

Bella, Giovanni

Working Paper

A BugFishes Life: Competition Among Species Towards the Environment

Nota di Lavoro, No. 18.2007

Provided in Cooperation with:

Fondazione Eni Enrico Mattei (FEEM)

Suggested Citation: Bella, Giovanni (2007) : A BugFishes Life: Competition Among Species Towards the Environment, Nota di Lavoro, No. 18.2007, Fondazione Eni Enrico Mattei (FEEM), Milano

This Version is available at:

<https://hdl.handle.net/10419/74301>

Standard-Nutzungsbedingungen:

Die Dokumente auf EconStor dürfen zu eigenen wissenschaftlichen Zwecken und zum Privatgebrauch gespeichert und kopiert werden.

Sie dürfen die Dokumente nicht für öffentliche oder kommerzielle Zwecke vervielfältigen, öffentlich ausstellen, öffentlich zugänglich machen, vertreiben oder anderweitig nutzen.

Sofern die Verfasser die Dokumente unter Open-Content-Lizenzen (insbesondere CC-Lizenzen) zur Verfügung gestellt haben sollten, gelten abweichend von diesen Nutzungsbedingungen die in der dort genannten Lizenz gewährten Nutzungsrechte.

Terms of use:

Documents in EconStor may be saved and copied for your personal and scholarly purposes.

You are not to copy documents for public or commercial purposes, to exhibit the documents publicly, to make them publicly available on the internet, or to distribute or otherwise use the documents in public.

If the documents have been made available under an Open Content Licence (especially Creative Commons Licences), you may exercise further usage rights as specified in the indicated licence.

A Bug's Life: Competition Among Species Towards the Environment

Giovanni Bella

NOTA DI LAVORO 18.2007

FEBRUARY 2007

NRM – Natural Resources Management

Giovanni Bella, *Department of Economics, University of Cagliari*

This paper can be downloaded without charge at:

The Fondazione Eni Enrico Mattei Note di Lavoro Series Index:
<http://www.feem.it/Feem/Pub/Publications/WPapers/default.htm>

Social Science Research Network Electronic Paper Collection:
<http://ssrn.com/abstract=965652>

A Bug's Life: Competition Among Species Towards the Environment

Summary

A model of different species competing for the same environment is presented, and possible explanations of peaceful coexistence or rather internecine conflicts are consequently derived. By means of a Lotka-Volterra dynamic system we describe the evolution of two populations (bees and locusts) that differently approach the management of those natural resources they contend for, and thus make a simple parable of today's societies playing the current environmental scenario.

Keywords: Competing, Species, Lotka-Volterra, Dynamics, Natural Resource Management

JEL Classification: C61, Q34, Q57

I would like to thank professors and colleagues of my department at the University of Cagliari for their support and discussions we had on the issues regarding environmental economics. Obviously, I take responsibility for all errors.

Address for correspondence:

Giovanni Bella
Department of Economics
University of Cagliari
Viale Sant. Ignazio, 84
09123 Cagliari
Italy
Phone. +39 070 675 3405
E-mail: bella@unica.it

1 Introduction

Since any species is part of a complex ecological system that includes preys, competitors and predators, modelling equilibrium dynamics with a single differential equation fails to account for such ecological interdependence, and can verisimilarly lead to wrong conclusions. The bulk of literature regarding species competition with one accord points out that spillovers occurring from one population to another might change crucially the optimal solution involving such systems of interdependent species (see Neugebauer, 2005).

In contrast to the single species model, some of the most interesting and important studies in this field basically involve the interactions between two or more biological populations occupying close surroundings.¹ A study on competition among different populations must then focus on the extent to which the living space of a species i is affected by the presence of a competitor j . Likewise, we may verify that the greater the competition among species, the lower their biological equilibrium stock levels.

The first attempt to formalise the principle of competition among species and its pessimistic consequence on the exploitation of natural resources is due to Verhulst (1838), whose logistic equation became the basic law to explaining population growth over time.² Although this equation is sometimes

¹See, for example, Finnoff-Tschirhart (2003), Fleming-Alexander (2002), and Tschirhart (2002).

²Theoretical bases of the relationship between a slow down in population growth and the lack of natural resources were formerly posited by Malthus at the end of the 18th century.

considered too simple for a complete analysis on population dynamics, it still represents a central point in the “predator-prey” framework.

In this light, we present a model of competing species towards the same resource, and focus on the different equilibrium solutions this interaction might eventually lead to.

We consider two species bravely competing with each other for the food available in their common environment, but while one species (*bees*) does care about the environment she lives in, and makes all possible (and sustainable) actions necessary for survivability of the ecosystem; the other species (*locusts*) is assumed to have no consideration of the natural belongings she is endowed with, and behaves in exploiting as much as she can, thus *free-riding* those natural resources bees have been so carefully and patiently managing day by day (see, Grimaldi-Engel, 2005).

Finally, we ought to make a simple parable of today’s societies where basically two type of agents coexist (compete) in the same environment, so affecting the natural resource management, given their peaceful or conflictual coexistence.

The rest of the paper is organised as follows. In section 2 we present the biological features underlying the two species we are going to deal with: *bees* and *locusts*. In section 3, we apply the Lotka-Volterra dynamics to our competing-species community, and derive the possible outcomes, either peaceful or conflictual, that could possibly arise therefrom. Moreover, we examine these results, and make a possible parable to explain current human

behaviour towards natural resource use. The final section concludes, and a subsequent Appendix provides all the necessary proofs.

2 The biology of species

2.1 Bee's life

“Social creatures are such as have some one common object in view; and this probably is not common to all creatures that are gregarious. Such social creatures are man, the bee...” (Aristotle, Book I, part 1, *History of animals*)

First Honeybees probably came to light in Tropical Africa at about 40 million years ago, as confirmed by fossil records of amber deposits where the ancestor bees have been eternally imprisoned. Later on, colonies of bees appeared in data of Northern Europe and Asia. Although so far in time, bees had already developed the same well-defined social behaviour that modern bees pursue up till now.

Let us then have a look to what this particular structural system gives rise to, and so try to infer some considerations about the development of such species in the surrounding environment.³

Bees are used to form social aggregations commonly called hives. A typical small hive contains about 20,000 bees, and amongst these we distinguish

³For a complete survey on this field, see also Maeterlinck (1901).

three kinds of characters: the Queen, the Drones, and the Workers.

The hive's life has to follow some hierarchical rules to let dwellers coexist peacefully and orderly. On the one hand, the Queen's main job is to lay eggs and let the colony be preserved and be furnished with new members within the sustainable capacity of the hive itself. In this light, she dare to keep control on new births, thus making workers uninterested in reproduction on their own, by secreting a chemical essence, the pheromone, which is then spread from body to body amongst the workers, starting with those being assigned to tend the queen more closely.

Such a task leaves the queen no time to eat or fly around. A group of five to ten handmaid workers provide her with food, each time she lays about 20 eggs. These workers are given a special tight role in the hive's preservation, let us think of it as a Crown Council. In fact, they can depose the queen whenever she stops making pheromone or laying eggs, and one of her most recently laid eggs is immediately moved to a specially prepared cell to produce a replacement queen.

In a bloodthirsty accession to the throne, the newly selected queen destroys her mother, and then takes her mating flight. This special wedding follows a specific pattern: the virgin queen flies to a selected area where hundreds of drones are gathered in and wait to be chosen. Drones, like queens, lack the body parts necessary to harvest nectar or pollen from flowers to feed themselves. Drones also lack a stinger for self-defence. They are designed for mating, and nothing else.

Unfortunately, it is worth to clarify that no room is left in this society for “outlawed” or “pitiful” expressions, in fact drones are tolerated in the hive only for those periods when there is a possibility they mate with a queen, mostly in spring and summer, but none in the winter. Cruelly, the workers turn the drones out of the hive to starve to death.

On the other hand are Workers that, as implied by the name, do most of the work necessary to the hive. For example, they secrete from the glands on their abdomens the wax necessary to build up the grid of the honeycomb. We are familiar with the shape of this comb containing hexagonal cells large enough to hold newly developed workers or drones, as well as the necessary amount of pollen or honey. In either case, when the cells are filled up, a worker put a cover to the cell and finally seals whatever content inside.

Bees development occurs through a metamorphosis process. As a matter of fact, three days after it is laid, the egg does change into a worm-like larva which is feeded continuously for about four days; it goes then into a resting stage (the pupa) for another few days, until the adult bee finally emerges. The complete process lasts for about three weeks depending on the season and the class of bee.

As evidence of a “never-ending” busy life, young workers are immediately enrolled in their duties, by tending larvae and using their new and strong wings to help ventilate the hive. Elderly bees — wiser and stronger — are instead mainly focused on cleaning out the old cells for reuse, and definitely tend the queen or young drones, to let the hive reproduction be guaranteed.

The second main task a worker is employed into does concern food provision. Depending on the season, the bee will then fly out of the hive and visit flowers looking for nectar and pollen to be stored, or will stop upon trees for gathering resin and make propolis to be used for sealing any cleft in the hive walls.

Last but not least, workers have also to defend the hive with the sting they are furnished with. However, in a tremendous act of self-sacrifice, honeybees do not survive to stinging the enemy. Conversely, honeybees are not likely to use their one-life sting unless really provoked.⁴

2.1.1 Bees and the environment

To understand why bees are commonly viewed as “environmental-friendly” agents, let us briefly sum up what this *liaison* does really look like.

Indeed, across ages flowers have evolved to attract honeybees, whose carrying pollen from flower to flower allows plants’ pollination and reproduction.

Competition among flowers is very hard. Their shape is different as are their colors and fragrances to let the bees recognise the plant who rewards them at most and make a repeated visit very likely to happen again. To this

⁴Remembering the famous fable “*The bee and Jupiter*” from Aesop: “A Bee from Mount Hymettus, the queen of the hive, ascended to Olympus to present Jupiter some honey fresh from her combs. Jupiter, delighted with the offering of honey, promised to give whatever she should ask. She therefore besought him, saying, ‘Give me, I pray thee, a sting, that if any mortal shall approach to take my honey, I may kill him.’ Jupiter was much displeased, for he loved the race of man, but could not refuse the request because of his promise. He thus answered the Bee: ‘You shall have your request, but it will be at the peril of your own life. For if you use your sting, it shall remain in the wound you make, and then you will die from the loss of it.’”

end, flowers reward bees with nectar and pollen. The nectar is converted to glucose and fructose, by means of some digestive enzymes, lately taken to the hive, and stored into cells for evaporation to make honey. On the other hand, pollen is transferred from flower to flower as soon as the bee cleans its legs whenever reaching a new different plant. In this way, flowers never lack sufficient pollination. Not surprisingly, this mutualistic relationship between flowers and bees has been observed for millions of years and both bee and plant have benefited from it.

Many studies have also quarrelled about the ability of bees to communicate their floral findings. Empirical studies have shown that whenever a bee returns from a place plenty of flowers, that is also rich of producing nectar, she starts a particular dance on top of the hive. The type of movements she makes — the orientation, and the frequency of wing vibrations — suggest to any other bee the direction and the distance of such a mass of flowers from the hive.

Very broadly, extending to the human species, we may think of a society which behaves sustainably when deciding about the amount of resources to be harvested, and let future generations satisfy their needs as much as they currently do themselves.

2.2 Locust's life

*“A nation has invaded my land, powerful and without number;
it has the teeth of a lion, the fangs of a lioness...” (Joel,1:1-2:27*

The Bible)

Grasshopper is the name given to a very broad group of insects. All members of this group are particularly characterised by crunching mouths, strong wings for crossing long distances, and powerful legs for high jumping. Amongst these we are mainly interested in locusts, the more plaguing insects of the group, and so perceived as a terrible threat to the human livelihood. Particularly, locusts differ from grasshoppers in their ability to swarm. Moreover, locusts are basically considered solitary insects, although some circumstances (e.g., the lack of food due to increasing population density) might facilitate a swarming behaviour. Basically, when young locusts concentrate in the same area, their wings will touch each other constantly, until they closely crowd together. This learning behaviour may last for about four hours. In this gregarious phase, with about 20,000 members per square meter, they do march together eating up every green field in their path.⁵

Grasshoppers' evolution takes three stages: egg, hopper (nymph), adult.

Briefly, eggs might be laid by a single female grasshopper every two or four days, and under favourable climate conditions she can produce on average more than 250 eggs in her whole lifetime. It is then theoretically possible that each generation multiplies of about one hundred times. Fortunately, Nature makes this dreadful event very unlikely to occur, as eggpods (laid in the ground) are exposed to many risks, such as climatic conditions (e.g.,

⁵Reports of locust invasions especially in North-Africa go back to the 9th century A.D., though precise records have only been collected from the 1990s.

dry weather and water floods) or rather predation contingencies.⁶ Eggs are usually laid in deep hollows of about 100mm in the soil. Soon after the clutch is made, the hole is immediately filled with a secreted slavering substance that keeps the eggbed sufficiently warm. Consequently, under these ideal conditions eggs hatch in 2-3 weeks, although time varies from species to species.

During the second evolutionary phase of new-born locusts (nymphs or hoppers), their size is pretty small, they are sexually immature, and above all they are flightless. Finally, a growth stage will be completed soon after 14 days, once maturity is finally reached.

As for locusts environmental *unfriendly* behaviour, we must note that green vegetation and humidity are necessary for breeding. When they lack both, adults can form dense aggregations of hoppers, called bands, and fly across countries in densities up to 5000 per m². Under the right climatic conditions, that is usually when rainfalls arise, locusts can cover long distances following the weather fronts, thus invading vast squared kilometers of country-side.⁷ Migration is then a survival strategy. When a place with rich green vegetation and constant rain for breeding is found, these locusts reproduce very rapidly and a plague is very likely to occur. Just to make things clear, in 1958 Ethiopia lost about 170,000 tons of harvest due to the tremendous locusts' swarm, that is roughly the exact amount of grain necessary to

⁶Predators like flies, beetles, or rather ants and birds feed on locusts' eggpods very *pleasently*.

⁷For example, Australian locusts might cover up to 500km in a night.

feed that population for a year.

A plaguing band of locusts can contain even a billion insects, devouring around 20 tons of vegetation a-day. If this happens, although all crops can be a potential prey, summer crops are highly at risk. Leaves, flowers, fruit, and seeds might all enter their devastating diet.

We can easily associate locusts behaviour to those members of the mankind, quite selfish perhaps in their decision making towards resource extraction and over-exploitation, and with no care of the possible consequences could possibly arise therefrom. It is indeed a sort of anarchic society, without any binding management rule to guarantee the same disposal of natural resources to those generations coming afterwards.

3 Ecosystem behaviour of competing species: Lotka-Volterra dynamics

The classical model of “predator-prey” interacting species was developed in the 1920s by the Italian mathematician Vito Volterra (1860-1940) in order to explain the recurrent alteration observed in the shark and food-fish populations in the Adriatic Sea (see also Berryman, 1992).⁸

In this model-type framework, choosing the proper functional form to describe a growing population is at least as important as determining the

⁸Basically, the first studies on this fields can be ascribed to Lotka’s *Elements of Physical Biology* (1925).

right parameter values to express the underlying biology of each species being considered.

Traditional studies concerned with population management basically rely upon single-species models, thus making the analysis simpler and leaving more space to exogenous, and not explained, influences. However, current research is paying more and more attention to the possible outcome arising from interactions amongst different species (see, for example, Barbier 2001).

A seminal work in this field is due to Flaaten (1991), still controversial nonetheless because of its conclusions that “sea mammals should be heavily depleted to increase the surplus production of fish resources for man”. In this light, the Norwegian government has found a possible economic justification against the international moratorium on whales hunting.⁹

In addition, it is meaningful to remind the biological concepts underlying the particular forms taken by the so-called “predator-prey” models. Clearly, the more complex applied studies in population dynamics usually employ still complex nonlinear functions, though containing an immense amount of information about the species being considered. Finally, the particular form assigned to these functions may serve to better understanding the particular species’ interaction we are going to deal with.¹⁰

To begin with, we must properly define a function for the growth of

⁹Conversely, a similar dispute concerns the problem of abundant *krill* created in Antarctic Sea because of the disappearance of its major predator: the whales (see, Nicol and de la Mare, 1993).

¹⁰See Castilho-Srinivasu (2005), Conrad-Salas (1993), and Tu-Wilman (1992).

each population, which might eventually slow down due to congestion of individuals of the same species living the same area. Secondly, we ought to focus on possible interactions between one species with the others, that is species evolve differently when coming into contact with other individuals to contrast their living activities. Not surprisingly, it might be also the case that individuals do not interfere with one another, or rather connections are not so strong as to affect their population dynamics. Such a situation is commonly described in the literature as a *laissez-faire* behaviour (see, Caughley and Lawton, 1976). On the contrary, species may interact so differently as to affect each population growth in a number of different ways (see, Yodzis 1994). For example,

1. they may compete either for food, reproduction or dwellings;
2. they may eat one another (i.e., strong adults that feed upon defenceless young members);

In any case, these forms of interference, in which a species hampers another, could be easily reversed, as the case of individual predators that may facilitate other predators' feeding activities.¹¹

A question of particular interest arises if we assume a population to survive when all the competitors are extinct. Formally, this is reflected by the shape of the surviving species isocline to be definite when every other species

¹¹Models that consider how the biology of feeding may affect their functional forms were largely developed during the 1960s. See, for example, Holling (1965), Ivlev (1961), Takahashi (1964).

does collapse to zero. In our case, the neighbourhood of the intersection point may represent the number of locusts that is consistent with an at least very small growth of bees population.¹²

To conclude, it is worth noting that biological peculiarities among species may affect the functional form taken by predator-prey models, but it remains still difficult to determine which function is to be chosen for the populations we are interested in. We need then to carefully delineate the biology of our species as to identify the more appropriate functional forms, and thus correctly understand the model we are going to build up.

3.1 Bees and locusts dynamics

Let assume competition between bee and locust populations be generally described by the following autonomous system of differential equations

$$\begin{cases} \dot{x} = f(x) + B(x, y) \\ \dot{y} = g(y) + L(x, y) \end{cases}$$

where x and y represent the densities (more properly, the number or biomass) of locusts and bees, respectively. Moreover, $f(x)$ and $g(y)$ stand for the growth rate functions of each population evolving with no contact with the competitor; whereas the so-called functional response terms $B(x, y)$ and

¹²The risk is to build a bioeconomic model where predators are extremely stout: they can survive although prey populations are pretty small. This is itself biologically absurd, and warns about the lack of these models at very small densities (see, for example, Hassell-Varley, 1969).

$L(x, y)$ represent the effects on each population due to a possible interaction between our two species. To make a deepen investigation, let us give the system the following explicit form

$$\begin{cases} \dot{x} = ax - bx^2 + [x(y + c)]^\alpha \\ \dot{y} = dye^{-\delta y} - \beta ye^{x^2} \end{cases} \quad (1)$$

where

1. $f(x) = ax - bx^2$ depicts the evolution of locusts according to the usual logistic form found in population dynamics, that is the number of members does grow rapidly in a first stage until a slow down then necessarily occurs because of congestion problems (see, Clark, 1976).
2. $B(x, y) = [x(y + c)]^\alpha$ shows the effect on locust population due to any interaction with bees. We assume this effect to be positive since locusts surely benefit from bees that live close, as they might pollinate flowers and help plants' reproduction, allowing fields to blooming grow up. If bees are then present, locusts are sure to find abundant food to be harvested (see, Shigesada-Kawasaki, 1997).

While a and b basically serve at parametrising the growth rate of a locust population in the absence of bees; parameter $c \in [0, 1]$ in the interaction function additionally shows that a population growth might react to some external effects other than biology and competition with other species. We assume henceforth these effects to be always positive ($c > 0$). It is the case,

for example, of natural rainfalls for we noticed before they facilitate locusts' breeding, and so make an increase in population very likely to occur.¹³ Finally, the power $\alpha \in (0, 1)$ is a parameter of scale, which points out the magnitude of such interaction.¹⁴

3. On the other hand, $g(y) = dye^{-\delta y}$ describes the evolution of bees in the absence of locusts in the surrounding environment, being d a measure for the rate at which bees grow when living free of contacts with any other competing species. Specifically, we assume this function to look differently from the logistic-shaped one, since a reduction in the hive's population is more likely to be observed. For example, drones are usually kicked-out of the hive when unnecessary, or rather new queens eventually leave the hive with a cohort when congestion does occur. To this end, notwithstanding the harmonious affair bees have established with the environment they live in, we introduce a parameter $\delta \in [0, 1]$ to capture for any potential exogenous effect that may affect a beehive's life.¹⁵ Basically, we take δ as a measure for human intervention (regulation) to keep the hive's reproduction be maintained

¹³Constraining c to be positive can also depict the case of a parasite getting used to new pesticides, thus letting population to grow anyway.

¹⁴We either assume an interaction always to occur ($\alpha > 0$), or rather to affect the growth function less than proportionally ($\alpha < 1$); for the remaining parameter space ($\alpha > 1$) is of no biological significance, and population densities may become negative. On the contrary, $\alpha = 1$ simply drives us back to the linear interaction effect noticed in the basic Lotka-Volterra framework.

¹⁵Let consider, for example, the benefit do bees receive for man building up a new hive where the exceeding members might hopefully move in, to avoid the colony leave his field instead.

within its carrying capacity.¹⁶ Henceforth, we will assume that locusts take advantage (i.e., *free-ride*) of any natural/external effect more than actually bees do themselves, so $\delta \leq c$.

4. Moreover, interaction with locusts devastating population will produce (undoubtedly) some tremendous negative effects, thus reducing bees population. Flowers being destroyed will force the hive to move aside in search of new fields to gather in. This situation can be synthesised by the following reaction function that describes the response of a bee population to the presence of a locust one, $L(x, y) = -\beta y e^{x^2}$. We already assumed that the presence of bees allows locusts to grow very rapidly, let us say a plague occurs at an exponential rate, e^{x^2} . As a consequence, bees population will decrease very rapidly, being $\beta \in [0, 1]$ a measure for the magnitude of this interaction, or rather the percentage of bees' reduction due to a noxious swarm of locusts.

The main question we want to answer to is then: “what the community equilibrium does finally look like?”

Our scope is consequently to observe how this society evolves when an interaction among competing species takes place. The rest of this paper will then point out the two possible outcomes of our dynamic system, and so — moving to a real world — try to infer some peculiar consequences of mankind competition towards the natural resource use. Briefly, we are considering two

¹⁶In this light, the more a man intervenes. the higher is δ . Consequently, the lower the bees' growth rate, the less congested (and the more productive) the hive itself.

kind of men: those interested in environmental protection (*bee-man*) and those who are not (*locust-man*), living close in a small area where whatever behaviour might affect one another's. The former are also supposed to form a bigger aggregation than the latter, even though interacting consequences are not so immediate and need a deeper investigation (see Stroebele-Wacker, 1995).

Remark 1 *When bees and locusts compete towards the same natural resource, the social equilibrium is unique (and peaceful coexistence arises) if, and only if, no species ever faces the danger of extinction.*

Trying to formalise what we stated before, let us check for the stability properties of our dynamic system (1) by means of the following Jacobian matrix, evaluated at the steady state (\bar{x}, \bar{y})

$$J_{(\bar{x}, \bar{y})} = \begin{bmatrix} \frac{\partial \dot{x}}{\partial x} & \frac{\partial \dot{x}}{\partial y} \\ \frac{\partial \dot{y}}{\partial x} & \frac{\partial \dot{y}}{\partial y} \end{bmatrix}$$

Let us then define $\frac{\partial \dot{x}}{\partial x}$ and $\frac{\partial \dot{y}}{\partial y}$ as a potential *inhibition* impact of each population on its own growth. It can be also thought as a sort of intraspecific *congestion* effect, probably due to any scarcity of food or space. In our community, too many locusts in the field or too many bees into the hive. In this light, we assumed hereinbefore that congestion problems are more likely to affect bees than locusts, for a colony of bees has a growing upper-bound in the dimension of the hive, thus letting exceeding members to eventually

leave the community *for good* ($\frac{\partial \dot{y}}{\partial y} < 0$); whereas locusts have more countryside at disposal to gather in, being the sign of this effect somewhat doubtful ($\frac{\partial \dot{x}}{\partial x} \geq 0$). Nevertheless, we can easily assume this inhibition effect to be more detrimental to bees than locusts, that is in absolute terms $\frac{\partial \dot{y}}{\partial y} > \frac{\partial \dot{x}}{\partial x}$. On the other hand, the cross-diagonal elements ($\frac{\partial \dot{y}}{\partial x}$ and $\frac{\partial \dot{x}}{\partial y}$) do simply measure an existing interspecific competition (interaction) among species. As we noticed in the previous section, locusts are indeed supposed to benefit from bees presence ($\frac{\partial \dot{x}}{\partial y} > 0$), whereas the same is not conversely for bees ($\frac{\partial \dot{y}}{\partial x} < 0$).

Just to give a flavour of what the system might eventually look like, let us now try to calibrate the model, and assign the appropriate parameter values by means of the biological information we have previously derived.

To make the analysis simpler, let assume a beehive colony located on a square meter field, with a small community of incoming (thus still solitary) locusts living in there. Yet we consider an horizon of two-weeks time, well enough for eggs of both species to hatch up. We assume around 300 bees to populate a medium-sized hive. Since we consider a type of European bees (*Apis Mellifera*), whose reproduction capacity is around 2,500 new-born fortnightly, we are therefore likely to observe the colony of about eight times more crowded then on its arrival (hence, $d = 8$). Moreover, we expect these bees to be highly negatively affected by a swarm invasion, what makes their population to collapse dramatically, let us say around 40%, in other words the magnitude of their interaction to be $\beta = \frac{4}{10}$. As for locusts population, we assume the first colony of dwelling locusts be composed of 10 units, whereas

its carrying capacity be estimated around 20 units per square meter (thus, $b = 0.1$). On the other hand, we imagine the case where locusts population is overshooting, and rises at an explosive growth rate, $a = 200\%$.¹⁷ If that is the way things are, a plague is very likely to occur in few days. As noted before, any external effect is somehow going to affect our dwelling populations. In fact, either we assume any small human activity taking care of a beehive to make the colony on about the 25% more productive ($\delta = \frac{1}{4}$); or we might expect a rainfall (or whatever natural event) to occur and let locusts breeding be favoured at most ($c = 1$). Finally, interaction with bees is supposed to affect locusts at the rate $\alpha = \frac{1}{2}$.

Under these circumstances, the autonomous system (1) describing our species competition consequently becomes

$$\begin{cases} \dot{x} = 2x - \frac{1}{10}x^2 + \sqrt{x(y+1)} \\ \dot{y} = 8ye^{-\frac{1}{4}y} - \frac{4}{10}ye^{x^2} \end{cases} \quad (2)$$

And since we assume environmental-damaging agents to be always present, that is $x > 0$, the system is therefore characterised by two possible outcomes: either do both species coexist harmoniously (x_p, y_p) , or internecine conflicts blow up, thus letting one species to survive, and the other to become locally extinct $(x_s, 0)$. The rest of this section is devoted to clearly understand this two possible solutions.

¹⁷Deriving from the standard logistic model the carrying capacity (k) of our population, this implies $k = \frac{a}{b}$.

3.2 Peaceful coexistence

Firstly, we assume a locust population to be pretty small, with no congestion problems arising. Indeed, as we noticed above, hoppers will keep their solitary behaviour intact, and no plaguing swarms do happen. On the other hand, bees will not dramatically suffer from interaction with these new neighbours, given their scanty amount; and though bee population might slightly decrease anyway, a peaceful coexistence is finally possible.

Graphically, the two isoclines will intersect in a point where a determinate equilibrium is achieved, and a stable focus is therefore obtained, as it is shown in the phase-portrait depicted in Figure 1.

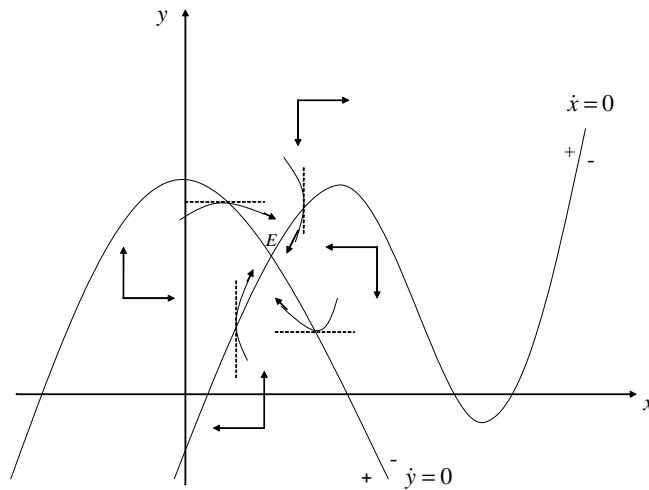


Figure 1: Peaceful coexistence

It can be the case of an economy where those members against environmental protection laws are quite trifling compared with interacting environmental-friendly agents.

Unfortunately, this is just a *knife-edge* solution, mainly depending on the value being assigned to the *externality* parameter, δ . In fact, the higher any human intervention to protect bees' existence, the less stable the optimal solution, and the more conflictual the social outcome finally achieved. A possible interpretation we may provide in this light is that the more any external agent (extensively, an international authority) intervenes to correct for market failures, and guarantee the environmental-friendly agents, the more willing are eventual "predators" to *free-ride* those natural resources the competitors have been so carefully taking care of. Mathematically written, the closer gets parameter δ to c (i.e., both species identically benefit from natural/external events) the more likely the social outcome is to become unstable instead, and no possible species coexistence could be achieved anyhow, as it

is shown in the following Figure 2 (where $\delta = c = 1$),

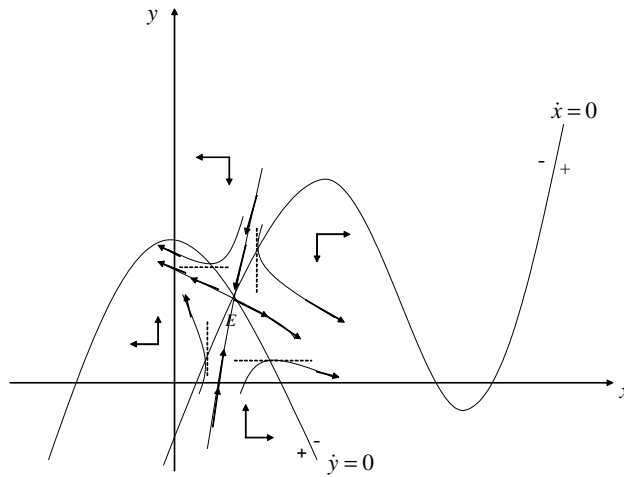


Figure 2: Unstable coexistence

which indeed describes an unstable saddle equilibrium.

3.3 Survival of a single species

Conversely, we may observe the case where things change to the worst. Locust population is dangerously increasing, swarming outbreaks are going to blow up, and a plague finally does occur. The upset caused by these bands keeps the established social order in suspense, until the hive does finally collapse. The dynamics originated by this interaction depicts a stable node equilibrium, as locusts might survive though having gotten rid of any com-

petitor. Basically, we may derive in Figure 3 that

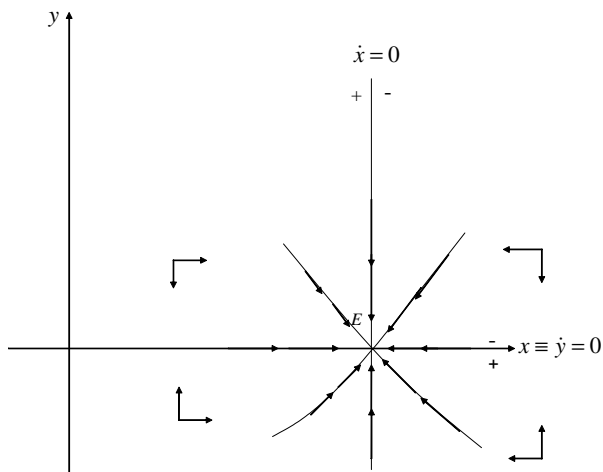


Figure 3: Survival of a single species

$E(x_s, 0)$ is a stable equilibrium point. It is the common case of a *laissez-faire* situation, where a population is living free of competition on the use of natural resources and easily blowing above its limits. Apparently, a stable solution can be reached even if no one does care about the surrounding environment. However, Nature has raised some self-defence barriers to avoid complete disruption. Hence, locusts will never be allowed to grow beyond their carrying capacity any further. If this temporarily happens then they will be driven back again to the equilibrium point, E .¹⁸

¹⁸Mathematical solvability of system (2), with bees population collapsing to zero ($y = 0$), needs locusts population density to be higher than 20 members ($x > 20$). Therefore, any other solution below this threshold is considered here of no biological significance.

This outcome basically confirms the so-called “competitive exclusion principle”, firstly formulated by Grinnell (1904), according to which “... *two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region.*” That is to say, the invader will crowd out the resident population until its complete extinction be reached.

It can be simply the case when skepticism about environmental protection is very high. In our society, agents that care about the environment are none, and foolish exploitation of natural resources has been carried on. Nevertheless, stability is achieved as Man and Nature have necessarily found a new deal to carry on their future life together on the Earth.¹⁹

4 Conclusions

Bees or *locusts*, to whom shall we identify ourselves with? By means of a competing species model, and the evolutionary dynamic rules described by the Lotka-Volterra equations, we characterised a community where bees and locusts are dwelling in, and *fratricidally* compete for their common environment. We assumed therefore these two populations to differently approach the management of the goods they are endowed with. Besides bees are supposed to be *environmental-friendly* agents, locusts are not; the latter mainly

¹⁹This is, for example, what probably did happen after the Ice Age when, even if some species did not survive that great event, some others did modify their living conditions, through adaptation to the new course of events.

free-riding those natural resources the former have been so patiently taking care of. Basically, our scope was to point out under what circumstances a peaceful coexistence among species might nonetheless be possible.

In this light, we noticed that a *peaceful* outcome is very uncertain to be achieved, being unstable equilibria more likely to happen instead. Even worst might be the case where only one population does survive, whereas the competitor is forced to an unavoidable decline and, ultimately, to an irreparable extinction.

Bearing the aforementioned *microcosm* story in mind, we took advantage of this parable to better explaining our real world evolution. It is in fact easily possible to share the mankind in those agents who care about the environment they live in, and those who conversely do not. While the former do manage sustainably the natural resources, acting the way future generations will enjoy the same welfare; the latter neither do care about how their foolish dissipation of the environment, nor do consider how might they negatively affect those members coming afterwards, and just behave at preserving their momentaneous, but still too high, standard of living.

This paper has also pointed out that any exogenous intervention, made by any force outside the community (e.g., Nature), can be of particular significance to properly determine the final social outcome. To this end, we noticed that, if a certain threshold is passed, any external intervention to favour those environmental-friendly agents, is anything but causing an increase in internecine species competition. Extensively, if an external intervention (ei-

ther due to a single government, or an international authority) to protect the environment is carried on, we might expect a free-riding behaviour to blow up, as “predators” have now more natural resources to feed upon.

On the other hand, if concentration of predators is too high, emulation among members will increase as well, such that nobody is therefore willing to take care of the environment he lives in anymore. Paraphrasing Gresham’s Law, “the *bad predator* drives out the *good competitor*”.

To conclude, nowadays our societies are indeed composed of members that differently approach the use of the natural resources they deal with. Nevertheless, a peaceful coexistence among these members can be achieved if, and only if, no exogenous intervention is such to arouse that anti-social behaviour that is mankind sometimes capable of, either leading to over-exploitation of any available natural resource, or ultimate extinction of any form of sound competition.

Appendix

Given the autonomous system (1) describing the evolution of our competing populations, we derive the associated Jacobian matrix

$$J = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \quad (\text{A.1})$$

where

1. $a_{11} = \frac{\partial \dot{x}}{\partial x} = a - 2bx + \alpha x^{\alpha-1}(y + c)^\alpha$
2. $a_{12} = \frac{\partial \dot{x}}{\partial y} = \alpha x^\alpha (y + c)^{\alpha-1}$
3. $a_{21} = \frac{\partial \dot{y}}{\partial x} = -2\beta x y e^{x^2}$
4. $a_{22} = \frac{\partial \dot{y}}{\partial y} = d(1 - \delta y)e^{-\delta y} - \beta e^{x^2}$

And then check for dynamic stability of the system by studying the sign of the associated trace (trJ) and determinant ($DetJ$), at the steady state values (\bar{x}, \bar{y}) .

On the one hand, since

$$trJ = a_{11} + a_{22} \quad (\text{A.2})$$

the sign of the trace gives us some useful information about a *congestion* problem which might affect each population's growth. Therefore, the species that suffers the most the congestion due to its members over-crowding evolution

($|a_{11}| \geq |a_{22}|$), is finally going to influence the sign of the trace ($|trJ| \geq 0$).

On the other hand, the sign of the determinant

$$DetJ = a_{11}a_{22} - a_{12}a_{21} \quad (A.3)$$

points out the magnitude of *competition* among our species. Formally, if $|a_{12}a_{21}| > |a_{11}a_{22}|$ then any interaction amongst our competing dwellers is going to affect each population growth more than it biologically grows itself.

To specify the analysis, let us calibrate the model by assigning the aforementioned parameter values derived from the biology of such species

a	b	c	α	d	β	δ
2	$\frac{1}{10}$	1	$\frac{1}{2}$	8	$\frac{4}{10}$	$\frac{1}{4}$

(A.4)

thus obtaining the system (2), with the associated steady-state values ($x_p = 1.42$, and $y_p = 3.93$), and the following explicit form of the Jacobian

$$J_{(1.42,3.93)} = \begin{bmatrix} 2.65 & 0.27 \\ -33.65 & -2.96 \end{bmatrix} \quad (A.5)$$

with

$$trJ = -0.31 < 0 \quad (A.6)$$

$$DetJ = 1.25 > 0$$

that is, equilibrium is unique, and the system describes a stable focus. Competition is small enough compared with inhibition, thus the two species can and do coexist.

On the contrary, we want to prove that an increase in parameter δ , necessarily drives the system to an unstable outcome. In fact, by assuming $\delta = 1$, the steady state values now become $x_p = 0.88$, and $y_p = 2.23$). The Jacobian matrix at the steady-state is therefore

$$J_{(0.88,2.23)} = \begin{bmatrix} 2.78 & 0.26 \\ -3.41 & -1.93 \end{bmatrix} \quad (\text{A.7})$$

and then

$$\begin{aligned} \text{tr}J &= 0.85 > 0 \\ \text{Det}J &= -4.48 < 0 \end{aligned} \quad (\text{A.8})$$

that is, the system is not stable, and a saddle path equilibrium is achieved. Competition is then too large in comparison with inhibition, and the two species will not steadily coexist together.

Conversely, solution to our system may lead to the case where one species survives and the other becomes locally extinct, at the point $(x_s = 22.16, y_s = 0)$. In our society, bees are going to disappear meanwhile locusts population

is overshooting. The Jacobian matrix therefore becomes

$$J_{(22.16,0)} = \begin{bmatrix} -2.32 & 2.35 \\ 0 & -7.43 \cdot 10^{212} \end{bmatrix} \quad (\text{A.9})$$

and consequently

$$\begin{aligned} \text{tr}J &= -7.43 \cdot 10^{212} < 0 \\ \text{Det}J &= 1.72 \cdot 10^{213} > 0 \end{aligned} \quad (\text{A.10})$$

that is, the system is now stuck at a point where a stable node is dynamically described. Unfortunately competition is no more possible, and one species gets rid of the other. In this case, the two population cannot coexist, natural resources are over-exploited, and no room is left for any environmental-friendly competitor.

References

- [1] Barbier, E.B. “A note on the economics of biological invasions”. *Ecological Economics* (2001), vol. 39(2), p. 197-202.
- [2] Berryman, A.A. “The Origins and Evolution of Predator-Prey Theory”. *Ecology* (1992), vol. 73(5), p. 1530-1535.
- [3] Caughley, G.; Lawton, J.H. “Plant-herbivore systems”, in R.M. May (ed.), *Theoretical Ecology: Principles and applications* (1981), p. 132-166. Blackwell Scientific Publications, Oxford, England
- [4] Castilho, C.; Srinivasu, P.D.N. “Bio-economics of a renewable resource in a seasonally varying environment”. *EEE Working Papers Series* (2005), n. 16.
- [5] Clark, C. *Mathematical Bioeconomics*. John Wiley & Sons, New York, 1976.
- [6] Conrad, J.M.; Salas, R. “Economic strategies for coevolution: timber and butterflies in Mexico”. *Land Economics* (1993), vol. 69, p. 404-415.
- [7] Finnoff, D.; Tschirhart, J. “Harvesting in an eight-species ecosystem”. *Journal of Environmental Economics and Management* (2003), vol. 45(3), p. 589-611.

- [8] Flaaten, O. "Bioeconomics of sustainable harvest of competing species". *Journal of Environmental Economics and Management* (1991), vol. 20, p. 163-180.
- [9] Fleming, C.M.; Alexander, R.R. "Single species versus multiple species models: the economic implications". *Discussion paper in Natural Resource and Environmental Economics*, (2002), n. 23.
- [10] Grimaldi, D.; Engel, M.S. *Evolution of the insects*. Cambridge University Press, 2005.
- [11] Grinnell, J. "The origin and distribution of the Chestnut-backed Chickadee", *Auk* (1904), vol. 21, p. 364-382.
- [12] Hassell, M.P.; Varley, G.C. "New inductive population model for insect parasites and its bearing on biological control". *Nature* (1969), vol. 223, p. 1133-1136.
- [13] Holling, C.S. "The functional response of predators to prey density". *Memoir of the Entomological Society of Canada* (1965), vol. 45, p. 5-60.
- [14] Ivlev, V.S. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Connecticut, USA, 1961.
- [15] Lotka, A.J. *Elements of Physical Biology*. Williams and Wilkins Company, Baltimore, 1925.

- [16] Maeterlinck, M. *The life of the Bee (La Vie des Abeilles)*. Dodd, Mead and Company, Chicago, 1901.
- [17] Neugebauer, T. "Bioeconomics of sustainable harvest of competing species: A comment". Mimeo, 2005.
- [18] Nicol, S.; de la Mare, W.K. "Ecosystem management and the antarctic krill". *American Scientist* (1993), vol. 81, p. 36-47.
- [19] Shigesada, N.; Kawasaki, K. *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford, 1997.
- [20] Stroebele, W.J.; Wacker, H. "The economics of harvesting predator-prey systems". *Journal of Economics* (1995), vol. 61, p. 65-81.
- [21] Takahashi, F. "Reproduction curve with two equilibrium points: a consideration of the fluctuation of insect populations". *Research in Population Ecology* (1964), vol. 6, p. 28-36.
- [22] Tschirhart, J. "Resource competition among plants: From optimising individuals to community structure". *Ecological Modelling* (2002), vol. 148, p. 191-212.
- [23] Tu, P.N.V.; Wilman, E.A. "A generalised predator-prey model: Uncertainty and management". *Journal of Environmental Economics and Management* (1992), vol. 23, p. 123-138.

- [24] Verhulst, P.F. “Notice sur la loi que la population poursuit dans son accroissement”. *Corr. Math. Phys.* (1838), vol. 10, p. 113-121.
- [25] Volterra, V. “Variazioni e fluttuazioni del numero d’individui in specie animali conviventi”. *Mem. R. Accad. Naz. dei Lincei* (1926), Ser. VI 2.
- [26] Yodzis, P. “Predator-Prey Theory and Management of Multispecies Fisheries”. *Ecological Applications* (1994), vol. 4(1), p. 51-58.

NOTE DI LAVORO DELLA FONDAZIONE ENI ENRICO MATTEI

Fondazione Eni Enrico Mattei Working Paper Series

Our Note di Lavoro are available on the Internet at the following addresses:

<http://www.feem.it/Feem/Pub/Publications/WPapers/default.htm>

<http://www.ssrn.com/link/feem.html>

<http://www.repec.org>

<http://agecon.lib.umn.edu>

<http://www.bepress.com/feem/>

NOTE DI LAVORO PUBLISHED IN 2007

NRM	1.2007	<i>Rinaldo Brau, Alessandro Lanza, and Francesco Pigliaru: <u>How Fast are Small Tourist Countries Growing? The 1980-2003 Evidence</u></i>
PRCG	2.2007	<i>C.V. Fiorio, M. Florio, S. Salini and P. Ferrari: <u>Consumers' Attitudes on Services of General Interest in the EU: Accessibility, Price and Quality 2000-2004</u></i>
PRCG	3.2007	<i>Cesare Dosi and Michele Moretto: <u>Concession Bidding Rules and Investment Time Flexibility</u></i>
IEM	4.2007	<i>Chiara Longo, Matteo Manera, Anil Markandya and Elisa Scarpa: <u>Evaluating the Empirical Performance of Alternative Econometric Models for Oil Price Forecasting</u></i>
PRCG	5.2007	<i>Bernardo Bortolotti, William Megginson and Scott B. Smart: <u>The Rise of Accelerated Seasoned Equity Underwritings</u></i>
CCMP	6.2007	<i>Valentina Bosetti and Massimo Tavoni: <u>Uncertain R&D, Backstop Technology and GHGs Stabilization</u></i>
CCMP	7.2007	<i>Robert Küster, Ingo Ellersdorfer, Ulrich Fahl (lxxx): <u>A CGE-Analysis of Energy Policies Considering Labor Market Imperfections and Technology Specifications</u></i>
CCMP	8.2007	<i>Mònica Serrano (lxxx): <u>The Production and Consumption Accounting Principles as a Guideline for Designing Environmental Tax Policy</u></i>
CCMP	9.2007	<i>Erwin L. Corong (lxxx): <u>Economic and Poverty Impacts of a Voluntary Carbon Reduction for a Small Liberalized Developing Economy: The Case of the Philippines</u></i>
CCMP	10.2007	<i>Valentina Bosetti, Emanuele Massetti, and Massimo Tavoni: <u>The WITCH Model. Structure, Baseline, Solutions</u></i>
SIEV	11.2007	<i>Margherita Turvani, Aline Chiabai, Anna Alberini and Stefania Tonin: <u>Public Policies for Contaminated Site Cleanup: The Opinions of the Italian Public</u></i>
CCMP	12.2007	<i>M. Berrittella, A. Certa, M. Enea and P. Zito: <u>An Analytic Hierarchy Process for The Evaluation of Transport Policies to Reduce Climate Change Impacts</u></i>
NRM	13.2007	<i>Francesco Bosello, Barbara Buchner, Jacopo Crimi, Carlo Giupponi and Andrea Povellato: <u>The Kyoto Protocol and the Effect of Existing and Planned Measures in the Agricultural and Forestry Sector in the EU25</u></i>
NRM	14.2007	<i>Francesco Bosello, Carlo Giupponi and Andrea Povellato: <u>A Review of Recent Studies on Cost Effectiveness of GHG Mitigation Measures in the European Agro-Forestry Sector</u></i>
CCMP	15.2007	<i>Massimo Tavoni, Brent Sohngen, and Valentina Bosetti: <u>Forestry and the Carbon Market Response to Stabilize Climate</u></i>
ETA	16.2007	<i>Erik Ansink and Arjan Ruijs: <u>Climate Change and the Stability of Water Allocation Agreements</u></i>
ETA	17.2007	<i>François Gusdorf and Stéphane Hallegatte: <u>Compact or Spread-Out Cities: Urban Planning, Taxation, and the Vulnerability to Transportation Shocks</u></i>
NRM	18.2007	<i>Giovanni Bella: <u>A Bug's Life: Competition Among Species Towards the Environment</u></i>

(lxxxi) This paper was presented at the EAERE-FEEM-VIU Summer School on "Computable General Equilibrium Modeling in Environmental and Resource Economics", held in Venice from June 25th to July 1st, 2006 and supported by the Marie Curie Series of Conferences "European Summer School in Resource and Environmental Economics".

2007 SERIES

CCMP	<i>Climate Change Modelling and Policy</i> (Editor: Marzio Galeotti)
SIEV	<i>Sustainability Indicators and Environmental Valuation</i> (Editor: Anil Markandya)
NRM	<i>Natural Resources Management</i> (Editor: Carlo Giupponi)
KTHC	<i>Knowledge, Technology, Human Capital</i> (Editor: Gianmarco Ottaviano)
IEM	<i>International Energy Markets</i> (Editor: Matteo Manera)
CSRМ	<i>Corporate Social Responsibility and Sustainable Management</i> (Editor: Giulio Sapelli)
PRCG	<i>Privatisation Regulation Corporate Governance</i> (Editor: Bernardo Bortolotti)
ETA	<i>Economic Theory and Applications</i> (Editor: Carlo Carraro)
CTN	<i>Coalition Theory Network</i>