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AN EXTENSION OF THE COMPLEXITY CONCEPT DERIVED FROM THE ANALYSIS OF COLONISATION PROCESSES IN SMALL ISLAND ENVIRONMENTS[1]

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Abstract. The concept of complexity has been and is currently used in association to that of stability in both theoretical and applied studies on natural communities. The reference to linear, totally or partially randomly connected systems, makes the search for a critical value of connectance, and its relation to stability, difficult to achieve. More relevant, the majority of investigations refer to complexity only the structural aspects (number of species and of known interrelations), but biological relationships of various kind affect the populations' dynamics with different mechanisms. Any connectedness index seems to be scarcely effective in measuring complexity, if it neglects the functional components of biological interactions.

This study presents some community assemblages as found and documented in small island environments. They have been investigated through qualitative methodology under the hypothesis of moving equilibrium. Ten models are presented and discussed: from the simplest one, with two competitors, to that of three competitors and one specialized predator; from a community organized at two trophic levels, to that at three trophic levels. For any situation, pairs of models are compared. They represent communities dynamically differently, but richness and connectedness are equivalent. Counterintuitive results following immigration/emigration processes, where modifications of the system network are often imposed by these processes, are also discussed.

Introduction

The relationship between complexity and stability in ecology is an open question. Nevertheless, the concept of complexity has been widely used in investigating the stability of natural communities. Most of the results obtained from theoretical studies do not agree with the empirical observations. Gardner and Ashby (1970) and Armstrong (1982) studied the stability of randomly constructed interaction matrices, and showed that, for partially connected systems, a critical value of connectance exists: below it, systems are stable; above it, they become unstable. The authors also stated that the probability of stability of totally connected models decreases as the number of variables increases; these results have been confirmed by May (1972).

But linear models, such as those considered by Gardner and Ashby, are unreal descriptions of ecological systems. Even though a critical value of connectedness has been found in partially connected non-linear models (Martens 1987), the presence of nonlinearities makes the concept of "critical connectance" hardly manageable (Somorjai and Gowsami 1972, Yodzis 1980).

A further restriction to randomly connected models refers to the feasibility of equilibrium states. Taking into account only feasible cases, Roberts (1974) showed that stability increases with the number of interacting species, while opposite results were obtained (Gilpin 1975) by considering the different interaction strengths operating into the model.

The main criticism against randomly connected models stems from the high number of functionally unfeasible assemblages. Ecological systems are composed of food webs with well-defined trophic structures; consequently a quasi-random links' allocation must be applied to obey the rules of natural selection, as expressed by specific ecological processes.

With the assumption that food web models agree with the conservation law (example: assimilation efficiency always below 100%), De Angelis (1975) documented real cases where increased connectance meant increased stability. Granero-Porati et al. (1982) showed that models with n-1 prey species and only one predator are asymptotically stable for any n, while the increment of predators lowers stability. King and Pimm (1983), instead, found that stability decreases when the number of species exceeds four, and that increased stability can be obtained through the addition of competitive interactions (increased connectance) among populations belonging to the same trophic

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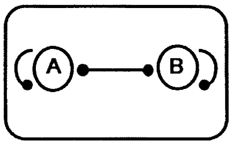

	A	B
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B	-	+

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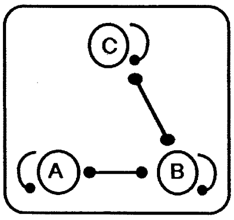

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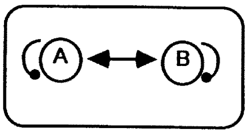

	A	B
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B	+	+

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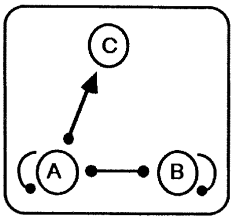

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C	-	+	?

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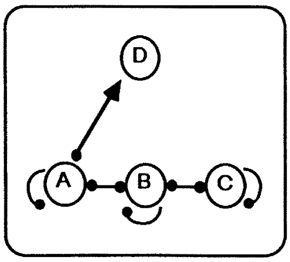

	A	B	C	D
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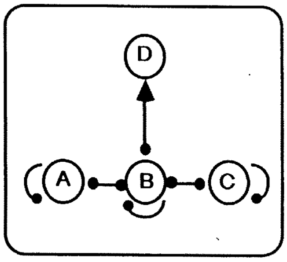
C	0	-	+	+
D	?	+	-	?

6



	A	B	C	D
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B	0	0	0	+
C	-	0	+	-
D	+	-	+	?

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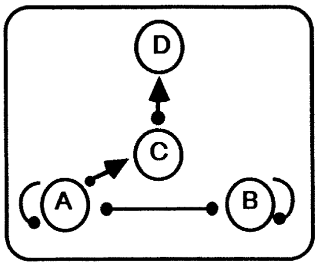

	A	B	C	D
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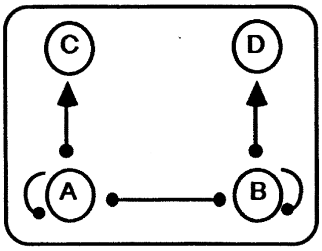
B	-	+	0	-
C	0	0	0	?
D	+	-	?	+

8



	A	B	C	D
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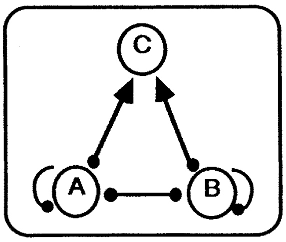
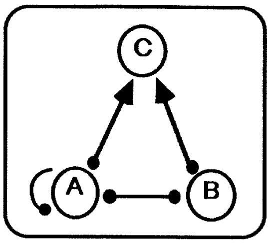
B	0	0	0	+
C	-	0	+	+
D	0	-	+	+

9



	A	B	C
A	+	-	?
B	-	+	?
C	?	?	?

10



	A	B	C
A	+	-	-
B	-	+	?
C	+	?	-

Model 1 - The simplest community with two competing species depicted in a totally connected system. A and B are also self-damped, as an expression of their logistic growth. Below the graph is the Table of predictions obtained by applying the loop analysis methodology.
Model 2 - Three competitors in a partially connected system and its table of predictions.
Model 3 - Simple system with two-species acting as direct mutualists. The system is totally connected.
Model 4 - Two competing species and a species preying upon one of them. C is not self-damped, because its growth is not completely regulated at the intraspecific level (not necessarily density-dependent).
Model 5 - An extension of model 4, with one added competitor at the lower trophic level.
Model 6 - A variant of model 5, with the predator feeding upon a species involved in two competition processes.
Model 7 - A three-trophic-level system with a chain of predation and two competitors.
Model 8 - Two species that prey separately upon two species in competition between themselves.
Model 9 - An almost totally connected system with two competitors and one predator.
Model 10 - A variant of model 9, where one of the two competitors is not self-damped.

level. Diverging conclusions, derived from mathematical analysis of more realistic models, could be explained in the frame of different ecological constraints and conceptual premises. In fact, neither the concept of stability nor that of complexity have been so far satisfactorily worked out.

Both the number of species (a measure of diversity, known as *richness*) and the connectance (or connectedness, percentage of non-zero elements of the interaction matrix) have been utilised for measuring complexity. Margalef and Gutierrez (1983) combined diversity (richness) and connectedness in a new index of complexity of ecological systems, and actually a relationship exists between the two aspects that seem to be inversely related.

In all the cases investigated, complexity refers only to the structural elements (variables and branches of interaction), while it is known that biological relationships affect differently the dynamics of the interacting populations (in two-species models, for instance, characteristic patterns in equilibrium abundances are found for each kind of interaction).

According to Patten (1982), who raised the question of indirect interaction, and Taylor (1985), who provided new suggestions about ecological complexity, when the number of system components increases, the corresponding pattern of equilibrium abundance change. Furthermore the feedbacks, which are associated with the circuits generated by intricate links' combinations, often determine unexpected, counterintuitive effects.

Because increased complexity is the first consequence of animal colonisation processes, this study examines some of these phenomena as they are known to occur (Simberloff 1970) in small island environments. It is documented (Bodini 1989; Bodini and Giavelli 1989) that in simple models, such as those describing island ecosystems, untrivial dynamics exist due to feedbacks associated with loops that even a few interrelations can generate.

Methods

The investigation has been carried out using loop analysis, under the hypothesis of moving equilibrium (Levins 1974; Puccia and Levins 1985). The phrase "moving equilibrium" is used with the meaning and extensions found in Levins (1974): when, in the system equation $dx_i/dt = f_i\ (x_1, x_2, \ldots, x_n; c_1, c_2, \ldots, c_p)$, the constant parameters c change at a rate slower than that of the x variable parameters, the system is in moving equilibrium.

The responses of equilibrium levels to changes in the growth rate of populations are determined, and arranged within tables of predictions for the moving equilibria. As such, the tables become tools for understanding both direct and indirect interspecific processes. In this context, we can extend the qualitative analysis and predict how the system will behave in response to a variation of one or more components.

Every model presents as many alteration entries as there are components belonging to it. Together the outcomes (arranged in tables of predictions) show how input on a variables' dynamical changes (growth rate increases) affect eventually the equilibrium values of all the components.

The responses of equilibrium levels to changes of growth rate of the species, organized in tables of predictions, are made up of symbols that express: (+) increase, (—) decrease, (?) unpredictable result, (0) no change. Symbols in parentheses mean that uncertainties occur for those predictions, and the outcomes have to be considered on a chance basis.

The table entries derive from the analysis of model's paths and feedbacks. A change in the equilibrium value of a generic j^{th} component (∂X_j^*; the star identifies the equilibrium value), produced by altering a parameter (∂c), is determined through the formula:

$$\frac{\partial x_i^*}{\partial c} = \frac{\sum_{i,\,k} \frac{\partial f_i}{\partial c} \cdot p_{ji}^{[k]} \cdot F_{n-k}^{[comp]}}{F_n}$$

applied n×n times (n: number of model components) to give the elements of the table. One can read the formula as follows:

- the i-indexed summation comprises all the functions f_i that include the altered parameter c ($\partial f_i + \partial c$);
- the k-indexed summation is for any *open path* $p_{ji}^{(k)}$ that leaves X_i towards the component X_j whose equilibrium value has to be computed. An *open path* is a circuit that connects two components without crossing any other component more than once. The length of the path is given by the k crossed components minus one (k-1). The summation is necessary because, depending on the model, several paths might exist that refer to the same pair of components;
- each path is multiplied by the corresponding *complementary feedback* F_{n-k}. To evaluate a complementary feedback of a given open path, the subsystem of n-k components is examined with interconnections not included into the previous path;
- the resulting quantity is divided by the overall feedback F_n, computed only once for the whole system of n components.

The analysis has been developed using generalized Lotka-Volterra equations (GLV)

$$\frac{dN_i}{dt} = N_i \left[r_i + a_{ii}\ N_i + \sum_{i=j=1}^{n} a_{ij}\ N_j \right]$$

where $a_{ii} = 0$ for the predators (only hampered by their source of food), and $a_{ij} < 0$ for the prey species (according to the logistic growth model). The linearization of these equations near equilibrium leads to a *community matrix*, represented by loop analysis as a signed digraph.

External perturbations act continuously on each population of any ecosystem, and are intrinsicly necessary to maintain their dynamical equilibrium (cf. Odum 1983). As an event occurring outside the system forces one or some parameters (birth rate, mortality rate, efficiency of predation, etc.) to change, the growth rate of the affected variable changes as well. If the growth rate increases, one can say that a positive input on the system has occurred. On the contrary, an event producing a decrease in the growth rate of a variable is called negative input. As a result of an input on the system, population abundances change, so that the system itself moves towards a new steady-state.

Colonization models: results and discussion

Small islands are inhabited by communities simpler than those occurring in open environments. Impoverishment, disharmony, dispersal, endemisms, and many other phenomena characterize the biota of small islands (Williamson 1981) and make these widely diffused places on earth perhaps the most interesting laboratories for assessing and validating ecological theories. Also for modeling needs, the natural communities in small islands are a suitable starting-point, as we can describe them mathematically with an acceptable degree of realism.

In the analysis, herbivores at the lowest trophic level were considered. The simplest model with interacting species is that of two competitors (model 1). As known, the stability of equilibrium for such a model requires the intraspecific competitions be stronger than the interspecific force. Because the populations considered in the model are competitors, a positive input in one of them increases its own equilibrium level, while the equilibrium level of the other decreases. The related prediction table shows this characteristic functional pattern.

An immigration event introduces a third species that could turn out to be, for those already present, competitor as well as predator. The prediction table of model 2 (a competitor interacting with one of the other species) is characterized by two question marks for the changes in the equilibrium level of A and C when a positive input occurs on themselves. Unpredictability results, because the complementary feedback for A on itself comes from the two-variable system (B-C): interspecific competition generates a positive feedback, while self-damping paths generate negative feedbacks, and, in terms of qualitative analysis, the sign of the overall feedback for the subsystem (B-C) remains undetermined. The same considerations hold for the unpredicability for C.

If the system is stable, however, the intraspecific forces are stronger than the interspecific ones, and the undetermined predictions can be resolved (two pluses replace the two question marks). Rows and columns for A and C show that a positive input increases their equilibrium levels so they help each other. Dynamically, A and C could be regarded as indirect mutualists: two mutualists, as drawn in the model 3, behave in such a way that an input on the growth rate of any of them produces the same changes in the abundance of both partners.

With the C predator feeding upon one of the competitors, the community can be described by model 4; this graph has the same number of variables and the same ratio of pair of species directly interacting (*i.e.* the same connectedness) than the previous one. An input on A leaves unchanged itself and B, while an input on B has no effect on A, but increases its own level. Species A and B do not behave as competitors, as one could intuitively deduce from the links in the model. In fact, direct interactions between A and B result in zero complementary feedbacks, due to the presence of the predator. The models 2 and 4 represent communities dynamically different, though richness and connectedness are equivalent.

A frequent colonisation event refers to a predator added to a three-competitor system (as that of model 2). Models 5 and 6 present two variants: in model 5 the predator leaves unchanged the B-C competition, while B and A, because of the predator, are not competitors at all; in model 6 neither B-C nor A-B are competitors. Depending on which one of the competitors becomes the prey, models change their dynamic patterns of interactions, even though the structural characteristics (richness and connectedness) are the same.

A new predator invading the environment by immigration yields to the scheme depicted in model 4. If such a new species is a top-predator (cf. model 7), it restores competition at the lowest trophic level: in fact the direct competitive links have a negative complementary feedback.

If the new predator feeds on the first trophic level, no A-B competition occurs (cf. model 8), as happens in model 4. Here too, different links combinations make the system dynamically different, but richness and connectedness do not vary.

The prediction table for a three-species community (one predator feeding on two competitors, model 9) confirms the untrivial role of the network effect: a dynamic pattern of competition is produced by indirect effects mediated by the predator, not as a linear consequence of direct interaction. Direct links between A and B have zero complementary feed back, and competition results only from the paths that connect the two prey species through the predator.

In addition to immigration processes, emigration might also be considered, provided that a negative term of flux is added to the dynamic equations. In the loop models, self-enhancing links on the variables involved in the emigration event have to be added. With reference to model 9, assuming that individuals belonging to one of the competitors (say B) move away, a self-enhancing term should be added on it, and a balance between the two opposite actions (emigration and logistic growth) determines how B affects itself: if they are equally strong, no self-loop on B must be imposed.

In model 10 no complementary feedbacks exist for the predation on A, so that these links are not bound up with any quantitative effect on the equilibrium levels of A and C. As a consequence, and also because C inhibits B (competitor of A), a positive input on the predator affects positively A's equilibrium level. Furthermore, a positive input on A decreases the abundance of its predator: the emigration process makes the predator presence advantageous for A, while the predator is not favoured when the growth rate of A increases. These results are counterintuitive, if compared to the dynamics of the predator-prey interactions, and depend on modifications of the system network imposed by the emigration process.

Conclusions

Loop analysis, under the ''moving equilibrium'' approach, can detect characteristic patterns of variation of equilibrium levels associated with any type of interaction (competition, mutualism, etc.). The addition of one or more species (as a result of colonisation processes), in increasing the system complexity, renders the network more and more rich in feedbacks: in two-species models these patterns of variation are enhanced by inputs that change the growth rate of the populations involved, but in complex systems the cause-effect aspects of the relationships are reassembled through the system network.

Connectedness, described as the quantity of non-zero interaction terms out of all those theoretically possible, accounts for structural aspects only, and as such does not seem to be an exhaustive measure of complexity. In fact the combination of links generates indirect interactions that, together with the direct ones, affect the equilibrium levels of all the species in real, multivariable systems. Such a feature cannot be neglected in dealing with the concept of complexity, and functional aspects of interactions must become an integral part of it.

According to the investigations discussed above, we found that: (i) dynamics associated with a single relationship change in unexpected ways; (ii) species not directly connected behave functionally as if they were directly connected; (iii) changes can be very different in systems with same values of diversity and connectedness.

To satisfactorily answer the dilemma of complexity of natural communities, it would be necessary to investigate and clarify the role of short and long loops on the dynamic properties of systems. It is still unclear how to handle these links, mainly because it remains mathematically difficult to come up with an answer for each effect on the equilibrium level for species buffered by the system network: links with no dynamic consequences, if considered as part of certain loops, can belong to other paths too, whose complementary feedbacks have an effect.

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