Chapter 1

How Communities Evolve

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1.1. Introduction

In Ecology, there is active debate about the nature of changes in large-scale biological systems, such as communities or even the whole ecosystem. The question is, are changes in communities the simply result of the replacement and evolution of its species? Or on the contrary, community change as a body. According to Niles Eldredge (1996), who has been working with these questions during the last decades, to accept these changes as evolutionary, these systems have to operate in an integrated way. According to the results of my research about the trophic organization of the communities of large mammals (Mendoza *et al.,* 2004), communities are and evolve as integrated dynamic systems.

1.2. Trophic Organization of Mammals Communities

To analyze the trophic organization of mammal communities, the faunal list of more than a hundred protected areas from Africa, such as national parks, sanctuaries, forest reserves, etc. were collected. All of them were classified into one of three general types of ecosystem (i.e., arid communities with sparse vegetation, open and closed wooded savannas, that share grass and trees in different proportion, and evergreen forests) and those communities that showed a mixture of ecosystems were excluded.

To obtain the trophic structure of each community, their large mammal species were classified into one of ,twelve feeding categories, further subdivided into different body size classes, obtaining, finally, 18 trophic-size categories:

Carnivores

Hypercarnivores: >70% of vertebrate flesh (three groups according to the size of their prey species)
Omnivores: small vertebrates, carrion, invertebrates, fruit and vegetal matter.
Bone crackers: feeding on carrion or on its own prey.

Ungulates

General grazers: >75% grass (GG I: <300kg, GG II: >300kg).

Fresh-grass grazers: >75% fresh grass (FG I: <300kg, FG II: >300kg).

Mixed feeders: 25-75% grass (MF I: <65 kg, MF II: 65-300 kg, MF III: 300-1000 kg, MF IV: >1000 kg).

Browsers: <25% grass (Br I: < 65kg, Br II: 65-300kg, Br III: >300kg).

Frugivores: <25% grass , >50% fruits and other non-fibrous plant foods.

Omnivores: non-fibrous vegetal matter, mushrooms and animal tissues.

If we consider the number of species of these 18 trophic-size categories as variables, a point in the 18-dimensional space defined by these variables could be considered as a good representation of the trophic structure of the mammal community. Thus, if those communities from the same type of ecosystem occupy a particular region of that trophic space, it can be accepted that they share a common pattern in their trophic structure. However, this 18-dimensional space cannot be represented over a bidimensional surface. Thus, two types of multivariate analysis were used to test if those communities from the same type of ecosystem share a common pattern in their trophic-size structure, using the number of species of the 18 feeding-size groups as independent variables: factorial analysis (Fig 1a), that is a variation of the principal components analysis, and discriminant analysis (Fig 1b).
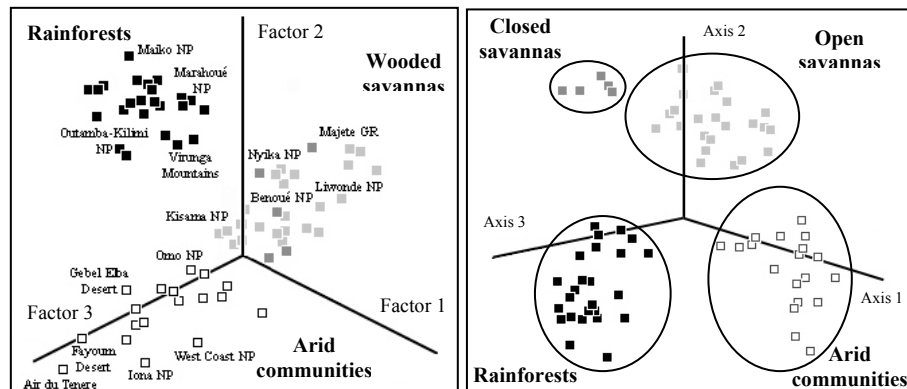

Figure 1. Projection of the real African communities on the trophic-size space defined by the three first factors (a) and the three first discriminant functions (b). Black: evergreen forests; Dark grey: closed wooded savannas; Light grey: open wooded savannas; Empty squares: arid communities with sparse plant cover. NP: National Park, GR: Game Reserve.

The factorial analysis is very interesting because it does not use direct information about the type of ecosystem; the only information provided to the analysis is that contained in the variables, in this case, the number of species from each trophic-size group. In spite of that, the three first factors (Fig 1a) reveal three broad groups of communities that correspond to the three broad ecological categories: arid communities with sparse plant cover, wooded savannas that share grass and trees, and evergreen forests.

However, a discriminant analysis, using direct information about the type of ecosystem, is the appropriate multivariate statistical method to check whether those communities from the same type of ecosystem occupy a particular region of that 18-dimensional space. Only in the case that definite patterns in the trophic structure characterize each type of ecosystem, will the discriminant functions obtained be able to separate them into discrete groups.

According to the results of the two types of multivariate analysis (Fig 1), there is no doubt about the existence of these definite patterns in the trophic structure, characteristic from these broad types of ecosystem. With the discriminant analysis, even was possible to highlight different patterns between open and closed wooded savannas, which the factorial analysis could not, probably because of the low number of closed wooded savannas available for the analysis. The discriminant functions provided clear predictive power even with communities from other continent (Asia) or time period (Pleistocene) that do not share any species with those African ones that were used to identify the patterns (Mendoza *et al.*, submitted). Thus, these patterns are an intrinsic property of the ecosystems, independent of their specific historical circumstances and taxonomic composition, at least of those ecosystems dominated by great mammals.

The appearance of so clear patterns led me ask about the origin of these patterns, and motivated me to develop a model, that is based on dynamic systems theory.

1.3. Explanation of the model

The model has a topological organization that is based on the observed mammal communities. It allows us to see and quantify how energy is distributed and canalized through the community and the consequences that follow for its structure and evolution.
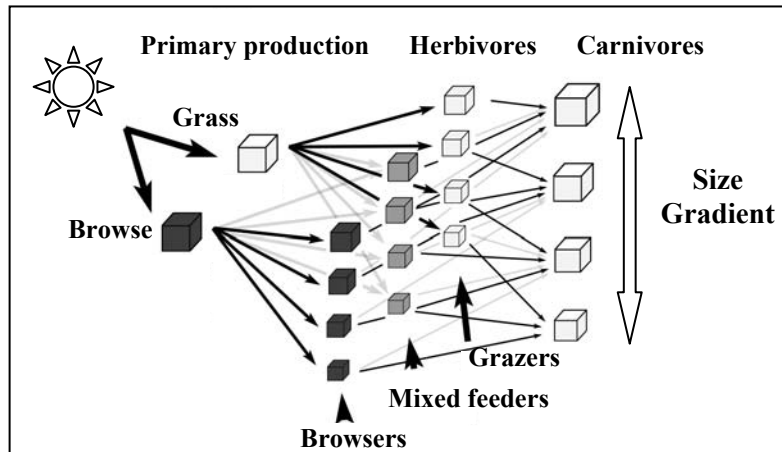

Figure 3. Relations of energy flux between the units of a large mammal community described as a system (see text).

Primary production provides to the herbivore species with different kinds of plant resources: grass, leaves, fruits, etc. That allows a first canalization and distribution of the energy, because different groups of herbivores (i.e., grazers, browsers, frugivores, etc.) show different feeding adaptations and consume these resources in different proportions (see Fig 3). These species show different body sizes, which allows a secondary canalization and distribution of energy: herbivores of different size are consumed in different proportions by different groups of carnivores. These carnivore groups are then characterized by the size of prey.

If we consider *n* groups of species with similar feeding habits as units of a system, each group process an amount of energy, and any real community of large mammals could be represented as a point in the *n-dimensional* space defined by the energy processed by each group. That *n-dimensional* space could be considered as the *trophic state space* of the system. The gradual change through time in the combination of the energy values would be represented as a trajectory. These trajectories, which represent the behavior of the variables of the system, correspond in general to solutions of a system of differential equations.

The continuous arrival of radiant energy from the sun, which is transformed into plant resources, keeps the system thermodynamically far from equilibrium, and the feedback relations between groups result in non-linear dynamics in the system. Both things together lead the trajectories to converge into *attractors*, which can be a single point, a limit cycle or something more complex known as a strange attractor. It is the appearance of these attractors that keep the stable self-organized structure in the system (Kauffman 1993, Goodwin 1994).

Like all the dynamic systems, communities have a set of parameters that determine their behavior. The control parameters of a terrestrial community, described as a system, would be environmental conditions such as precipitation, mean temperature or soil fertility. The way that these parameters control the dynamic of the system is through the growth rates of different types of plant (i.e., trees, bush, grass) that provide to the herbivores with different types of resources (i.e., leaves, fruits, seeds, grass). In this way, if communities are selforganized as a consequence of the appearance of a steady-state point attractor, communities with similar soil and climatic conditions will have similar rates of production of each primary resource, and thus similar properties in their community organization. In other words, communities with similar environmental conditions will have similar combinations in the processed energy values for every group of species defined by feeding characteristics.

This approach describes communities in terms of the energy processed by each feeding group of species. However, given that those species of a particular trophic level of a community process a similar quantity of energy (Damuth, 1995), there is a correspondence between the number of species that a group contains and the amount of energy that this group of species process. In this way, communities with similar environmental conditions not only will have similar values for processed energy by each trophic group, but also similar numbers of species within each group; that is, a similar trophic structure.

That is the way that the model proposes to explain the origin of the pattern revealed in the trophic structure of the large mammals communities. Given that this process cannot be directly observed in real communities, the proposed dynamic was tested with a system simulated by computer.

1.4. Computer simulation

Eighteen differential equations, grouped in three sets, were used to simulate the model:

Growth rate:
control parameters

Intergroups
Inhibition rate   Consume by herbivores   Small inmigration rate

$$\frac{dx_i}{dt} = a_i x_i - b_i x_i^2 - g_i x_i x_j - x_i \left(\sum_{k=1}^{3} c_{ik} \left(\sum_{l=1}^{4} y_{kl} \right) \right) + n; \quad i,j = 1, 2; \ i = j \quad (1)$$

Intragroup Inhibition rate

Two equations of the this first set (1) define the energy processed by two types of plants, browse and grass, which provide to herbivores two different types of resource. Each of these two equations involve one of the control parameters, their growth rates, that according to the model depend on the environmental features, which would be the true control parameters of the system.

Natural death   Plant intake   Predation by Carnivores
rate = 0

$$\frac{dy_{ij}}{dt} = y_{ij} \left(-f + \sum_{k=1}^{2} s_k c_{ij} x_k - \sum_{k=1}^{4} d_{jk} z_k \right) + n; \quad i = 1,\dots, 3; \ j = 1,.., 4 \quad (2)$$

Equations of the second set (2) represent the energy processed by the species of each herbivore feeding-size group (i.e., grazers, mixed-feeders and browsers, with different body-size class), and those of the third set (3), the energy processed by each carnivore group, characterized by the body size of their prey.

Natural death   Predation on Herbivores
rate ≠ 0

$$\frac{dz_i}{dt} = z_i \left(-e_i + \sum_{j=1}^{4} d_{ij} \left(\sum_{k=1}^{3} y_{kj} \right) \right) + n; \quad i = 1,\dots, 4 \quad (3)$$

As the model predicts, the simulated communities are selforganized as a consequence of the appearance of attractors (Fig 4), and those communities simulated with similar combinations of control parameters usually showed similar trophic structure.

In order to analyze the trophic structure of these communities, a region of the control space was explored (Fig 5a). More than 500 points, set by random combinations of both growth rates, the control parameters, were selected to obtain the trophic structure of a large number of simulated communities. To analyze that trophic structure we used the same types of analyses used with the real mammal communities, factorial analysis (Fig 5b) and discriminant analysis (Fig 6b).

Is interesting that, in spite of the fact that the control parameters were homogeneously distributed, discrete groups of communities arose (Fig 5b), in addition, with a remarkable and unexpected relationship with the real ones (Fig 6).
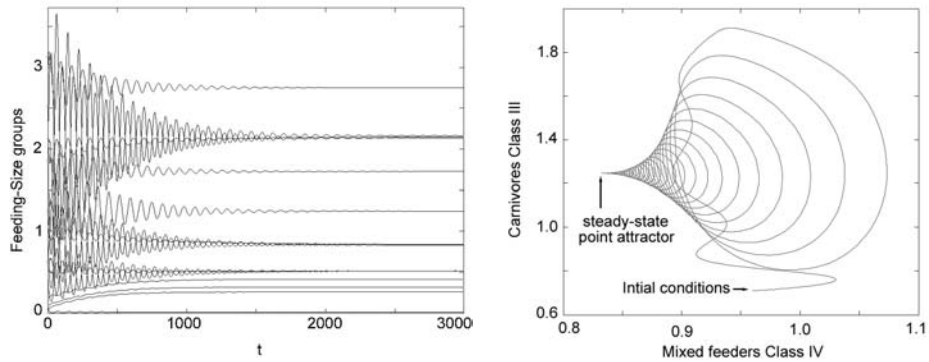
Figure 4. Representation of the first 3000 iterations. a) Energy processed by all the feeding-size groups. b) Space defined by two of the feeding-size groups, partial representation of the trophic-size state space (a1 = 10, a2 = 20).

Figure 6 allows us to compare the results obtained by discriminant analyses with the real communities and the simulated communities. In both cases, there is no doubt about the discrete distribution of the groups in the *trophic state space*. Regard to the simulated communities, one of the groups is characterized because, when their variables are stabilized (the trophic groups), both types of plants show very low abundance, two groups of samples reaches a steady state with different ratios between browse and grass, and the last group stabilizes with trees and no grass. The resemblance with the real ones is amazing, and it was completely unexpected.
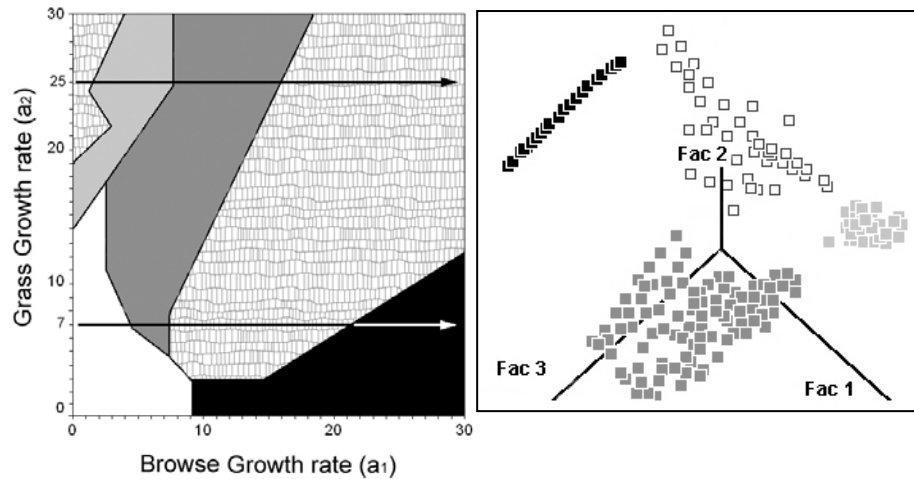

Figure 5. a) Approximate distribution of different regions in the control space which communities stabilize into relatively discrete groups (black, dark and light grey, and white) and those for which variables do not stabilize as a consequence of the appearance of limit cycles or strange attractors (pattern); arrows: see fig 7. b) Projection of the simulated communities of large mammals on the trophic-size space defined by the three first factors. Black: communities stabilized without grass; dark grey: communities stabilized with higher percentage of browse; light grey: communities stabilized with higher percentage of grass; white: communities stabilized with very low amount of both types of plants.
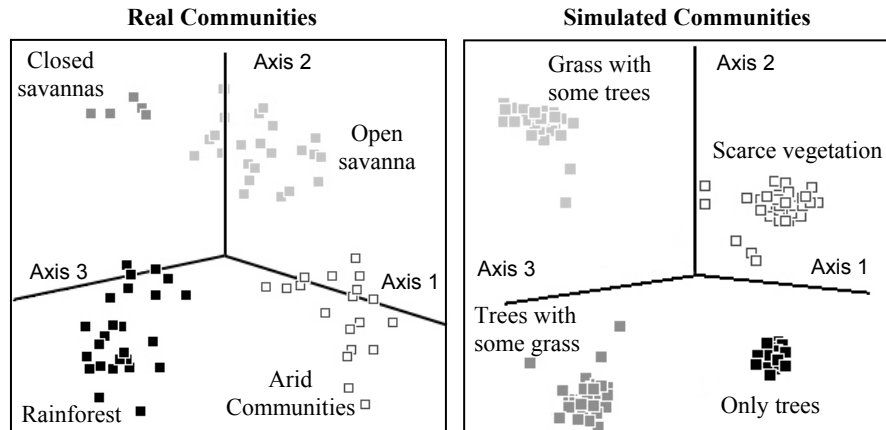
Real Communities   **Simulated Communities**

Figure 6. a) Application of the three first discriminant functions to African communities. Black: evergreen forests; Colors: see Fig 1. b) Application of the three first discriminant functions to the simulated communities. Colors: see Fig 5.

In order to understand the cause of the emergence of these discrete groups new simulations were run but, instead of using fixed combinations of the control parameters, one of them (a_1) changed slowly (Fig 7). The other axis represents the first discriminant axis, a linear combination of the energy processed by all the feeding groups once they are stabilized, that could be considered as a representation of the trophic organization of the community. As you can see (Fig 7), bifurcations are the cause of the appearance of discrete groups of samples that correspond to different ways of trophic organization.
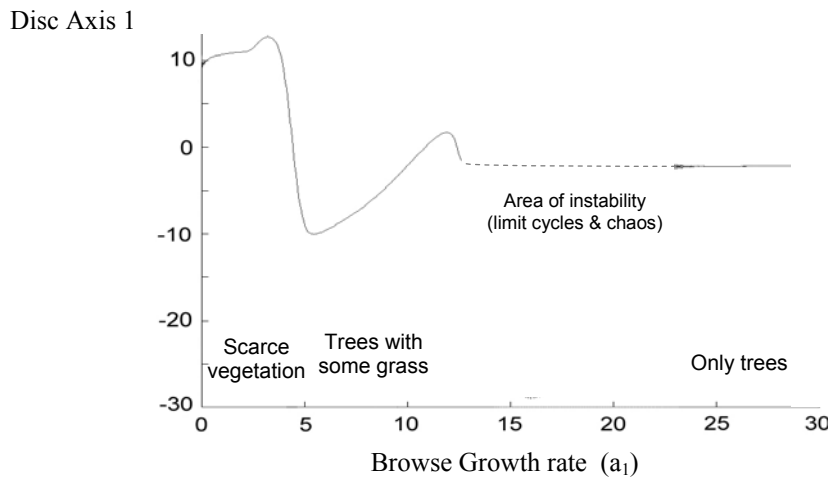
Disc Axis 1

Figure 7. Projection of the first discriminant function tuning a_1 from 0 to 30, keeping constant $a_2 = 7$. Correspond to the lower arrow in Fig. 5a.

1.5. How Communities Evolve

According to these results (Mendoza *et al.*, 2004), communities are unitary structures with coherent properties that result from the self-organizing dynamic of the whole system. Thus, communities evolve as integrated dynamic systems. Through the production rates of different types of plant resources, climatic conditions and soil fertility fix, through a process of self-organization, the energy that every trophic group process, constraining the possible combinations of species.

Seasonal and year-on-year fluctuations of these conditions are compensated by communities changing the number of individuals, and even their weight, so only persistent environmental changes end up affecting the number of constituent species.

A modification in the trophic-size structure of a community implies the extinction from this community of some species and the appearance of others. This can occur by local extinction of some species and the immigration of some others. However, when that immigration is not possible, due to biogeographical barriers or other reasons, similar results can be obtained in a longer term by the evolution of some species towards other feeding habits. In this way, the evolution of a community as a whole system could determine the evolution of their constituent species.

Bifurcations, moreover, would be the cause underlying the remarkable observation that nature appears to be organized in discrete kinds of ecosystems, in spite of the gradual change of most of environmental conditions.

This approach to the biological communities could explain, moreover, the significant correlation between various environmental factors and herbivore abundance and/or diversity, shown by a variety of authors (Olff *et al.*, 2002 and references therein). If the trophic structure of the communities is controlled by these environmental factors through a process of self-organization, that correlation would be an obvious consequence. In addition, this approach also allows us to understand how and why some rules constrain the assembly of the communities, which also has been showed by different authors (Fox, 1999 and references therein).

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