Symbology from set theory applied to ecological systems: Gause’s exclusion principle and applications

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Abstract: We introduce a symbolic representation like set theory to consider ecologic interactions between species (ECOSET). The ecologic exclusion principle (Gause) is put in a symbolic way and used as operational tool to consider more complex cases like interaction with sterile species (SIT technique), two species with two superposed sources (niche differentiation) and N+P species competing by N resources, etc. Displacement (regional or characters) is also considered by using this basic tool. Our symbolic notation gives us an operative and easy way to consider elementary process in ecology. Some experimental data (laboratory or field) for ecologic process are re-considered under the optic of this set-theory.

Keywords: Coexistence and competition; Food web theory; Ecology; Set theory.
I Introduction.

Interactions between species in ecology is after some time the object of study of mathematical branches (Gertsev et al (2004) and references therein). For instance, mathematical models for predator-prey are usually treated with nonlinear coupled differential equations like Lotka-Volterra (Begon et al. (1999), Murray (1993), and references therein). It is true that, as a general rule, modelling of ecological systems is a difficult task since complexity in biological sciences is almost always present. For instance, the more known application of Lotka-Volterra system, that is, the Hare-Lynx predator-prey data recorder by Hudson Bay Company in 1953, presents some troubles. The expected periodic solution between prey and predator is not determined from data (Murray (1993)). The reasons are not clear but one can expect a complex dynamics for real predator-prey system in a not isolated region. Very refined experiment in laboratories are actually realized (Costantino et al. (1995)), nevertheless the more impressive laboratory experiments were carried out some time ago by ecologist G. F. Gause with protozoan Paramecium species. These experiments have determined some general principles applied to inter-competition and coexistence in ecology. The more basic for us is the statement that: when we have two species competing by (exactly) the same niche then one of them disappear (Gause (1934)). That is, finally, one species full the niche. The statement is very restrictive since it requires quite special conditions (section IV) and in this paper it will be used as a basic principle to consider more complex situations.

Mathematical models like Lotka-Volterra for two species in competition predict coexistence for some range of parameters (high intraspecific competition). In fact, any mathematical system with attractors (out-side of the axis) in this two dimensional phase-space makes the same prediction. So, for us this mathematical result is not proof of real violation of the principle. Gause’s exclusion principle will be assumed for interspecific competition as a basic statement in this paper. Nevertheless, we accord that the distinction between the minimum amount of niche differentiation (in real ecological system) to produce its break is a difficult point to consider in practice. For an appropriate discussion see reference (Begon et al. (1999)).

In this paper we will consider a mathematical modeling for ecological systems but using a symbology, called ECOSET, similar to basic set theory. This schema has the advantage of a condensed notation for a variety of
ecological interacting systems. There are some similarities with usual set theory but also some differences. For instance, Gause’s exclusion principle (16) has not equivalence in the usual set theory. In our construction, Gause’s exclusion principle will be used as a basic operational tool to consider complex situations like more than one species and more than one resource. A great part of field and laboratory examples found in this article were hold from reference Begon et al (1999).

In this paper, species will be represented by capital letter like \( A, B, \ldots \). We will use the symbol \( S \) only for a primary source at the basis (consume) of a ecological chain. We will give to \( S \) a stronger sense: it will design a defined ensemble of sources which make viable the development of species. Namely, it is considered in the sense of an ecological niche. We assume that this primary resource is auto-sustained or externally sustained. The absence of species in a given region will be denoted by \( \phi \) in analogy with the symbol of usual set theory.

II Symbology for depredation (\( > \)) and basic definitions.

Consider a primary resource \( S \) and species \( A, B, C \ldots \). The notation

\[
A > B \quad (B \text{ consumes } A),
\]

means: species \( B \) exploits species \( A \) as a resource in a sense of depredation. In this way, a basic chain becomes for instance

\[
S > A > B > \phi \quad (a \text{ basic depredation chain }),
\]

namely, species \( B \) exploits \( A \) as a resource and, \( A \) exploits the primary resource \( S \). Note that the species \( \phi \) at the end of the chain means that \( B \) is not prey for others.

For two no-interacting species \( A \) and \( B \) (also for ecological process) in a given ecological region we write \( A \oplus B \). When two species (\( A \) and \( B \)) consume the same primary resource (\( S \)), in a not depending way, we write
\[ S > (A \oplus B), \text{ (independent depredation).} \quad (3) \]

When two species \((A \text{ and } B)\) exploit the same resource \((S)\) in an interdependent way we write

\[ S > (A \otimes B) \quad \text{(interdepending depredation).} \quad (4) \]

The notation \(S > A \otimes B\) (without braces) means: species \(A\) consumes \(S\) with the help of species \(B\).

Note that when one of the interdependent species is \(\phi\) then, after a time, no depredation on \(S\) must occur. In a symbolic way,

\[ \{ S > (A \otimes \phi) \} \Rightarrow S > \phi, \quad (5) \]

where the symbol \(\Rightarrow\) has a temporal interpretation or, it defines a temporal direction. Namely, if we have the ecological system \(X\) then, after a time we have \(Y\) \((X \Rightarrow Y)\). For instance, the ecological proposition: \text{when one species \(A\) has not source for depredation then it dies,} could be written as:

\[ \{ S > \phi > A \} \Rightarrow \{ S > \phi \}. \quad (6) \]

We also define the symbol \(\Leftrightarrow\) which will be interpreted as equivalence between ecological process. For instance, in the process \((3)\) we always assume implicitly the equivalence:

\[ \{ S > (A \oplus B) \} \Leftrightarrow \{(S > A) \oplus (S > B)\}. \quad (7) \]

Two notes: (a) An ecological process like \(S > A > B\) does not mean that \(S > B\). If it is true that also \(B\) consumes \(S\) we must write \((S > A > B) \oplus (S > B)\). (b) We have the equivalent notation \(A > B \Leftrightarrow B < A\).

As a field example consider the food web with four trophic levels from New Zealand stream community (Begon et al (1999) page 836). This ecological systems is composed by Algae \((A)\), Herbivorous insects \((H)\), Predatory insects \((P)\) and Brown trout \((B)\). The web food is:

\[ \{ A > H > P > B \} \oplus \{ A > H > B \}, \quad (8) \]

and then

\[ (8) \Leftrightarrow A > \{(H > P) \oplus H\} > B. \quad (9) \]
So, $A$ is a primary resource and $B$ the final predator. Note that if $P \Rightarrow \phi$ (extinction), the web food does not disappear completely since $\{A>H>B\}$. As expected, biodiversity leads stability of ecological systems.

As another field example consider the ecological trophic level at the Lauca National Park (Arica-Chile). There is a biodiversity group represented by ancient flora and fauna under extreme climatic condition (3.0 to 4.5 Km of altitude). The highly adapted species conform almost a close system. Particularly we have a partial food-chain composed by different species like: basic herbs, including the so-called bofedal, $(H)$; a kind of camel called Vicunas $(VC)$; a kind of rodent called Vizcacha $(VZ)$; two predators (Puma $(P)$ and Zorro $(Z)$). Also we have the carrion-eat species condor $(K)$. A basic process of Lauca National Park is represented by

$$H > (VC \oplus VZ) > \{(P \ominus Z) \otimes K \ominus (P \ominus Z)\}.$$  

(10)

In fact, species $P$ and $Z$ are natural competitors in this region. Naturally, the web is more complex of that represented by (10), for instance species $K$ also depends on natural dead of $VC$ and $VZ$; but is only a basic notation example for us.

III Symbology for competition ($\supset\subset$) and basic definitions.-

To consider species in competition (no depredation) we will use the symbol $\supset\subset$ (see later). Here we give some basic definitions, for instance, consider species $A$ and $B$ in struggle for some source like water, space, etc. The symbol:

$$A \supset B \quad (A \text{ is perturbed by } B),$$

(11)

means that species $B$ perturbs (interferes) $A$. Note that for depredation we use other symbol ($\succ$). The above process could also written as $B \subset A$ or in the equivalence language

$$A \supset B \quad \Leftrightarrow \quad B \subset A.$$  

(12)

The symbols $\oplus, \otimes, \Rightarrow$ and $\Leftrightarrow$ are used in the same way that in the above section.
With this basic definitions we can represent competition between species. In fact, if $A$ and $B$ are two species in competition (no depredation) we write

$$(A \supset B) \oplus (B \supset A), \ (A \text{ and } B \text{ compete}). \quad (13)$$

By simplicity we will use the alternative symbol $\supset \subset$ for competition. Namely,

$$\{(A \supset B) \oplus (B \supset A)\} \leftrightarrow \{A \supset \subset B\}, \ (\text{symbol for competition}). \quad (14)$$

Before to ending this section we give a useful definition which will be used in some cases. The notion of “potential competitors” is related to two species who put together then compete. In our symbolic notation, it could be written as

$$\{S > (A \oplus B)\} \Rightarrow \{S > (A \supset \subset B)\} \ (\text{potential competitors}). \quad (15)$$

IV Gause’s exclusion principle for interspecific competition and symbolic notation.

Gause’s exclusion principle (or competitive exclusion principle) in ecology states that: when we have two species $A$ and $B$ which compete (interspecific competition) for the same invariable ecological primary resource $S$ (realized niche), then one of them disappear (Begon et al (1999), Gause (1934), Hast- ing (1996), Flores (1998)). It is important to note that Gause’s exclusion principle holds when no migration, no mutation and no resource differentiation exist in the ecological systems. Note that it refers to interspecific competition. The case of intraspecific competition will be touched briefly in section IX. The principle assures that the more stronger species in the exploitation of primary resource survives. Applications could be found in many text of ecology. A direct application of this principle to Neanderthal extinction in Europe could be found in reference (Flores (1998)).

In our symbolic notation the principle could be written as:
\{S > (A \supset \subset B)\} \Rightarrow \{(S > A) \text{ or } (S > B)\}, \text{ (Gause).} \quad (16)

The above statement (16) will be a basic operational tool to consider more general cases or application like two sources and two predators, or more general. So, (16) is our start-point. The logic operator \textit{or} (some times written as $\lor$) is the usual exclusion symbol in set theory.

The more famous example of exclusion comes from the classic laboratory work of ecologist G. F. Gause (1934), who considers two type of \textit{Paramecium}, namely, \textit{P. caudatum} and \textit{P. aurelia}. Both species grow well alone and reaching stable carrying capacities in tubes of liquid medium and consuming bacteria. When both species grow together, \textit{P. caudatum} declines to the point of extinction and leaving \textit{P. aurelia} in the niche.

As said before, other examples could be found in literature. For instance, competition between \textit{Tribolium confusum} and \textit{Tribolium castaneum} where one species is always eliminated when put together (Park (1954)).

V Application: interaction with sterile individuals and eradication (SIT).

A corollary of the above principle can be found when one of the species in competition is sterile. In fact, we define a sterile specie \(M\) as a species which exploits a resource \(S\) and then disappear. Namely,

\[\{S > M\} \Rightarrow \{S > \phi\}, \text{ (sterile species).}\quad (17)\]

Now, we consider this definition together to the exclusion principle. Let \(A\) be a species which exploits the resource \(S\), and let \(M\) be a sterile species introduced which exploits the same resource. The application direct of the principle (16), and definition (17), tell us that

\[S > (A \supset \subset M) \Rightarrow (S > A) \text{ or } (S > M), \text{ (Gause applied).}\quad (18)\]

and then,

\[\Rightarrow \{S > A\} \text{ or } \{S > \phi\}, \text{ (M is sterile ).}\quad (19)\]
Putting together (18) and (19), we have the ecological process:

\[ \{S > (A \supset \subset M)\} \Rightarrow \{(S > A) \text{ or } (S > \phi)\}, \quad \text{(Gause for sterile)} \]  

(20)

so, at least one species of both disappear and then there is the possibility of total extinction in the niche \((S > \phi)\). The known SIT (Sterile Insect Technique, Barclay (2001)) uses this principle to eradicate undesirable insects. In fact, sterile insects compete with native ones for a source and there is the possibility of total extinction (eradication, \(S > \phi\)). The fruit flies (medfly) eradication program carried out in many regions of the world, for instance in Arica-Chile, could be understand partially with the above results (Flores (2000) and (2003)). If \(S\) is the female-native group then the native male group \(A\) and the sterile male group \(M\) compete by the “resource \(S\)”. In this way using (20) there is the possibility of \(S > \phi\) corresponding in this case to extinction of all type of male and then the wild species disappear.

VI Application: two species, two resources, and niche differentiation.

As other application of our symbology for the principle of Gause, consider two resources \(S_1\) and \(S_2\) and two species \(A\) and \(B\) in competition by these resources. Namely, consider the ecological systems where

\[ (S_1 \oplus S_2) > (A \supset \subset B), \]

(21)

or

\[ (21) \Leftrightarrow \{S_1 > (A \supset \subset B)\} \oplus \{S_2 > (A \supset \subset B)\}, \]

(22)

the equivalence becomes since both species consume any of two resources. From the exclusion principle (16), we have

\[ (22) \Rightarrow \{S_1 > A \text{ or } S_1 > B\} \oplus \{S_2 > A \text{ or } S_2 > B\}, \quad \text{(Gause applied)} \]

(23)

8
and the four final possibilities:

(a) \{S_1 \oplus S_2\} > A. Species A exterminates B.
(b) \{S_1 \oplus S_2\} > B. Species B exterminates A.
(c) \{S_1 > A\} \oplus \{S_2 > B\}. Species A exploits S_1 and B exploits S_2.
(d)\{S_1 > B\} \oplus \{S_2 > A\}. Species A exploits S_2 and B exploits S_1.

The last two possibilities (c) and (d) tell us that both species could survive by resources exploitations in a differential (partitioned) way. Some time this coexistence is considered a violation of Gause’s exclusion principle; but it is not. In fact, we have more than one resource (realized niche).

The behavior found in the above process (a-d), has been observed in laboratories (see Begon et al (1999) page 311, or Tilman (1977)) where two diatom species (Asterionella formosa and Cyclotella meneghimiana) compete by silicate (S_1) and phosphate (S_2) as elementary resources. In fact, for different proportions of this components one can see extermination or stable coexistence (Tilman (1977)). This is a valuable laboratory experimental example which support our theory as a clear and efficient operational tool.

VII General case with \(N+P\) species competing by \(N\) resources.

Considering the above result of section VI for two sources and two species in competition, it seems natural to extend it to a more general case. This will be do in this section. Consider \(N\) primary resources \(S_i\) \((i = 1, 2, ...N)\) and \(N+P\) \((P \geq 0)\) species \(A_j\) \((j = 1, 2, ...N+P)\) competing by the resources. We will consider this species as potential competitors in the sense defined by expression (15). In this section, the mean result is that at least \(P\) species disappear. So, we are considering the ecological systems given by the process

\[
\left\{ \sum_{i=1}^{N} S_i \right\} > \left\{ \sum_{j\neq k}^{N+P} (A_j \supset A_k) \right\}, \tag{24}
\]
where the summation is understood in the sense of independent species in a region, explicitly,

\[
\sum S_i = S_1 \oplus S_2 \oplus S_3 \ldots ,
\]

the ecological process (24) is equivalent to

\[
(24) \Leftrightarrow \sum_{i=1}^{N} \left\{ S_i > \sum_{j \neq k}^{N+P} (A_j \supset A_k) \right\},
\]

because any species consumes any resources. Using Gause (16) for every pair \( i, k \) then we have

\[
(25) \Rightarrow \sum_{i=1}^{N} \left\{ S_i > (A_1 \text{ or } A_2 \text{ or } A_3 \text{ or } \ldots \text{ or } A_{N+P}) \right\}, \text{ (Gause applied). (26)}
\]

So every \( S_i \) is consumed by one species; but note that one species could consume more than one resource. In this way, at least there are \( P \) species extinct. The extrema option are:

(a) One species, called the exterminator, finally uses the \( N \) resources.
(b) \( N \) species coexist. That is, one species for every source (niche differentiation).

VIII Regional and character displacement.-

As said before, Gause competitive exclusion principle is a basic tool which could be applied to more complex cases as two resources or more. In this section we want to show how our notation is so coherent that it could be applied to other cases. In fact we will consider displacement of species. We will see it in a very operative way.

We define displacement of a species \( D \) from a source \( S_1 \) to \( S_2 \) as

\[
\{(S_1 > D) \oplus (S_2 > \phi)\} \Rightarrow \{(S_1 > \phi) \oplus (S_2 > D)\}, \text{ (displacement). (27)}
\]

Note that displacement could be understood in two ways:
(a) Regional or spatial displacements (migration). Namely, $S_1$ and $S_2$ are sources in different spatial locations.

(b) Character displacements. Namely, $S_1$ and $S_2$ are sources in the same spatial place but species $D$ changes (displaces) its sources necessities, for instance due to mutation.

Consider two species, $A$ and $D$, competing by the same resources $S_1$. Assume that $D$ displaces to the unoccupied resource $S_2$ before to apply Gause. The ecological system is given by

$$\{S_1 > (A \supset D)\} \oplus \{S_2 > \phi\}, \quad (28)$$

$$\Leftrightarrow \{S_1 > (D \supset A \oplus A \supset D)\} \oplus \{S_2 > \phi\}, \quad (29)$$

$$\Leftrightarrow \{S_1 > D \supset A\} \oplus \{S_1 > A \supset D\} \oplus \{S_2 > \phi\}, \quad (30)$$

$$\Leftrightarrow \{(S_1 > D) \oplus (S_2 > \phi)\} \supset A \oplus \{S_1 > A \supset D\}, \quad (31)$$

where we have used $\phi \supset A \Leftrightarrow \phi$. In this stage, assuming that species $D$ displaces to $S_2$ (see (27)) we have

$$\Rightarrow \{S_1 > \phi \oplus S_2 > D\} \supset A \oplus \{S_1 > A \supset D\}, \quad (32)$$

$$\Leftrightarrow \{S_1 > \phi \supset A\} \oplus \{S_2 > D \supset A\} \oplus \{S_1 > A \supset D\}, \quad (33)$$

using newly $\phi \supset A \Leftrightarrow \phi$ we obtain

$$\Leftrightarrow \{S_2 > D \supset A\} \oplus \{S_1 > A \supset D\}. \quad (34)$$

In resume, from (28) and (34) we have:

$$\{S_1 > (A \supset D)\} \oplus \{S_2 > \phi\} \Rightarrow \{S_1 > A \supset D\} \oplus \{S_2 > D \supset A\}, \quad (35)$$

and both species survive due to displacement. A practical example for displacement comes from the same Gause classic experiments. In fact, when two protozoan $P. caudatum$ and $P. bursaria$ were grown together neither
species suffered a decline to the point of extinction. They were in competition with one another but although they lived together in the same tube, they were spatially separated. *P. caudatum* lived suspended in the liquid medium and *P. bursaria* was concentrate at the bottom of the tube (Begon (1999)). So, coexistence is related here with displacement.

An example where character displacement gives coexistence is provide by mud snails *Hydrobia ulvae* and *Hydrolia ventrosa* (Saloniemi (1993)). When they live apart, their sizes are almost identical. Nevertheless, when put together they reach different sizes in time. In fact, when they are similarly sized (apart) they consume similarly sized food; but when they are put together, the more larger tends to consume larger food particles.

**IX Intraspecific competition : Gause does not hold.-**

As mentioned in the introduction, an important and debated question is related to the validity of Gause’s principle when high intraspecific competition exist (individuals of the same species compete themselves by resources). So, we have two species *A* and *I* exploiting a resource *S*; but *I* presents high intraspecific competition. In this case it seems that both species could co-exist (Begon (1999)). That is, assume species *A* is a weak consumer of *S* and then in principle it must disappear face to the strong consumer *I*; but *I* presents a so high degree of intraspecific competition that *A* has a chance to survive.

Our formalism does not respond the question about coexistence, or not, in this case since Gause does not hold here. In fact, we define a species *I* with intraspecific competition as

\[(S > I) \Rightarrow (S > (I \supset I)), \quad \text{(intraspecific competition)} . \]  

(36)

Now, consider species *I* competing with *A* by the resource *S*, namely,

\[(S > I \supset A) \oplus (S > A \supset I), \quad \text{(37)} \]

since *I* is (high) intraspecific competitor

\[ (37) \Rightarrow (S > (I \supset I) \supset A) \oplus (S > A \supset I), \quad \text{(38)} \]
and Gause does not hold since $(I \supset I) \Leftrightarrow I$ (with exception of $\phi$). Note that we use the term high intraspecific competition. This is so because in the above process we use intracompetition before applying Gause to process (37). Weak intraspecific means that in (37) we use Gause and after the intraspecific character of species $I$. In this case we have exclusion.

**X Virtual process generation.**

In this section we consider a virtual (speculative) possibility to generate new processes from some known. In this sense, the new processes constructed are not necessarily real process. The advantage of this generation processes is to explore some future symmetries of ecological systems.

We define the **dual ecological process** of a given process as this one where the changes $(>) \rightarrow (\supset)$ and $(\supset) \rightarrow (>)$ operate. We define the **inverse ecological process** as this one where the changes $(>) \rightarrow (<)$ and $(<) \rightarrow (\subset)$ operate. For instance, the dual of $(A > B)$ denotes by $(A > B)^D$ is $(A \supset B)$, namely, $(A > B)^D \Leftrightarrow (A \supset B)$. The inverse of $(A > B)$ is $(A < B)$, namely $(A > B)^I \Leftrightarrow (A < B)$.

For instance, consider the ecological process of two species $A$ and $B$ in mutual depredation $(><)$ which consume also a primary resource $S$. Moreover, since individual of every specie dies, the primary resources uses this as a food resource (nutrients). So, consider the idealized process where

$$S > (A >< B) > S,$$

obviously, this process is invariant under inversion operation. Namely,

$$\{S > (A >< B) > S\}^I \Leftrightarrow \{S > (A >< B) > S\}.$$

(40)

As other hypothetical example, consider the process $(S > B \supset S)$. From the above definition for dual and inverse operations we have $(S > B \supset S)^{DI} \Leftrightarrow (S > B \supset S)$, namely, we have an invariant ecological process under dual and inversion operations.
XI Time for exclusion (number of generations).

In this last section we will be concerned with a basic discussion of time for exclusion. That is, Gause is a time evolutive process; but it does not refer explicitly to how long is this time for exclusion. It seems quite natural to think that when more similar species in competition are, then more longer the extinction time becomes. To be more explicit, Consider two species $A$ and $B$ in competition according with Gause. Assume species $B$ is excluded in a number $N_B$ of generations. We will assume that all similitude between both species could be quantified by one parameter $s$. That is, $s = 1$ both species are completely similar (same species). Opposite, $s = 0$, means that they are completely different species (genotype, phenotype, etc.). The two parameter $N_B$ (the extinction generation number) and the similitude parameter $s$, are related by the simple expression $N_B = 1/(1 - s)$, proposed originally in reference Flores (1998). So, more similar the species in competition are ($s \rightarrow 1$), a much longer time (number of generation) is necessary to exclusion.

XI Conclusions.-

We have presented a symbology like to set theory applied to ecological interacting process (ECOSET). Chains of depredation or competition were explicitly studied. Particularly, Gause’s exclusion principle was considered in this notation and used as a basic operational tool. For instance, it was applied to competition with sterile individuals (SIT), two species with two resources and, more general, to $N + P$ species with $N$ resources. The symbology is so coherent that: displacement breaks exclusion was obtained with basic operations of our theory. Examples from laboratory and field were explicitly considered.
Resume for symbols

⊢ Perturbation (no depredation).
> Depredation.
⊕ Two independent species in a region (eventually independent process).
⊗ Two interdependent species.
⇒ Temporal evolution.
⇔ Equivalence.
⊃⊂ Abbreviation for competition.
>< Mutual depredation.
or Exclusion (some times ∨).
∑ Independent species (eventually process): A ⊕ B ⊕ C ⊕ D ⊕ ....

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