An axiomatic theory for interaction between species in ecology: Gause’s exclusion conjecture

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Abstract: I introduce an axiomatic representation, called ecoset, to consider interactions between species in ecological systems. For interspecific competition, the exclusion conjecture (Gause) is put in a symbolic way and used as a basic operational tool to consider more complex cases like two species with two superposed resources (niche differentiation) and apparent competitors. Competition between tortoises and invaders in Galapagos islands is considered as a specific example. Our theory gives us an operative language to consider elementary process in ecology and open a route to more complex systems.

I Introduction

After Ryall (2006), theoretical works in ecology are almost completely ignored for empirical searchers. The cause becomes related to inaccessibility of theoretical studies because its presentation. In fact, most of the time, a theoretical paper requires a specialized background knowledge. In this sense, a simple technical language in ecology could be desirable. The purpose of this paper is related with an axiomatic nomenclature (set theory) to describe ecological process and consider, also, predictive events. More important, inference rules are proposed, particularly, the exclusion conjecture is put in an axiomatic way.

Gause’s Exclusion Conjecture GEC (or competitive exclusion conjecture) widely cited in ecology states: \textit{when we have two different species}...
A and B competing for the same invariable (temporal and spatial) ecological primary resource $S$ (niche), then one of them disappear (Begon et al (1996), Emmel (1973), Gause (1934), Hasting (1997)). It is important to note that GEC (which refers to species, not to process) holds when no migration, no mutation and no resource (niche) differentiation exist in the invariable ecological systems. Moreover, it refers to interspecific competition. Applications could be found in many texts of ecology (see for instance Odum (1971)). A direct application of this conjecture to Neanderthals extinction in Europe could be found in references Flores (1998) and Murray (2002). New studies about Neanderthals and Modern Human competition could be found in Mellars (2006).

II Symbology for depredation and competition: basic definitions

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

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

means, species $B$ exploits species $A$ as a source in a sense of depredation. For two no-interacting species $A$ and $B$ (also for ecological process) in a given region we write $A \oplus B$. So, when two species ($A$ and $B$) use the same primary resource ($S$), in a not depending way, we write

$$S > (A \oplus B), \quad \text{(independent depredation)}. \quad (2)$$

The symbol $\Leftrightarrow$ will be interpreted as equivalence between ecological process or species. In the process (2) we always assume implicitly the equivalence:

$$\{S > (A \oplus B)\} \Leftrightarrow \{(S > A) \oplus (S > B)\}. \quad (3)$$

An ecological process like $S > A > B$ does not mean $S > B$ (no transitivity). If also $B$ consumes $S$ we must write: $(S > A > B) \oplus (S > B)$.

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, refuge, etc. The symbol

$$A \supset B, \quad (A \text{ perturbed by } B), \quad (4)$$
means that species $B$ perturbs (interferes) $A$. We note that for depredation we use other symbol ($>$). With these basic definitions we can represent competition between species. In fact, if $A$ and $B$ are two species in competition (no depredation) then we write

$$(A \supset B) \oplus (B \supset A), \quad (A \text{ and } B \text{ compete}). \quad (5)$$

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

$$\{(A \supset B) \oplus (B \supset A)\} \Leftrightarrow (A \supset \subset B), \quad \text{(symbol for competition)}. \quad (6)$$

Before ending this section, we give a useful definition. The notion of potential competitors is related to two species which put together then ($\Rightarrow$) compete. In our symbolic notation:

$$\{S > (A \oplus B)\} \Rightarrow \{S > (A \supset \subset B)\}, \quad \text{(potential competitors)}. \quad (7)$$

Where the symbol $\Rightarrow$ has a temporal interpretation or it defines a temporal direction.

III Gause’s Exclusion Conjecture (GEC)

In our notation the Gause’s exclusion conjecture, discussed in section I, is written as the inference rule,

$$\{S > (A \supset \subset B)\} \Rightarrow \{(S > A) \text{ or } (S > B)\}, \quad \text{(GEC)}. \quad (8)$$

The above statement will be a basic operational tool to consider more general cases or applications like two sources and two predators or, eventually, others (Flores (2005)). The more famous example of exclusion comes from the classic laboratory work of Gause (1934), who considers two type of Paramecium, namely, $P. caudatum$ and $P. aurelia$. Both species grow well alone and reaching a stable carrying capacities in tubes of liquid medium and consuming bacteria and oxygen. When both species grow together, $P. caudatum$ declines to the point of extinction and leaving $P. aurelia$ in the niche.

As said before, other examples of GEC could be found in literature. For instance, competition between Tribolium confusum and Tribolium castaneum where one species is always eliminated when put together
(Park (1954)). In this case is the temperature and humidity which determine usually the winner. In fact, in a medium range of these parameters is only a probabilistic approach which determines the victorious species.

To ending this section, a caution note, in the case of “competition between process” usually GEC does not hold directly.

IV Two species and two resources

Consider two resources $S_1$ and $S_2$ and two species $A$ and $B$ in competition: $(S_1 \oplus S_2) > (A \supset B)$, or $\{S_1 > (A \supset B)\} \oplus \{S_2 > (A \supset B)\}$. Using directly GEC (8) we have the ecological process:

$$(S_1 \oplus S_2) > (A \supset B) \Rightarrow \Rightarrow \{(S_1 > A) \text{ or } (S_1 > B)\} \oplus \{(S_2 > A) \text{ or } (S_2 > B)\},$$

and then the excluding final states:

(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 survives by resource exploitations in a differential (partitioned) way.

The results found in the above process (a-d), have been observed in laboratories where two diatom species (Asterionella formosa and Cyclotella meneghiniana) compete for silicate ($S_1$) and phosphate ($S_2$) as elementary resources. In fact, for different proportions of these components one can see extermination or stable coexistence (Tilman (1977)).

V Extinction of giant tortoises in Galapagos

Concerning to evolution and selection, Galapagos islands are still a prolific resource of study in ecology (Grant (2004)). For instance, native giant tortoises $T$ live in Galapagos islands after centuries exploiting its
natural resources ($S > T$). With the arrivals of humans being ($H$) some invaders ($I$), like goats and pigs, were introduced in the islands and reaching a wild state. Invaders and tortoises, considered as potential competitors (7), compete for primary resources ($S > (T ⊂⊂ I)$). There is a real risk for extinction of species $T$ in Galapagos. From 1995, international agencies are developing an eradication program (Isabela project) to eliminate invaders $I$ and re-introducing species $T$. In our symbolic notation: $S > \{(T ⊂⊂ I) ⊕ (I ⊂⊂ H_T)\}$. Where $H_T$ is the human being re-introducing species $T$ and not compete with. Under this conditions, Gause’s exclusion conjecture (8) could be applied as a first approach and we have the four final process: (a) $S > T$, (b) $S > I$, (c) $S > H_T$ (d) $S > (H_T ⊕ T)$. So, species $T$ is in three (of four) possible final scenarios. Note that if $H_T ⇔ \phi$ (no eradication) species $T$ occupies only one of two final scenarios and then with a mayor risk to extinction.

VI Apparent competition

It is well known (Holt (1984), Jeffries & Lawton (1985)) that sometimes there is apparent competition between two kind of no-competitive species. This is due to the intervention of another (ignored) species which is a real competitor. Examples of this curious process could be found in Begon et al (1996). Let $A$ and $B$ be no-competing species exploiting a resource $S$, namely, $S > (A ⊕ B)$. Let $C$ be a potential competitor (of both) introduced in the system, and consider the process:

$$S > \{(A ⊂⊂ C) ⊕ (C ⊂⊂ B)\}. \quad (10)$$

Like to section V, a direct application of the basic tool (8) permits to obtain the four mutual excluding possibilities:

(a) $S > C$.
(b) $S > (A ⊕ B)$.
(c) $S > A$.
(d) $S > B$.

The process (a) and (b) correspond to the elimination of $(A ⊕ B)$ or $C$. The more interesting cases ((c) and (d)) could be interpreted erroneously as the result of competition between species $A$ and $B$ when the existence of the true competitor $C$ is ignored. The process (10) will
be written in an abbreviate way as:

\[(10) \iff S > (A \supsetsubset C \supsetsubset B). \tag{11}\]

For more general cases like \( S > \{A \supsetsubset B \supsetsubset C... \supsetsubset Z\} \), which does not contain some direct competitors like \( A \) and \( Z \), the result is the same. So, the existence of (ignored) intermediate competitors could be interpreted erroneously as apparent competition.

**Conclusions:**

Gause’s exclusion conjecture was put in a operative symbolic nomenclature (III). It could be applied to different cases like more than one resource or more than two species (IV). The case of apparent competitors was also explicitly treated (VI). Other cases like exclusion with sterile individuals, regional displacement and others, could also be considered (Flores 2005). In resume, this theoretical framework (ECOSET) corresponds to an axiomatic theory to describe, and predict, ecological process.

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**Resume for symbols**

- \( \supset \) Perturbation (no depredation).
- \( > \) Depredation.
- \( \oplus \) Two independent species in a region (eventually independent process).
- \( \otimes \) Two interdependent species.
- \( \Rightarrow \) Temporal evolution.
- \( \iff \) Equivalence.
- \( \supsetsubset \) Abbreviation for competition.
Mutual depredation.
or Exclusion (some times $\vee$).
$\sum$ Independent species (eventually process): $A \oplus B \oplus C \oplus D \oplus ....$

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