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THE ECOSYSTEM AS AN ALGEBRAIC CATEGORY: A MATHEMATICAL BASIS FOR THEORY OF COMMUNITY AND ECOSYSTEM IN ANIMAL ECOLOGY

B.S. Niven, School of Science, Griffith University, Nathan, Brisbane, Australia, 4111

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Abstract: A formal definition of 'ecosystem' is shown to obey the axioms of category theory. The definition makes use of a previously published symbolic definition of an animal's environment and includes also the formalized notion of an animal community. A product of the category is a food web in the ecosystem. Methods of classification and comparison of real-life communities and ecosystems result from the definitions. Non-overlapping communities within the same habitat may be differentiated precisely. Illustrative examples of communities and ecosystems are given using the ecology of the Common Octopus *(Octopus vulgaris)*. An analysis of R.L. Kitching's water-filled treehole communities is also given.

Introduction

Rosen (1958) showed how the algebra of categories might be useful in general in theoretical biology. In the present paper it is shown that the 'ecosystem' of animal ecology obeys the three axioms of category theory (see for example Manes 1976). The ecosystem will be defined by using a formal symbolic definition of the environment of an animal which has been found useful in field ecology. The definition of ecosystem given here incorporates a definition of community. Both definitions lend themselves to simple classifications of observed communities and ecosystems which accord well with present practices of field ecologists. A product in the category is a food web in the ecosystem.

An animal's environment

A symbolic definition of an animal's environment was published by Niven (1980). This was used by Andrewartha and Birch (1984) as a basis for their own approach to animal ecology. These authors also used the definition to classify the environments of a number of animal species including limpets, insects, a moose and a buffalo. They introduce a diagram called an 'envirogram' which displays objects in the environment in their correct place according to the formal definition. The environment is defined as a structured set of objects. There are two subsets, called the 'centrum' and the 'web'.

The *centrum* includes those objects which affect the subject animal directly; it is subdivided into four subsets called 'Resources', 'Mates', 'Predators' and 'Malentities'. Resources are objects such as items of food, packages of energy (heat, light etc.) and places such as suitably-placed rocky shelves for breeding purposes. The definition of 'Mate' requires that an offspring will probably result from the union, thus a sterile animal of the opposite sex would not be classified as a mate. Self-matings are allowed. The subset 'Predators' includes also the parasites of the subject animal; these objects benefit from the encounter with the subject animal. A 'Malentity' is an object which adversely affects the subject animal without itself benefitting by the encounter. A typical malentity is the person who steps on an ant; the human probably does not even notice the encounter whereas the subject animal (the ant) is damaged or destroyed.

The *web* includes those objects which affect the subject animal indirectly. It is subdivided into various orders of 'modifiers'. First-order modifiers are objects which modify elements of the centrum. Thus a person acting as a malentity in the environment of an ant may be 'modified' by being stung by a wasp and hence removed from the scene so that the ant does not encounter the person at all; the wasp is classified as a first-order modifier in the environment of the ant. Second-order modifiers modify first-order modifiers, and so on. The web is formally defined as an infinite set of modifiers. In practice animal ecologists rarely use modifiers of order greater than two, nevertheless these do sometimes form part of an ecological study, for example Andrewartha and Birch (1984) give some third-order modifiers for the limpet *Cellana tramoserica* and Kitching (1983) gives an envirogram for the aquatic snail *Lymnaea peregra* which includes some third-order modifiers. It is often convenient in theoretical work to refer to objects in the *centrum* as 'zero-order modifiers'.

The definition of environment incorporates four primitive terms special to the theory of animal ecology. The interpretation of one of these includes stochastic variables. In addition the definition of a mate is a probabilistic sentence. Thus the proposed mathematical basis is probabilistic in two different ways both of which are at a foundational level. Since the definitions of community and ecosystem given in this paper are dependent on the environment definition they too are fundamentally stochastic. Also since the environment definition is a functional one it follows that the definitions of 'community' and 'ecosystem' are likewise functional. Each subset of the environment is defined for a specific animal at some specific time. In practice this is no obstacle to the use of the resulting classification in a practical case, since results observed from studies of many animals of the same species during intervals of time are concatenated to yield an envirogram. More formally we may replace the sub-index 't' in the definitions by 'τ' representing an interval of time.

Community

There are at least three notions of community in current ecology literature:

(i) In human ecology 'community' is used to mean a set of humans usually in a specific place. This set would be called a 'population' by animal ecologists.

(ii) In plant ecology 'community' is often used to mean the set of all plants in a particular area, which may or may not interact in an obvious way.

(iii) In animal ecology 'community' is often used to mean a set of interacting populations in which the interactions are fairly obvious and easily measured.

In the present article the third meaning is used, except that the interactions are formally among individuals instead of populations.

The idea of 'habitat' is required in order to define an animal community. Unfortunately the word has been used in at least two quite different ways in animal ecology. In this article 'habitat' is used to mean "... a place that might be habitable for the animal whose ecology is being studied. The boundaries of the habitat and the qualities that determine the boundaries are fixed arbitrarily by the ecologist". This is the meaning accepted by Andrewartha and Birch (1984). The quotation is from Elton (1949). So a habitat is a specific place, not a class of places. 'Habitat' will now be used as the fifth primitive term special to animal ecology.

In lieu of "animal 'a' is a kth-order modifier of animal 'b' " we now write "Mod^k: a $\rightarrow$b", *i.e.* "a kth-order modifier sends animal 'a' to animal 'b' ". The idea of modifiers in an environment is thus transformed into the mathematical notion of a morphism. Then an nth-order animal community C_n within a habitat is a structured set of animals a, b, ... such that for every ordered pair (a, b) we have Mod^k: a $\rightarrow$b, k = 0, 1, 2, ..., n, where k is the smallest integer for every pair.

If n is small then C_n will be a set of animals which are closely knit together and several different communities may occur. Animal ecologists usually work with such communities. If for the moment we imagine that the elements of C_n are plants and their connecting morphisms are known then the plant ecologists' notion of community would be satisfied when n is large. For this definition to be helpful certain universal modifiers must be excluded. Oxygen and thermal energy are examples of universal modifiers. In any group of animals units of oxygen or heat are resources for all the animals, thus an animal 'a' which uses some particular unit of energy, say, is removing this resource from animal 'b' and is thus formally a first-order modifier in b' s environment. So all animals in a habitat are sent to each other by the morphism Mod^1 (first order modifier). For this reason we exclude the universal modifiers when classifying a community.

Ecosystem

The nth-order ecosystem $\mathcal{E}_n$ associated with the animal community C_n is a category. The morphisms of $\mathcal{E}_n$ are the modifiers in the environments of the animals a $\in C_n$ of order not greater than n. The objects of $\mathcal{E}_n$ are the elements of C_n. The universal modifiers which were excluded when classifying C_n we now include in $\mathcal{E}_n$.

The ecosystem obeys the three axioms of category theory (see *e.g.* Manes 1976) as follows:

I. The associative law. For example if animal 'a' is a mate of (a third-order modifier of a predator) of animal 'b' then animal 'a' is (a mate of a third-order modifier) of a predator of animal 'b'.

II. Identity morphism. An identity morphism in $\mathcal{E}_n$ may be obtained as follows. We have, for animals 'a' and 'b', that a = b iff Ea = Eb, where Ea and Eb are the two environments (Niven 1983). If now we write E^{-1} X for the animal whose environment is X then E^{-1} Ea = a thus E^{-1} E: a $\rightarrow$ a and 'E^{-1} E' is identity morphism in $\mathcal{E}_n$.

III. If for animals a, b, a', b', (a, b) $\neq$ (a', b') then Hom (a, b) $\cap$ Hom (a', b') = 0 i.e. the set of morphisms connecting one pair of animals is disjunct from the set of morphisms connecting any different pair of animals. This must be so if we include the end animals.

Notice that Hom (a, b) may well include non-animal objects such as plants, viruses, particles of soil or mineral matter, quantities of water, units of energy and so on. In most field studies many hundreds of animals of scores of different species are likely to form the community and the non-animal objects in the ecosystem may be extremely numerous. It may sometimes, in a specific case in the field, seem sensible to add some extra non-animal objects, which would not normally be included in $\mathcal{E}_n$ because, although they are modifiers of some animal in the community, they do not enter into a connecting link between some pair of animals. We shall call these 'external modifiers'. An example is given in the ecosystem of the following section.

An interesting mathematical object within the category $\mathcal{E}_n$ is the product $X^{\mathrm{Pred}}\, Y$ where X and Y are sets included in C_n and for all x $\in$ X and all y $\in$ Y we have that Pred: x $\rightarrow$ y, 'Pred' standing for 'predator'. The product may be extended to more than two sets. It may also be defined in terms of 'resource' instead of 'predator'. This mathematical object is the analogue of an interesting object in field ecology called a 'food web'. Food webs are well explained by Cohen (1978), who gives an example in which a species of snake eats a certain species of frog which in turn eats two species of insect. If we refer to the four sets of these animals in the habitat as S, F, I_1 and I_2 then the two products are:

$S^{Pred} F^{Pred} I_1$

and $S^{Pred} F^{Pred} I_2$

Cohen also includes three species of the willow, *Salix*, in his example; for the purposes of this paper, however, we omit the sets of plants.

Illustrative examples of communities and ecosystems

The Common Octopus, *Octopus vulgaris*, is particularly well-known in the Mediterranean. Its food consists mainly of crabs, lobsters, bivalves and gastropods (Mangold 1983; Ambrose and Nelson 1983). R.F. Ambrose (pers. comm. 1984) remarks "Crabs seem to be the favourite food everywhere. Octopuses often hunt 'speculatively' by feeling under rocks and in cracks; all the hunting I have observed in the field has been of this sort." However if the anemone *Calliactis parasitica* is present on the crab *Dardanus arroser*, the octopus will not eat that crab (Ross 1971; Ross and von Boletzky 1979). Thus a crab of this species is a resource of a subject octopus and an anemone of the right species is a first-order modifier. An octopus constructs a lair which affords a certain amount of protection from its predators, the most important of which are large eels, in particular the Common Moray, *Gymnothorax mordax* (Grzimek 1974, Lane 1960). Thus the lair is a first-order modifier of an eel of this species in the environment of a subject octopus.

As an illustrative example consider a small habitat in the Mediterranean containing an octopus lair. The animals present are:

1 *Octopus vulgaris*;
2 crabs *(Dardanus arroser)* of opposite sex;
1 anemone *(Calliactis parasitica)*;
1 eel *(Gymnothorax mordax)*;
2 passing fish.

We have the following morphisms:

Pred: octopus → $crab_1$
Res: $crab_1$ → octopus
Pred: octopus → $crab_2$
Res: $crab_2$ → octopus
Mat: $crab_1$ → $crab_2$
Mat: $crab_2$ → $crab_1$

All these morphisms are zero-order modifiers, so a zero-order community C_0 in the habitat is the set {octopus, $crab_2$, $crab_2$}.

If now we add the eel to C_0 we may write down the following morphisms:

Pred: eel → octopus
Res: octopus → eel
Mod^1: $crab_1$ → eel
Mod^1: eel → $crab_1$
Mod^1: $crab_2$ → eel
Mod^1: eel → $crab_2$

The crabs are resources of a resource of the eel and are thus first-order modifiers in the environment of the eel. The eel is a predator of a predator of the crabs and is thus a first-order modifier in the environments of both crabs. Thus the set {octopus, $crab_1$, $crab_2$, eel} is a first-order community C_1 in the habitat.

If now to the zero-order community of {octopus, $crab_1$, $crab_2$} we add the anemone, we may add the following morphisms:

Mod^1: anemone → octopus
Mod^2: octopus → anemone
Mod^1: anemone → $crab_1$
Mod^1: $crab_1$ → anemone
Mod^1: anemone → $crab_2$
Mod^1: $crab_2$ → anemone

As explained above the anemone is a first-order modifier in the environment of the octopus. When we consider the anemone as the subject animal we find that a crab enters its environment as a first-order modifier by conveying the anemone to its food; we can find an item of food which is such that it does not become a resource of the anemone without the intervention of the crab. Thus the octopus, as a predator of the crab, is a second-order modifier in the environment of the anemone. Notice that the crab is not a resource, mate, predator or malentity of the anemone, *i.e.* it is not a zero-order modifier in the anemone's environment. So there is a basic asymmetry in the morphisms between anemone and octopus. When we examine the functional relations between crab and anemone, however, we find symmetry; a crab is a first-order modifier of the anemone and the anemone is a first-order modifier of the crab. These arguments lead, then, to the conclusion that the set {octopus, $crab_1$, $crab_2$, anemone} is a second-order community, C_2, in the habitat.

Now consider the set {octopus, $crab_1$, $crab_2$, eel, anemone}. The morphisms to be added are:

Mod^3: eel → anemone
Mod^2: anemone → eel.

The first of these comes about because in the environment of the anemone the octopus is a second-order modifier so the eel acts as a third-order modifier if it eats the octopus. The second morphism is true because the octopus is classified as a resource in the eel's environment; the crab is a resource of the octopus and the anemone a modifier of that resource. Thus the given set is C_3, a third-order community in the habitat. The two passing (anonymous) fish may possibly enter into the scheme if high order morphisms are considered, or if they happen to be suitable octopus prey. However two large fish of suitable species are unlikely to be elements of an animal community of low order which contains the octopus.

The ecosystems associated with C_0, C_1, C_2 and C_3 will include such objects as oxygen and thermal energy, both of which are resources of all the animals. The octopus lair, which is a first-order modifier, may be added to $\mathcal{E}_1$, $\mathcal{E}_2$ and $\mathcal{E}_3$ as an external object, since it does not link any pair of animals. The lair protects the octopus from the eel and so is a first-order modifier in the eel's environment by modifying a resource. It is also a first-order modifier in the octopus' environment by modifying a predator. However we cannot write Mod^k: eel $\rightarrow$ octopus for some small k via a path which includes the lair. So the lair is an 'external modifier'. In a real-life habitat in the Mediterranean containing large numbers of many species of animals the lair would almost certainly be incorporated in the ecosystem via chains of modifiers connecting pairs of animals and it would be unnecessary to add any external modifiers.

An analysis of a water-filled treehole community

R.L. Kitching has studied communities of animals, mainly insects, in water-filled treeholes in England, Australia and Indonesia (Kitching 1986, pres. comm.). In this analysis only the first of these studies is used (Kitching 1971). It was undertaken in the beech forests of Wytham Woods, Berkshire, England. The following animals were found:

(i) Two species of mosquito, *Aedes geniculatus* (Olivier) and *Anopheles plumbus* Stephens, referred to here as 'A_1' and 'A_2'.

(ii) Two species of midges, *Metriocnemus martinii* Thienemann and *Dasyhelea dufouri* Laboulbène, referred to as 'M' and 'D'.

(iii) The hoverfly *Myiatropa florea* (Linnaeus), referred to as 'Y'.

(iv) A small detritus-eating beetle *Prionocyphon serricornis* Müller, referred to as 'P'.

The mosquitoes require sugar secretions to provide flight energy and the females require a blood meal to ensure maturation of eggs. Herbs provide the sugar and vertebrates the blood. Midge D requires plant juices for food and the females probably feed on the blood of other adult insects. The hoverfly requires pollen meals provided in Wytham Woods by flowers of teasel and ivy. All the insects in the water-filled treeholes are preyed upon by birds, spiders, other insects and a variety of other insectivorous animals. They may be blown away and be unable to find further treeholes in which to lay eggs. Heavy rain or extreme temperatures will cause considerable mortality. The larvae of A_1, A_2, M, D, Y and P are all saprophages *i.e.* they eat rotten compostlike particles present in the water.

In order to deal with the insects throughout a lifecycle we choose a suitable interval of time during which the modifiers in the insects' environments may act. Since all the larvae in one particular treehole have as resources the rotting particles in the water they are first-order modifiers of each other. Thus if we choose just one water-filled treehole as the habitat the community is a first-order one which includes all members of all six species. If now we use a larger habitat then the predators of the adult insects should be included in a higher order community, such as web-spinning spiders (there may perhaps be a dozen of these), seven or eight species of insectivorous birds, a few species of entophagous insects and possibly a bat (Kitching, pers: comm. 1986). The corresponding first-order ecosystems include the compost-like particles in the water, the water itself and the universal modifiers oxygen and thermal energy. To include the vertebrates which supply the blood meals for the mosquitoes we need to consider higher-order modifiers.

Discussion

The definitions of community and ecosystem provide a simple method for differentiating communities and ecosystems in the field even when in the same habitat. It will often be possible for a field ecologist to observe two nonoverlapping nth-order communities in one habitat providing n is small. The method of classification also provides a means of comparison across the boundaries of habitats and animal species.

The point that the system described here is a stochastic one at a fundamental level accords well with the view of many ecologists that stochastic systems have validity in ecology (See *e.g.* Wiens 1984). It is also widely accepted that population ecology is a basis for community ecology (Southwood 1980, Strong *et al.* 1984), an attitude with which the definitions of this article are in accord.

The environment definition has been used by Andrewartha and Birch (1984) for classifying the environment of our own species. However I myself believe that psychological and cultural matters are of such importance in human ecology that a separate definition should be constructed for our species. Work on this definition is in progress. It may well be that analogues of the community and ecosystem definitions will hold also for humans; for the moment it seem preferable to exclude humans from the system. Future work also is planned for an extension to plant ecology. The morphisms connecting plants and modular organisms have not yet been studied. A more complete definition of ecosystem should be possible once these morphisms are written down.

The use of such a general algebra as the theory of categories lends itself to the construction of a further axiom once the work on plants, modular organisms and humans has been completed. Only with a complete axiomatic system will it be possible to derive theorems which relate directly to ecology and enable us to do the necessary arithmetic to manipulate and predict ecological systems in much the same way as we manipulate and predict physical systems.

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