, this also implies that a stochastic event could move the system in an alternative basin of attraction less likely in the Security zone than in the Risky Region.

Fig. 8 also clarifies that if we are in the Risky Region (point A in Fig. 7) and reduce the effort of human control on the wild boar population (i.e. decreasing the $E$ values), we enter Region III (point B in Fig. 7) with two possible outputs: (i) if $E$ is slightly reduced, coexistence is still possible by the means of an oscillatory dynamics. Panel Region III (NH) in Fig. 8 shows the basins of attraction related to this

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Table 5
The aggregated model (5). Existence and stability properties for the equilibria of the aggregated system (5) in the four regions of the two-parameter bifurcation diagram in Fig. 5.

<table>
<thead>
<tr>
<th>Region</th>
<th>$P_0$ stable</th>
<th>$P_1$ stable</th>
<th>$P_2$ stable</th>
<th>$P_3$ stable</th>
</tr>
</thead>
<tbody>
<tr>
<td>Region 0</td>
<td>$P_0$ stable</td>
<td>$P_1$ unstable</td>
<td>$P_2$ unstable</td>
<td>$P_3$ stable</td>
</tr>
<tr>
<td>Region I</td>
<td>$P_0$ unstable</td>
<td>$P_1$ unstable</td>
<td>$P_2$ unstable</td>
<td>$P_3$ unstable</td>
</tr>
<tr>
<td>Region II</td>
<td>$P_0$ stable</td>
<td>$P_1$ unstable</td>
<td>$P_2$ unstable</td>
<td>$P_3$ unstable</td>
</tr>
<tr>
<td>Region III</td>
<td>$P_0$ unstable</td>
<td>$P_1$ unstable</td>
<td>$P_2$ unstable</td>
<td>$P_3$ unstable</td>
</tr>
</tbody>
</table>

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Fig. 7. A detail of the $(d, E)$ bifurcation diagram in Fig. 5 which specifically focuses on Region II. The bifurcation parameter $d$ is related to the wolf migration processes between patches whereas the bifurcation parameter $E$ represents the effort of the human control on the wild boar population. In Region II coexistence between wolf and wild boar population can be ensured through a stable equilibrium. Theoretical results suggest that, from the point of view of the control strategies, such region can be divided in two different sub regions: a Security Region and a Risky Region. (For interpretation of the references to color in text, the reader is referred to the web version of the article.)

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case: the smaller (light green region) refers to the stable limit cycle born by supercritical Hopf bifurcation in the neighboring of the now unstable equilibrium $P^2$; the other one (red region) represents the two species extinction equilibrium $P_0$ (ii) whenever $E$ is greatly reduced, the bistability situation ceases and system dynamics tends toward the unique system attractor which drives both the species to extinction, Panel Region III (AH). Both these situations should be looked upon with some caution: the former because of the potential for oscillatory behavior to trigger extinction when stochastic forces are involved (May, 1972), the latter because it represents a sharp transition toward extinction.

Finally, Fig. 8 outlines that if we are in the Risky Region (point A in Fig. 7) and – acting unwisely – we increase the amount of human control on the wild boar population (i.e. increasing the $E$ values), we enter Region I (point D in Fig. 7) where a bistability situation occurs between the two species extinction equilibrium $P_0$, whose basin of attraction is the red region, and the only wolf extinction equilibrium $P_2$, whose basin of attraction is the light red region (Panel Region I in Fig. 8).

3.4. Implications for the conservation of the wolf in the Alta Murgia Park

The achieved results strongly suggest that Region II may represent the most desirable situation in terms of a sustainable management of the wolves in the Alta Murgia Park. In this regard, we can identify those factors crucial for wolf conservation: human wild boar control and wolf migration. Indeed, a careful combination of processes such as human control of the wild boar population – through proper planning programs – and wolf migration between patches – through the existence of suitable ecological corridors – should be used in order to properly limit the wild boar population while preserving the wolf population from extinction.

Our findings give some qualitative warnings for the specific case study. In primis, either too low $d$ values and high $E$ values have to be avoided. Moreover sufficiently low values of the control parameter $E$ have to be combined with intermediate values of the migration parameter $d$ in order to ensure coexistence between the wolf and wild boar populations and hence wolf survival in the Alta Murgia Park.

Now, the obvious question is: which Region in the two-parameters bifurcation diagrams of Figs. 5 and 7 can currently represent the Alta Murgia case? As far as the parameter $d$ is concerned, we observe that it can be reasonable to suppose that the densities of wolf population in Alta Murgia and Monti Dauni sites in 2012 correspond respectively to the fast equilibria $d_2$ and $d_3$ of the full model (1). It follows that $d_2 = 0.0363$ and $d_3 = 0.02$ so that – according to (6) – one gets $d = 0.6446$. Recalling the formula (A.8), it follows that the threshold $E_2 = 0.1788$.

Moreover, as explained above, the parameter $E$ is related to the abatement level of wild boars decided by the management authority of the Alta Murgia Park. In the official act of 2012, an abatement proposal was launched to reduce the estimated population of 1540 individuals to a value in the range 550–839. By choosing the maximum value for the huntability coefficient $q$ (i.e. $q = 1$), such abatement can be estimated with values of $E$ in the range $E_{min}, E_{max}$ where $E_{min} = \log(1540)/839 = 0.673$ and $E_{max} = \log(1540)/550 = 1.0296$. For this chosen value of the parameter $d$, the considered range $E_{min}, E_{max}$ is such that $E_{min} > E_2$ and our analysis predicts the extinction of the wolf population as a long-term system behavior. We are in fact in Region I of Fig. 5. Our results suggest that, to ensure wolf population survival, we have to enter the coexistence Region II. To this aim, the value of the effort $E_{max}$ should hence be lowered below the threshold value $E_2$. Such findings are completely confirmed by numerical investigations on the full model (1). Fig. 9 shows how a situation of wolf extinction, corresponding to the effort value $E = E_{min} = 0.673$, can be avoided simply by lowering the effort $E$ to the level $E = 0.16$. However, even in this last situation, we would be in the Risky zone of Region II whereas, for a sustainable management of the wolf and wild boar populations, it
would be preferable to move into the security zone of Region II. Still keeping $E = 0.16$, this can be obtained by acting on the parameter $d$ which has hence to be lowered below the threshold $d_{\text{opt}} = 0.6413$. Since the parameter $d$ is related to the existence of ecological corridors between the Alta Murgia and the Dauni Mountains sites, this last observation could throw new light on the role of the ecological corridors for species survival in multi-patch environments.

A suitable control policy could be designed by acting on either the corridors or the abatement rate or on both. In the case of the Alta Murgia Park where the managing authorities have little – if any – control on the corridors, our findings may recommend the monitoring of corridors to provide estimation of migration rates. Since we are dealing with ‘natural’ corridors, their control is mainly related to the impact of human activities and to the alterations of the landscape generated by changes in the land use and land cover (new roads, different agricultural practices, reforestation, poaching), which might be managed to some extent. Our study also highlights qualitative estimates on the strength of the abatement rate in order to favor the onset of a coexistence equilibrium of the two species, advising that the wild boar abatement proposal by the Apulian regional authorities should not be too severe if one has to ensure a long-term survival of wolf population in the Alta Murgia Park. Moreover, by looking at the structure of the coexistence equilibrium (A.6) that represents the asymptotic level to which the abundances of the predator and prey populations will tend for extremely long times, it is possible to observe that the long-term effect of increasing the control parameter $E$ is to increase the average wild boar population level and to decrease the average wolf population level. Even if for certain aspects counterintuitive, this result can be interpreted as a clear admonition against non-specific control measures that affect indistinctly both preys and predators with possible catastrophic consequences (De Bach, 1974; Kot, 2001).

A further interesting result is the evidence of an ambivalent role of the corridors for the wolf and wild boar dynamics. We point out that the spread and impact of antagonistic species, i.e. predators, is generally considered as a negative effect of corridors connecting otherwise separated habitat patches. This effect turns out to be highly wanted, of course, if the antagonistic species are the endangered and protected ones, whereas the preys are of no interest with respect to conservation policies, as in our case. Recent studies (e.g. Haddad et al., 2014), have shown that the effect of corridors on the predator–prey dynamics and the coexistence conditions does not have a definite sign: negative, neutral and positive effects are all likely to occur and there is currently no theoretical approach capable to explain that. This appears to be a point in favor of our model which stresses this double-role of ecological corridors and suggests the existence of different dynamical scenarios which qualitatively match behaviors actually observed in nature.

However, for the model to provide quantitative estimations useful for management purposes, some key processes have to be explicitly included. First of all, stochasticity. In fact, although deterministic models are sufficient to predict average behaviors at the population level, stochasticity is critical for small populations and could intervene in several processes such as control, population growth, predation strength and, more importantly, migration that is here considered as individual movements between patches. Besides, wolves are reported to have a very strong social structure and a more careful description of the development stages should be considered in the model. Enriching the system with compartments referring to an age structure (young/adults) and to a sex structure (male/female) may in fact significantly influence the population dynamics involved. This feature can in particular affect migration since differences have been observed in migration patterns of older and younger individuals or of individuals of the two sexes. Last but not least, a more realistic description of the control process has to be developed. In fact in the model the control of wild boars is considered as a continuous process but it should be more realistically modeled as a discrete event since the actual control procedures are based on the calculation of quotas on annual basis.

4. Concluding remarks

We have used a modeling approach to gain qualitative insights for the management of the wild boar and wolf population dynamics in the Alta Murgia Park. For this purpose, a two-patch predator–prey model has been considered where both migration processes between patches and prey control policies have been

Fig. 9. Long-term behaviors of the full model (1) when the parameters $d_1$, $d_2$ and $E$ are chosen so that the parameters $d$ and $E$ are (a) $E = E_{\text{min}} = 0.673$ and $d_1 = 0.02$ $d_2 = 0.0363$ so that $d = 0.6446$; (b) $E = 0.16$ and $d_1 = 0.02$ $d_2 = 0.0363$ so that $d = 0.6446$. The other parameter values are fixed as in Table 1. For the reasons detailed in the text, the chosen initial conditions are: $n(0) = 14$, $p_1(0) = 0.0363$ and $p_2(0) = 0.02$. In (a) it is shown that, after a brief transient, the wild boar population $n(t)$ and the wolf population in both the patches $p_1(t)$ and $p_2(t)$ become extinct. In (b) it is shown that, after a rather long transient, the wolf populations $p_1(t)$, $p_2(t)$ and the wild boar population $n(t)$ coexist via a stable equilibrium.
taken into account. The full model has been simplified by applying the aggregation model to get a reduced dynamical system whose properties have been theoretically analyzed. Numerical investigations on the two-patch model have provided evidence of the capability of the reduced system to mimic the dynamics of the full model with respect to equilibria and stability properties. In addition, we have showed the existence of four different dynamical scenarios which suggest that a suitable control policy could be designed by acting on either the corridors or the abatement rate or on both. In the case of the Alta Murgia Park our findings may recommend the monitoring of corridors to provide estimations of the migration rates.

We stress that the proposed model is meant to be used as a means for qualitative scenario building more than as a quantitative tool to support environmental decision making on protection policies. This is because of the many assumptions that make model quantitative estimations not fully reliable for practical purposes. This is perfectly consistent with the modeling framework used in this paper, the top-down approach, where one starts with a simple, deterministic, macroscopic description and then adds successive levels of details. With reference to the present case study, enriching our model with elements such as stochasticity, sex/age structure and more refined control procedures, corresponds to increasing the complexity of its mathematical representation and of the related theoretical analysis to the point that some results could only be obtained with the help of case-dependent numerical simulations. On the other hand this case-oriented implementation would seem to limit the overall theoretical power of the model as a means to understand general ecological principles and patterns but, on the other hand, it could significantly refine the capability of quantitative estimates on the specific case under examination. This is a clear example of how developing realistic ecological models for practical decision support is indeed a complex and challenging task, often requiring a very careful and calibrated compromise between the top-down and the bottom-up modeling approaches.

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Appendix A. The aggregated model: equilibria and stability properties

In this mathematical appendix we analytically derive the thresholds, expressed in terms of the system parameters, for the existence and stability properties of the equilibria. The following results hence provide the theoretical bases for the dynamical scenarios described in Section 3.3 for the specific case study.

Preliminary remarks – Let us introduce the following threshold quantity for the control parameter $E$,

$$E_{of} = \frac{r_k (k-A)^2}{4 Ak^2},$$  \hspace{1em} (A.1)

and further consider the threshold quantities for the wild boar intrinsic growth rate parameter $r$,

$$r_{1/2} = k A e a \frac{(k-A)^2}{2 \sqrt{Ak}},$$  \hspace{1em} (A.2)

$$r_r = e a / k A (k-A)^{-1}.$$  \hspace{1em} (A.3)

It is easy to recognize that $r_1 < r_r < r_2$. As a preliminary step let us introduce the quantities

$$C_1 = 4 r_k^2 \mu e a^2 k A,$$

$$C_2 = q^2 \mu e a^2 [r^2 (k-A)^2 - 2 r_k A k + A + e a^2 k^2 A^2].$$

and observe that $C_1$ is always a positive quantity whereas $C_2 > 0$ for

Existence results – The following result allows us to get an insight into the different kinds of equilibria of the aggregated model:

**Theorem Appendix A.1.** The aggregated model

(i) admits the extinction equilibrium $P_0 = (0, 0)$ for every value of the positive parameter $E$ and the predator’s extinction equilibria $P_1 = (n_1, 0)$ and $P_2 = (n_2, 0)$ for $0 < E < E_{of}$.

(ii) admits a feasible coexistence equilibrium $P^* = (n^*, p^*)$ if one of the following cases (ii.a)–(ii.d) holds:

(ii.a) Let $r > r_1$ and $\mu / (eaA)$. Then two real positive values of the control parameter exist, $E_1$ and $E_2$, such that $P^*$ is feasible for $E_1 < E < E_2$.

(ii.b) Let $r < r_1$ and $\mu / (eaA)$. Then two real positive values of the control parameter exist, such that $P^*$ is feasible for $0 < E < E_2$.

(ii.c) Let $r < r_1$ and $\mu / (eaA)$. Then two real positive values of the control parameter exist, $E_1$ and $E_2$, such that $P^*$ is feasible for $E_1 < E < E_2$.

(ii.d) Let $r > r_1$ and $\mu / (eaA)$. Then one real positive value $E_2$ of the control parameter exists, such that $P^*$ is feasible for $0 < E < E_2$.

**Proof.** System’s equilibria are the real positive roots of the system

$$n \left[ r \left( 1 - \frac{n}{k} \right) \left( \frac{n}{A} - 1 \right) - a e d f - q E \right] = 0,$$

$$p - \mu e a d n - q E = 0.$$  \hspace{1em} (A.4)

(i) A straightforward analysis of system (A.4) shows that $P_0 = (0, 0)$ is always an equilibrium. Moreover it is easy to check that the prey parameters $n_i, i = 1, 2$ of the predator’s extinction equilibria $P_i = (n_i, 0)$ are given by the real positive solutions of the following algebraic equation:

$$n^2 - (A + k) n + \frac{4 k E}{r} = 0.$$  \hspace{1em} (A.5)

Observe that $\Delta = (k - A)^2 - 4 E_{of}$, so that $\Delta > 0 \Leftrightarrow E < E_{of}$. Holding this, the Descartes’ rule of signs ensures that both the roots of Eq. (A.5) are positive and hence feasible. As a consequence, for $0 < E < E_{of}$, $P_i = (n_i, 0)$ exist with $n_i$ given by $n_i / A = (1/2)(A + k) \pm \sqrt{\Delta}$.

(ii) The coexistence equilibrium $E^* = (n^*, p^*)$ can be easily deduced by system (A.4) which gives:

$$n^* = \frac{\mu e a d}{q E}, \hspace{1em} p^* = \frac{1}{4 a d} \left[ r \left( 1 - \frac{n^*}{k} \right) \left( \frac{n^*}{A} - 1 \right) - q E \right].$$  \hspace{1em} (A.6)

This is feasible when $p^*$ is a positive quantity. Namely:

$$p^* > 0 \Leftrightarrow B E_2^2 + B_1 E + B_0 < 0,$$  \hspace{1em} (A.7)
where
\[ B_2 = rq^2d^2, \quad B_1 = qd(2\mu + e^2a_1^2dA - r\alpha d(k + A)), \]
\[ B_0 = \mu(e\alpha d - \mu)(e\alpha d^2 - \mu). \]

Inequality (A.7) can be verified if and only if the quantity \( \Delta_1 = B_2^2 - 4B_1B_0 = d^3(C_2d + C_1) > 0 \). It follows that if (a) \( r < r_1 \lor r > r_2 \) or if (b) \( r_1 < r < r_2 \) and \( 0 < d < -C_1/C_2 \), then inequality (A.7) is verified for \( E_1 < E < E_2 \), where
\[ E_{1/2} = \frac{-B_1 \pm \sqrt{\Delta_1}}{2B_2}. \]

Next step for the feasibility of the coexistence equilibrium \( P^* \) is to search for conditions in order that at least one of the thresholds (A.8) is a positive quantity. Applying the Descartes’ rule of sign it follows that Eq. (A.7) has exactly one positive root, \( E_2 \), if \( \mu/(e\alpha d) < d < \mu/(e\alpha A) \) whereas it admits exactly two positive roots if the following system is verified:
\[
\begin{align*}
\frac{\mu}{e\alpha A} &< d < \frac{\mu}{e\alpha A}, \\
\frac{2\mu}{e\alpha A} &< \frac{2\mu}{e\alpha A} - \frac{2\mu}{e\alpha A} \\
\frac{\mu}{e\alpha A} &< \frac{\mu}{e\alpha A} - \frac{2\mu}{e\alpha A} \\
\frac{\mu}{e\alpha A} &< \frac{\mu}{e\alpha A}.
\end{align*}
\]

Recalling system (A.9), one gets that if
\[ r > r_\ell \& d > \frac{\mu}{e\alpha A}, \]
then Eq. (A.7) admits two positive roots \( E_1 \) and \( E_2 \). By combining the above results on positivity with on the reality of the roots \( E_1 \) and \( E_2 \), we can conclude that: (ii.a) if \( r > r_2 \) and \( d > \mu/(e\alpha A) \), then \( P^* \) is feasible for \( 0 < E < E_2 \); (ii.b) if \( r > r_2 \) and \( \mu/(e\alpha A) < d \mu/(e\alpha A) \), then \( P^* \) is feasible for \( 0 < E < E_2 \); (ii.c) if \( r > r_2 \) and \( \mu/(e\alpha A) < d < -C_1/C_2 \), then \( P^* \) is feasible for \( 0 < E < E_2 \); (ii.d) if \( r > r_2 \) and \( \mu/(e\alpha A) < d < \min \{ \mu/(e\alpha A), -C_1/C_2 \} \), then \( P^* \) is feasible for \( 0 < E < E_2 \).

**Stability properties of \( P^* \)** - We set:
\[
\begin{align*}
d_{\text{low}} &= \frac{\mu}{e\alpha A}, & d_{\text{up}} &= \frac{\mu}{e\alpha A}.
\end{align*}
\]

In view of the application to the specific case of study, we will focus on the cases (ii.a) \( r > r_2 \) and \( d > d_{\text{up}} \) and (ii.b) \( r > r_2 \) and \( d_{\text{low}} < d < d_{\text{up}} \) of Theorem Appendix A.1. We hence restrict all the following investigations to the case: \( r > r_2 \) and \( d > d_{\text{low}} \). In addition, to be more precise on the expected kind of coexistence, we look at the stability properties of the coexistence equilibrium \( P^* \).

**Theorem Appendix A.2.** Let \( r > r_2 \) and \( d > d_{\text{low}} \). Then the coexistence equilibrium \( P^* \) is feasible for max \( 0, E_1 \) \( < E < E_2 \), where \( E_1 \) and \( E_2 \) are given by the formula (A.8). Define:
\[
\begin{align*}
d_{\text{stab}} &= \frac{2\mu}{e\alpha A} + \frac{2\mu}{e\alpha A}, & E_{cr2} &= \left[-2\mu + e\alpha d(k + A)\right]/2qd.
\end{align*}
\]

(i) If \( d_{\text{low}} < d < d_{\text{stab}} \), then the coexistence equilibrium \( P^* \) is stable for every value of max \( 0, E_1 \) \( < E < E_2 \); (ii) If \( d > d_{\text{stab}} \), then a positive value \( E_{cr2} \) of the control parameter \( E \) exists such that the coexistence equilibrium \( P^* \) is unstable for max \( 0, E_1 \) \( < E < E_{cr2} \) and locally asymptotically stable for \( E_{cr2} < E < E_2 \). The bifurcation value \( E = E_{cr2} \) is a Hopf bifurcation point.

**Proof.** The Jacobian matrix \( J(n, p) \) of the aggregated system (5) is given by:
\[
J(n, p) = \begin{bmatrix}
G & -na d \\
pea d & -\mu - qEd + ea d 
\end{bmatrix},
\]
with
\[
G = 2 \frac{rn^2}{A} - 3 \frac{rm^2}{A} - r + \frac{2m^2}{k} - a_1 dp - qE.
\]

By evaluating the Jacobian matrix (A.12) in \( P^* \) one obtains that
\[
\text{det}(J(n^*, p^*)) = (\mu + qEd)P^* a_1 d,
\]
which is always positive in the range of the parameters, so that \( P^* \) is feasible. Moreover,
\[
\text{tr}(J(n^*, p^*)) \geq 0 \Rightarrow F_2 E^2 + F_1 E + F_0 \geq 0,
\]
with:
\[
F_2 = -2rq^2d^2, \quad F_1 = rdq[4\mu + de\alpha A],
\]
\[
F_0 = \mu[2\mu + de\alpha A].
\]

It straightforwardly follows that if \( d > d_{\text{stab}} \), then \( \text{tr}(J(n^*, p^*)) > 0 \Leftrightarrow E_{cr1} < E < E_{cr2} \) and \( \text{det}(J(n^*, p^*)) < 0 \Leftrightarrow E < E_{cr1} \lor E > E_{cr2} \), where \( E_{cr1} = -\mu/(qEd) \) and \( E_{cr2} \) given by equation (A.11). Moreover \( \text{tr}(J(n^*, p^*)) > 0 \Rightarrow E < E_{cr2} \). Hence a couple of complex imaginary eigenvalues of \( J(n^*, p^*) \) crosses the imaginary axis and a Hopf bifurcation occurs. In the strict neighborhood of \( E_{cr2} \), \( P^* \) is a stable focus for \( E > E_{cr2} \) and unstable focus for \( E < E_{cr2} \). In this latter range and close enough to the bifurcation value, an asymptotically stable limit cycle appears for the system (5) that surrounds the unstable equilibrium \( P^* \). If \( d_{\text{low}} < d < d_{\text{stab}} \), then \( \text{tr}(J(n^*, p^*)) < 0 \) for every \( E > 0 \). By combining the above results with the requirements about the feasibility of the coexistence equilibrium \( P^* \), theses (i) and (ii) of Theorem Appendix A.2 easily follow. □

**References**


