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# FORMALIZATION OF SOME BASIC CONCEPTS OF PLANT ECOLOGY

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**Abstract.** Formalization of the concepts of the 'environment' of a plant and of a 'community' of plants is given using mainly first-order logic, with some symbols and concepts taken from probability theory, modern algebra and engineering mathematics. The primitive terms from the biological sciences are those used for the analogous animal ecology definitions with two extra added to mean 'plant' and an indication of the well-being of the plant. The functional definitions may be used for classifying objects in the environment and for classifying communities. Examples are given.

## 1. Introduction

Research presently being carried out on the formalized theory of ecology extends over animal, plant and human ecology. The *modus operandi* is to construct a new branch of pure mathematics, using the concepts of modern formal logic. These require, in outline, first the establishment of a semantic basis, the universe of discourse. Secondly primitive terms, undefined in the system, are laid down, followed by formal definitions (usually symbolized), axioms, rules of deduction and, finally, theorems. The theorems are then used as a basis for the arithmetic necessary for management and prediction of real-life systems. For instance when we perform an analysis of variance we use formulae which stem from theorems about the normal, chi-square and F distributions. A second example comes from the physical sciences; the enormously complex calculations required to send the space probe Voyager II on the correct course to Neptune would have been impossible without the underlying theorems of dynamics and space science. So, too, the precise management of complex ecosystems will require appropriate theorems on which formulae that the ecologists will use will be based.

This article contains mathematical definitions of certain concepts basic to plant ecology. Initially, as a basis for the formalization, I have used the ideas of the population biologists H. A. Gleason (1926) and J. L. Harper (1977). Central to their theory is the individualistic concept. Gleason writes "... a logical classification of associations into larger groups, or into successional series, has not yet been achieved." Gleason's work has been greatly extended by Harper and this paper, which is based largely on Harper's work, presents one possible "logical classification" as called for by Gleason. Thus I start with the idea of an individual plant or module (for a discussion of modular organisms see Harper, 1981). The individual is surrounded by objects, both animate and inanimate. My universe of discourse is the set of substantive objects; it includes other plants or modules, animals, soil, rocks, air... and, most importantly, energy, treated in this paper as measurable energy packages. Kinetic energy in the form of light energy, thermal energy or wind, is of particular importance. My universe of discourse includes thermal energy but not temperature, which is assumed in this paper to be defined as in modern physics and thus is not a substantive object. Some of the objects near the individual plant or module will interact directly with it, others will interact only indirectly, many very indirectly indeed. Following Maelzer (1965) I distinguish sharply between those objects which directly affect the individual of interest, plant or module, from now on referred to as the 'subject' and those objects which affect the subject only indirectly. The two sets of objects are, respectively, finite and (potentially) infinite. They are then split into subsets. From this simple but powerful notion will be developed first a mathematical definition of the 'environment' of the subject and secondly a mathematical definition of a functionally related 'community' which includes the subject and also includes in a natural way the loose association of plants in the same habitat referred to by Miles (1979) as a 'patch'. The word 'habitat' here is from Elton (1949); it is used as a primitive term (see below) and means a particular place, not a class of places.

The formalization in this work is non-standard in the sense that I have not restricted myself to first-order logic as is usual in a formalization. I have used ideas and symbolism from engineering mathematics, probability theory and modern algebra, as well as set theory and first-order logic.

Animals are necessarily incorporated in the system. The analyses for animals are available in a series of published papers (see Niven, 1989).

## 2. Symbols and primitive terms

The following symbols from symbolic logic are used in this paper:

(i) The existential quantifier $\exists$. '$\exists$ leaf' means "there is at least one leaf".

(ii) The negation $\sim$. '$\sim$ ($\exists$ leaf)' means "it is not the case that there is at least one leaf"

(iii) The subjunctive conditional $\supset$. '$A \supset B$' means "if A then B".

(iv) The conjunction &. '$A \& B$' means "A and B".

(v) The disjunction V. '$A V B$' means "A or B" (or both).

The symbols $>$, $<$ and $\leq$ are from ordinary arithmetic and mean "greater than", "less than" and "less than or equal to" respectively.

The 'hard' conditional $|$ is the conditional used by statisticians and probabilists for conditional events and conditional probabilities (Feller 1959). '$A \mid B$' means "A (occurs) given that B (occurs)".

The symbol $\rightarrow$ is from modern algebra. $A{:}B \rightarrow C$ means that the morphism A sends B to C.

The symbol t_ used as a subindex comes from engineering mathematics. It means "just before t". So 'the event $A_{t\_}$' means "the event A occurs at a time just before time t".

The brackets $<...>$ are used for ordered pairs, so the pair $<a,b>$ is not the same as $<b,a>$ unless a is the same object as b.

There are seven primitive (undefined) terms from biology used in the definitions. They are:

(i) 'Pl' standing for plant or plant module.

(ii) 'Off' standing for offspring.

(iii) 'An' standing for animal or animal module.

(iv) 'Hab' standing for habitat.

(v) The well-being primitive for plants, G, which is a number.

(vii) The survival and reproduction primitive for animals, H, which is a number.

(viii) The directed-interaction primitive $\xi$, which ensures that the system is totally interactive.

Explications of all primitives are given in the following section.

## 3. The explication of the primitive terms Pl, Off, An, Hab, G, H and $\xi$

In any formalized system such as a branch of mathematics it is necessary to include certain undefined words or phrases called 'primitive terms'. It is not possible to construct a branch of mathematics in which all terms are defined within the system. The primitive terms are then used in definitions, which are incorporated into the axioms from which the rules of inference of the system enable us to prove theorems. Choice of primitive terms which involve notions from the biological sciences results in a formalized system which has a foundation of biology, not physics, as is the case for most modern mathematics.

3.1 $Pl_t(p)$ means that the object 'p' is, at time t, a plant or modular organism which is part of a plant. 'Plant' is a blanket word in this context which is used in this paper to mean the Plantae, Fungi, Protoctista and Monera of Margulis and Schwartz (1982). A module is a "a repeated unit of multicellular structure, normally arranged in a branch system" (Harper 1981). Modules which are not arranged in a branch system are also used in this paper.

3.2 $q\ Off_t p$ means that the object 'q' becomes an offspring of object 'p' at time t, for the first time, *i.e.* q is 'born', becoming a separate object from p at time t.

3.3 $An_t(a)$ means that the object 'a' is, at time t, an animal or modular organism which is part of an animal. 'Animal' is used in this paper to mean the Animalia of Margulis and Schwartz (1982). 'Module' is used as explained in 3.1.

3.4 B Hab b means that the object 'b' occupies the region of physical space 'B' at time t. 'B' is called "the habitat of b". It is a specific place, not a class of places. "The boundaries of the habitat and the qualities that determine the boundaries are fixed arbitrarily by the ecologist" (Elton 1949). The object b must be either a plant or an animal, in the sense used in this paper, *i.e.* either $Pl_t(b)$ or $An_t(b)$.

3.5 The well-being primitive G is a number which expresses the general well-being of the subject plant or module. Following Harper (1977) such things as the rate of increase of dry weight, the amount of wilt and the amount of leaf-blackening are included in G. Also included in G is the probability of reproduction. The number $G_t(p)$ refers to G at time t of object p and it is obligatory that $Pl_t(p)$. Since G includes a probability it is itself probabilistic.

3.6 The survival and reproduction primitive H is a number which is a function of:

(a) The expectation of life at birth.

(b) The probability of reproduction, sexual or asexual.

Since H includes a probability it is itself probabilistic. The number $H_t(a)$ refers to H at time t of object 'a' and it is obligatory that $An_t(a)$. H is non-decreasing with respect to (a) and (b).

3.7 The directed interaction primitive $\xi_t xy$ means that an interaction occurs between the object 'x' and the object 'y' which evokes immediately in 'y' some physical, physiological or behavioural response or a change of position and no other object (other than 'x') reduces or enhances this effect of 'x' on 'y' ie 'x' affects 'y' directly. The objects 'x' and 'y' must be elements of the universe of discourse; in particular they may be plants or animals. Judgement as to whether the response is significant is to be made by the ecologist.

In all cases the subindex 't' may be replaced by '$\delta t$' implying that the observation or action takes place during an interval of time instead of at an instant.

## 4. The direct environment

The direct environment of a plant is the set of objects which affect the subject directly. There are five subsets called resources, associates, co-reproducers, predators and malentities.

### *4.1 Resources*

A resource of an individual subject plant is an object which is such that when it interacts with the subject in the sense of the directed interaction primitive, the G of the subject is increased. In the case that the object is itself a plant or an animal, its G or H is decreased or unchanged. The formal definition for object 'r' to be a resource of a subject plant (or module) 'm' is:

$$\{G_t(m)>G_{t\_}(m)\} \mid \xi_t rm\&[Pl(r)\supset\{G_t(r)\leq G_{t\_}(r)\} \mid \xi_t rm]$$
$$\&[An(r)\supset\{H_t(r)\leq H_{t\_}(r)\} \mid \xi_t rm]$$

This string of symbols is a (mathematical) sentence which reads, approximately: The general well-being of the subject plant (or module) at a particular time t is greater than its well-being just before t given that at time t the object acts significantly on the plant; furthermore if it is the case that the object is itself a plant then the general well-being of the object at time t is less than or equal to its well-being just before t given that at time t the object plant acts significantly on the subject plant; further to this if it is the case that the object is an animal then its survival and reproductive ability is less than or equal to its survival and reproductive ability just before t given that at time t the object animal acts significantly on the subject plant.

Objects such as a package of light energy or thermal energy, an amount of water (some specific quantity of water), an amount of oxygen, carbon dioxide or mineral nutrient are all resources. Semi-formally, when dealing with water, say, we may write, for a subject plant, say a maize plant:

G(maize) is increased $\mid \xi$ (water)(maize).

Since water is neither plant nor animal the second part of the definition is not applicable. The semi-formal sentence is a useful device which helps to check the accuracy of the classification. It is implied that:

(i) The time constraint is to be understood.

(ii) The maize referred to is a specific individual plant.

(iii) The water referred to is a specific quantity; it is a particular individual 1cc (say) of water, not the set of all possible 1cc amounts of water or a subset of that set.

Now as the subject consider a module of the brown rot fungus *Monilinia fructicola* and as the object another module which is one particular cherry (Weier *et al.* 1982). Then the cherry is a resource of the fungus, since we may write:

G(fungus) is increased and G(cherry) is decreased $\mid \xi$ (cherry)(fungus).

Now consider a case in which the resource is an animal. Suppose the subject is an individual Venus fly trap, *Dionaea muscipula* and the object some suitably-sized insect (Weier *et al.* 1982). Then we may write:

G(Venus f. t.) is increased and H(insect) is decreased $\mid \xi$ (insect)(Venus f. t.).

A plant may not be a resource of itself, since a contradiction appears in the definition if 'r' is replaced by 'm'; we have that G(m) is both increased and decreased at time t.

### *4.2 Associates*

An associate of an individual subject plant is an individual plant or animal which is such that when it interacts with the subject in the sense of the directed interaction primitive the G of the subject is increased. In the case that the object is a plant its G is also increased. In the case that the object is an animal its H is increased. The formal definition for object 'a' to be an associate of a subject plant (or module) 'm' is:

$$\{G_t(m)>G_{t\_}(m)\} \mid \xi_t am\&[Pl(a)\supset\{G_t(a)>G_{t\_}(a)\} \mid \xi am$$
$$\&[An(a)\supset\{H_t(a)>H_{t\_}(a)\} \mid \xi am]$$

In English, this reads, approximately: The general well-being of the subject plant at a particular time t is greater than just before t given that at time t the object acts significantly on the plant; furthermore if it is the case that the object is itself a plant then its general well-being at time t is also greater than just before t given that at time t the object plant acts significantly on the subject plant; further to this if it is the case that the object is an animal then its survival and reproductive ability at time t is greater than just before t given that at time t the object animal acts significantly on the subject plant.

An example of an associate is given by Harper (1977). This is the fungus *Epichloe typhina*, described as an "intriguing... exception..." (to the normal interaction between pathogen and host). The fungus "sterilizes its grass hosts by preventing the emergence of an inflorescence. Such eunuch plants have high vegetative persistence in pastures and apparently greater vegetative vigour. It may be that some of the resources diverted from flowering are available for the more rapid production of tillers..." The fungus is an associate of the subject grass since:

G(grass) is increased and G(fungus) is increased $\mid \xi$ (fungus)(grass).

An example of a case in which the associate is an animal is not known, but has been allowed for in the mathematical definition.

Formally speaking, a plant may be an associate of itself, since no contradiction appears in the definition if 'a' is replaced by 'm' for the case of a plant as object. This does not, at present, seem to be a useful inference.

### *4.3 Co-reproducers*

A co-reproducer of an individual subject plant is an object which is such that when the interaction in the sense of x occurs the probability is greater than zero that a new individual will come into existence. The formal definition for an object 'o' to be a co-reproducer of a plant 'm' is:

$$\mathrm{Prob}[(\exists x)(x\mathrm{Off}_{t+\beta}m \;\&\; x\mathrm{Off}_{t+\beta}o)\ \xi_t om] > o.$$

Examples of dioecious plants are asparagus, date palms and some mosses (Weier *et al.* 1982). Thus, for instance for a subject male asparagus and an individual female asparagus as object we may write, semi-formally:

The probability is greater than zero that an offspring of both male asparagus and female asparagus will appear after a time $\beta \mid \xi$(female asparagus)(male asparagus).

If 'o' is replaced by 'm' in the mathematical definition we have the case that a plant is a co-reproducer of itself. This applies to monoecious plants such as walnut, squash and some mosses (Weier *et al.*, 1982). It also applies to a subject tiller of the infected grass of section 4.2 since we have:

The probability is greater than zero that the tiller will produce an 'offspring' tiller after a time $\beta \mid \xi$(tiller)(tiller).

The expression $\xi$(tiller)(tiller) means that the subject tiller interacts with itself. The time $\beta$ is the 'gestation' period *i.e.* the time from the start of the interaction to the time when a new individual appears, say a seed which is separate from the parent, or a new tiller or other module. $\beta$ may be very short, perhaps only a few minutes, or very long, perhaps many months. The object 'o' is normally a plant, however the definition allows for 'o' to be an artefact.

### *4.4 Predators*

A predator of an individual subject plant is an individual plant or animal which is such that when the object interacts with it in the sense of $\xi$ the G of the subject is decreased. If the object is a plant its G is increased; if it is an animal its H is increased. Predators of plants include grazing animals and humans. The formal definition for object 'p' to be a predator of a subject plant (or module) 'm' is:

$$G_t(m) < G_{t\_}(m) \mid \xi_t pm \& [Pl(p) \supset \{G_t(p) > G_{t\_}(p)\} \mid \xi_t pm]$$
$$\& [An(p) \supset \{H_t(p) > H_{t\_}(p)\} \mid \xi_t pm]$$

The blight *Endothia parasitica* attacks chestnut trees in North America (Harper 1977). This parasite is formally a predator in the environment of a subject chestnut tree since we may write:

G(chestnut) is decreased and G(blight) is increased $\mid \xi$(blight)(chestnut).

Notice that once again in the semi-formal sentence the time constraint is to be understood and the blight is either a whole individual or a module. An example of an animal predator is the caterpillar of the olethreutid moth *Ecdytolopha* sp. which feeds on the Red mangrove (*Rhizophora mangle*), (Strong *et al*, 1984). The semiformal sentence is:

G(mangrove) is decreased and H(caterpillar) is increased $\mid \xi$ (caterpillar)(mangrove).

A plant may not be a predator of itself, since if we substitute 'm' for 'p' in the mathematical definition a contradiction appears, *i.e.* G(m) is required to increase and decrease, both at time t.

### *4.5 Malentities*

A malentity of an individual subject plant is an object which is such that when it interacts with the subject in the sense of $\xi$, the G of the subject is decreased. In the case that the object is itself a plant its G is decreased or remains unchanged. In the case that the object is an animal its H is decreased or remains unchanged. The formal definition for object 'c' to be a malentity in the environment of a subject plant (or module) 'm' is:

$$[\{G_t(m) < G_{t\_}(m)\} \mid \xi_t cm] \& [Pl(c) \supset \{G_t(c) \leq G_{t\_}(c)\} \mid \xi_t cm$$
$$\& [An(c) \supset \{H_t(c) \leq H_{t\_}(c)\} \mid \xi_t cm].$$

Inanimate objects such as a falling rock, a violent wind (the kinetic energy is the object), a hailstone, a blast of lighting (electrical energy), fire (thermal energy) are all malentities. The semi-formal sentence for a subject plant and lightning as the malentity is:

G(plant) is decreased $\mid \xi$ (lightning)(plant).

A banyan which destroyed some small plant by forcing its roots through that plant is acting as a malentity; the small plant is destroyed, the banyan is unaffected:

G(small plant) is decreased and G(banyan) is unchanged $\mid \xi$ (small plant)(banyan).

An example of a human acting as a malentity is given by Liddle and Thyer (1986). Ramets of the grass *Entolasia stricta* were significantly harmed by human trampling. The semi-formal sentence for a subject ramet is:

G(ramet) is decreased and H(human) is unchanged $\mid \xi$ (human)(ramet).

The definition allows for both subject and malentity to be adversely affected by the encounter. An example would be a human trampler whose foot was pierced by the trampled plant (bearing thorns for instance).

Formally, a plant may be a malentity of itself. There is no logical contradiction involved if 'c' is substituted for 'm'.

## 5. The indirect environment

The indirect environment of a plant is the structured set of objects which affect the subject indirectly. These objects are called 'modifiers', a term due to Maelzer (1965) writing on animal ecology. First-order modifiers modify the effect on the subject of objects in the direct environment. Second-order modifiers modify first-order ones; third-order modify second-order, and so on. The formal mathematical definition is given in Section 5.3 below. Modifiers of all orders may be either negative or positive.

### *5.1 First-order Modifiers*

These are objects which interact directly with the resources, associates, co-reproducers, predators or malentities in the environment of the subject plant. Harper (1977) records that the larvae of the cabbage white butterflies *Pieris brassicae* and *P. rapae* are attracted by mustard oil glycosides in their food plants and will eat other leaves (or even filter papers) if treated with sinigrin or sinalbin. Thus a leaf of the 'wrong' species becomes a resource if treated. For a subject leaf, say, an individual larva is a predator, since:

G(leaf) is decreased and H(larva) is increased | ξ (larva)(leaf).

The glycoside is a positive first-order modifier in the environment of the subject leaf since:

(∃ larva)[(larva)Pred(leaf) | ξ(glycoside)(leaf) &

~(larva)Pred(leaf) | ~ξ(glycoside)(leaf)].

That is, there is at least one larva, such that the larva is a predator of the leaf given that there is significant interaction between glycoside and leaf in the sense of ξ and it is not the case that the larva is a predator of the leaf given that there is no interaction between glycoside and leaf. The interaction primitive (section 3.7) in this case should be interpreted as evoking a physiological or physical response, depending on whether the glycoside is incorporated in the structure of the leaf or merely smeared on.

Also from Harper (1977) we have that the cyanogenic glycosides protect plants of *Trifolium repens* against slugs. Without the glycoside the slug would be a predator, so the glycoside in this case is a negative first-order modifier, since we may write, for a subject *T. repens* individual:

(∃ slug)[(slug)Pred(T.repens) | ~ξ(glycoside)(T.repens) &

~(slug)Pred(T.repens) | ξ(glycoside)(T.repens)].

That is, there is at least one slug such that it is a predator of the subject *T. repens* plant given that it is not the case that there is an interaction in the sense of ξ between glycoside and plant, and it is not the case that the slug is a predator given that there is an interaction between glycoside and plant. Notice the difference between positive and negative modifiers brought out by these two examples. The time constraint applies throughout.

Symbiosis between two organisms is often a first-order-modifier situation. An interesting example is a lichen, which consists of two plants, an alga and a fungus, in symbiosis. The fungus hyphae enmesh the alga, introducing haustoria into it which absorb food material from the alga. The fungus provides the thallus which supports the alga (Weier *et al.* 1982). Consider first a subject alga, the thallus which supports it being a resource, since:

G(alga) is increased and G(thallus) is unchanged | ξ (thallus)(alga).

The fungus which supplies the thallus is a positive first-order modifier, since:

(∃ thallus)[thallus)Res(alga) | ξ(fungus)(alga) &

~(thallus)Res(alga) | ~ξ(fungus)(alga)].

Now consider a subject fungus. The food it gains from the alga is a resource, since:

G(fungus) is increased | ξ (food)(fungus).

The alga which supplies the food is a positive first-order modifier, since:

(∃ food)[(food)Res(fungus) | ξ(alga)(fungus) &

~(food)Res(fungus) | ~ξ(alga)(fungus)].

Grime (1979) remarks that the treatment of productive vegetation with the growth retardant maleic hydrazide tends to suppress potential dominants and to increase species density. In the environment of a small plant as subject, the dominant is either a predator or a first-order modifier by shading the subject. If the dominant is a predator then the maleic hydrazide is a negative first-order modifier since:

(∃ dominant)[(dominant)Pred(small plant) | ~ξ(mal. hyd.) (dominant) &

~(dominant)Pred(small plant) | ξ(mal. hyd.)(dominant)].

The shading situation is dealt with in the following section.

Another interesting example of symbiosis is that of a mycorrhiza which associates with the roots of a higher plant (Weier *et al.* 1982). The endomycorrhizal fungi which live within individual root cells are, formally, classified as predators. More interesting, from the logical point of view, are the ectomycorrhizal fungi, the hyphae of which grow between the root cells but do not form haustoria; but contact between root and fungus is nevertheless close enough for metabolites to be transferred in both directions. In this case each plant provides resources for the other and is therefore a positive first-order modifier in the other's environment since, for a subject fungus we may write:

(∃ metabolite)[(metabolite)Res (fungus) | ξ(plant root)(metabolite) &

~(metabolite)Res(fungus) | ~ξ(plant root)(metabolite)].

Similarly, for a subject plant:

(∃ metabolite)[(metabolite)Res(plant) | ξ(fungus)(metabolite) &

~(metabolite)Res(plant) | ~ξ(fungus)(metabolite)].

The rules of construction of the semi-formal sentences allow, in the term starting with ξ, for the second individual to be either the subject or an object in the direct environment of the subject.

### *5.2 Second- and Third-order Modifiers*

Second-order modifiers are objects in the environment of the subject which modify first-order modifiers. Third-order modifiers modify second-order modifiers. To continue with the example of the previous section from Grime (1979) suppose the dominant is shading the subject small plant and thereby interfering with the thermal energy or light energy that it requires. Some one particular package of thermal energy corresponding to a suitable temperature is a resource since:

G(small plant) is increased | ξ(thermal energy)(small plant).

The dominant is a negative first-order modifier, since:

(∃ thermal energy)[(therm. en.)Res(small plant) | ~ξ(dominant)(therm. en.) &

~(therm. en.)Res(small plant) | ξ(dominant)(them. en.)].

The maleic hydrazide is a positive second-order modifier, since:

(∃ dominant)[(dominant)$\text{Mod}^1$(small plant) | ξ(mal.hyd.)(dominant) &

~(dominant)$\text{Mod}^1$(small plant) | ~ξ(mal.hyd.)(dominant)]

If we now introduce the human who treats the vegetation with maleic hydrazide we find that the human is a third-order modifier in the environment of the small plant, since:

(∃ mal. hyd.)[(mal. hyd.)$\text{Mod}^2$(small plant) | ξ(human)(mal. hyd.) &

~(mal. hyd.)$\text{Mod}^2$(small plant) | ~ξ(human)(mal. hyd.)].

In this latter case the interaction primitive is interpreted as meaning that the response is a change of position of the maleic hydrazide. Notice that the notation $\text{Mod}^1$ and $\text{Mod}^2$ is being used here for first and second-order modifiers.

Harper (1977) writes that the jay *Garrulus glandarius* carries acorns of *Quercus* spp. up to a distance of one kilometre for burial. They search for them during the autumn and winter and eat them, but a number of seedlings survive. The burial may be vital for the viability of the acorn. The thermal energy associated with above-ground temperatures is a malentity, since:

G(acorn) is decreased | ξ(therm. en.)(acorn).

The soil which covers the acorn is a negative first-order modifier:

(∃ therm.en.)[(therm.en.)Mal(acorn) | ~ξ(soil)(therm en.)&

~(therm.en.)Mal(acorn) | ξ(soil)(therm.en.)].

In this case a physical change is induced on the thermal energy by the soil.

The jay which buries the acorn is a positive second-order modifier:

(∃ soil)[(soil)$\text{Mod}^1$(acorn) | ξ(jay)(acorn) &

~(soil)$\text{Mod}^1$(acorn) | ~ξ(jay)(acorn)].

### *5.3 Modifiers of all Orders*

The formal definition of the set of modifiers (which is potentially infinite) is given here. First, we shall refer to objects in the direct environment of a subject plant m as 'modifiers of order zero'. A modifier is an object w. Thus for a resource, an associate, a co-reproducer, a predator or a malentity referred to as w we have $\text{wMod}^0{}_t\text{m}$. Then:

$$\text{wMod}_t{}^{+(n+1)}\text{m} =_{df} (\exists x)\,[\{\text{xMod}_t{}^{n}\text{m} \mid (\xi_t\text{wx} \vee \xi_t\text{wy})\}\ \&$$
$$\{{}^{\sim}\text{xMod}_t{}^{n}\text{m} \mid \sim(\xi_t\text{wx} \vee \xi_t\text{wy})\}]$$

$$\text{wMod}_t{}^{-(n+1)}\text{m} =_{df} (\exists x)[\{\text{xMod}_t{}^{n}\text{m} \mid \sim(\xi_t\text{wx} \vee \xi_t\text{wy})\}\ \&$$
$$\{{}^{\sim}\text{xMod}_t{}^{n}\text{m} \mid (\xi_t\text{wx} \vee_t\text{wy})\}]$$

$n=0,1,2,\ldots;$

y is either m or a modifier of order $\leq n$

$$\text{Mod}_t{}^{n}\text{m} =_{df} \text{Mod}_t{}^{+n}\text{m} \vee \text{Mod}_t{}^{-n}\text{m}$$

A set of objects connected by the modifier definitions, taken in order, is called a 'modifier chain'.

Notice that we have the choice of either ξwx or ξwy when writing down the justifying sentence for a modifier. Thus in second example of section 5.2 above the first-order modifier definition includes ξ(soil)(therm. en.) *i.e.* ξwy where y is a modifier of order zero. For the second-order modifier semi-formal sentence we use ξ(jay)(acorn) *i.e.* ξwm.

## 6. The total environment

The total environment of a plant or module m is the structured set which is the union of direct and indirect environment of m in which the structure of the five subsets of the direct environment and their attached modifier chains is preserved. The environment is total in the sense that all possible increases or decreases of G(subject) and G(object) (or H(object)) are included in the direct environment. If G(subject) does not change the object being considered does not belong to the direct environment. If it exists (*i.e.* belongs to the universe of discourse) then it must necessarily be, in this case, a modifier.

The 'environment', as mathematically defined in this paper, is an extremely complex network, since any one object may occupy many logical positions in the environment of a subject plant, all at the same instant. This occurs because of the use of the conditional |

(given that) in the definitions. In ordinary English objects in the environment would be referred to as '*potential* resources', '*potential* associates', '*potential* co-reproducers', '*potential,* predators', '*potential* malentities' and '*potential* modifiers'. The situation is similar to that in the related formalized theory of animal ecology and an example is given by Niven (1989) from a study of the environment of the three-spined stickleback (*Gasterosteus aculeatus*) in which a parasitic worm Schistocephalus solidus appears in six logical positions in the known environment --- once as a predator, three times as a first-order modifier and once as a third-order modifier. This conceptual difficulty is significantly resolved by the use of a brilliantly simple diagram called an 'envirogram', which was invented by H G Andrewartha, using the mathematical definition of the total environment of an animal given by Niven (1980). The diagram was introduced into the animal ecology literature by Kitching (1983) and used extensively by Andrewartha and Birch (1984). The envirogram opens out the complex network of the environment and projects it on to a flat surface, making it very easy to scan. Envirograms are now being constructed for plants, using the definitions in this paper. Until recently drawn by hand, these diagrams may now be computer-constructed (Abel *et al.* 1989).

## 7. Communities

The modifier chains which formalize the functional relations between plant and plant, or plant and animal will now be treated as the functional linkages which knit together a plant or plant-and-animal community. I now introduce a change of notation; instead of saying "plant 'q' or animal 'a' is a kth-order modifier in the environment of plant 'p'" I shall say

"$\mathrm{Mod}^k$ sends plant 'q' or animal 'a' to plant 'p'" and write this symbolically as:

$\mathrm{Mod}^k: q \rightarrow p$, or

$\mathrm{Mod}^k: a \rightarrow p$.

The idea of modifiers in the environment of a subject plant is thus transformed into the mathematical notion of a morphism.

We can now define an nth-order community $C_n$ within a habitat as a structured set of plants, animals and modules a,b,c,........ such that for every ordered pair $<a,b>$ we have $\mathrm{Mod}^k: a \rightarrow b$, $k=0,1,2,\ldots,n$, where k is the maximum of the smallest integer for every pair. The time constraint holds as for environment, *i.e.* we allow for a change within a community from instant to instant. Thus we start with a specific habitat B, say, which is such that for every plant, animal and module, p, to be considered, B Hab p. We consider each pair in turn. Each pair is considered twice, taking the ordering into account. For the first pair, $<a_1,a_2>$ say, we write down the modifier connection. We repeat this for $<a_2,a_1>$. If n is small then $C_n$ will be a set of plants (modules, animals) which is closely knit together. Several such communities (non-overlapping) may occur in a large habitat. If n is large then Miles' (1979) idea of patch is satisfied. In some cases the functional relation between two plants in a patch will be very tenuous indeed; this is catered for in the definition since there will be at least one modifier chain, which may contain scores of objects, which connect the two.

For the definition to be helpful certain universal modifiers must be excluded. Oxygen and thermal energy are examples of universal modifiers, which will knit together, since they are resources for all, even extreme 'logical outliers' in a Miles 'patch'.

### *7.1 A zero-order community*

Consider the example of a predator from Harper (1977) in Section 4.4. The blight *Endothia parasitica* attacks chestnut trees and is formally classified as a predator of a subject chestnut tree. We rewrite this as:

$\mathrm{Mod}^0$:blight → tree. ("Mod zero sends blight to tree.")

Now take an individual blight as the subject. Then:

G(blight) is increased and G(tree) is decreased | $\xi$(tree)(blight).

We rewrite this as:

$\mathrm{Mod}^0$: tree → blight.

The two individuals, chestnut tree and blight, constitute a zero-order community. If now we add another chestnut tree, then this second tree is a first-order modifier in the environment of the first tree; it "competes" for blight (or nutrient) and we write, semi-formally:

(∃blight)[(blight)Pred(first tree) | ~$\xi$(blight)(second tree)&
~(blight)Pred(first tree) | $\xi$(blight)(second tree)].

In other words:

$\mathrm{Mod}^1$: second tree → first tree.

Thus we no longer have a zero-order community.

A zero-order community, then, is one in which the plants (modules, animals) are linked together by being in one another's direct environments; they are usually very small, with only two or three individuals. The concept is a useful one when classifying communities, but is not usually appropriate to real-life communities in the wild.

### *7.2 Higher-order communities*

Consider the example of section 5.2 taken from Grime (1978), in which a dominant, which normally shades a small plant, is adversely affected by maleic hydrazide sprayed by a human. We have:

$\mathrm{Mod}^3$: human→ small plant.

It is not clear from the example what the converse relation is. The dominant is a (negative) first-order modifier of the small plant, thus:

$\mathrm{Mod}^1$: dominant → small plant.

The converse relation is not clear, but it may well be that the small plant 'shares' nutrient with the dominant, in which case:

$\mathrm{Mod}^1$: small plant → dominant.

The human who sprays the maleic hydrazide on the dominant is also a first-order modifier in the environment of the dominant, so

$\mathrm{Mod}^1$: human → dominant.

Finally, for this rather artificial community containing one small plant, one dominant and one human in some definite fixed habitat B we have:

$\mathrm{Mod}^3$: human → small plant.

$\mathrm{Mod}^1$: dominant → small plant.

$\mathrm{Mod}^1$: small plant → dominant.

$\mathrm{Mod}^1$: human → dominant.

The community, therefore, is classified as a third-order community within the habitat B, as far as our knowledge extends. We lack the information about the two missing morphisms small plant→human and dominant→human.

### *7.3 Example of an Observed Community.*

Boyd (1988) studied a Searocket community as follows:

"Two species of searockets (*Cakile maritima* and *C. edentula* ssp. *edentula* var. *edentula*) have been sequentially established on the West Coast of North America since the 1880's. In California, *C. maritima* has replaced *C. edentula* in the southern 1000 km of their former sympatric distributions. This research tested the hypothesis that differential herbivory contributed to the ascendance of *C. maritima*. Choice experiments were conducted with three herbivores (two insects and a rodent) which consume *Cakile* at Point Reyes National Seashore, California, where only *C. maritima* now occurs. Larvae of the moth *Platyprepia virginalis* (Arctiidae) displayed a significant preference for foliage of *C. maritima* in a laboratory test. No evidence of any foliage preference was found for a short-horned grasshopper *Microtes occidentalis* (Acrididae) in laboratory and field experiments. Field experiments with deer mice (*Peromyscus maniculatus*) demonstrated a significant preference for *C. edentula* seedlings and fruits. Degree of preference by mice for seedlings was affected by the distance from the experimental location to patches of introduced beachgrass (*Ammophila arenaria*), which mice use for nesting sites and cover, but this distance-dependence did not occur for fruit predation. Herbivory by the two insect species was not a factor in this case of species replacement. *Peromyscus* preference for seedlings and fruits of *C. edentula* would have affected the rapidity of local species replacement at Point Reyes, but this preference does not explain the current distribution of *Cakile* on the Pacific Coast. I concluded that differential predation by mice was not the ultimate cause of *Cakile* species replacement in California."

We start the mathematical analysis by choosing the habitat, say a bounded area in the same region as that used by Boyd, but still containing both species of *Cakile*. Now consider two individual *C. maritima* and *C. edentula*. Since they compete for nutrients they are first-order modifiers of each other. Call them 'm' and 'e'. Then

$\mathrm{Mod}^1$:m→ e, and

$\mathrm{Mod}^1$:e→ m.

Now consider other plants of the same species in the habitat, $m_1, m_2 \ldots$ and $e_1, e_2, \ldots$ For any pair, we have:

$\mathrm{Mod}^1$:m→ e,

$\mathrm{Mod}^1$:m→ m,

$\mathrm{Mod}^1$:e→ m, and

$\mathrm{Mod}^1$:e→ e.

Now introduce the moth larvae, $l_1, l_2 \ldots$ say. For any larva, and m or e:

$\mathrm{Mod}^0$:l→ m,

$\mathrm{Mod}^0$:l→ e,

$\mathrm{Mod}^0$:m→ l, and

$\mathrm{Mod}^0$:e→ l.

Among larvae, since they are predators of the same plants,

$\mathrm{Mod}^1$:$l_1 \to l_2$, and

$\mathrm{Mod}^1$:$l_2 \to l_1$.

The same argument applies to the grasshoppers $g_1, g_2, \ldots$ and rodents $r_1, r_2 \ldots$

We now add plants of the beachgrass, $b_1, b_2, \ldots$ which serve as protection for the rodents (from unknown predaters or malentities). Thus for any m or b:

$\mathrm{Mod}^1$:b→ m.

It follows from this that the beachgrass is a second-order modifier in the environment of a Searocket:

$\mathrm{Mod}^2$:b→ m, and

$\mathrm{Mod}^2$:b→ e.

We now have to consider the Searockets as objects in the environment of the beachgrass, similarly moth larvae and grasshoppers. If the beachgrass and Searockets use the same nutrients, which seems a reasonable assumption, then we have, for any b and e or m:

$\mathrm{Mod}^1$:m→ b, and

$\mathrm{Mod}^1$:e→ b.

Since larvae and grasshoppers attack first-order modifiers of the beachgrass they are both, therefore, second-order modifiers in the environment of a subject beachgrass, thus, for any larva and grasshopper:

$\mathrm{Mod}^2$:l→ b, and

$\mathrm{Mod}^2$:g→ b.

Altogether there are three species of plants and three species of animals mentioned in this example. It is advisable when doing the analysis to consider two individuals of each species, to ensure that the analysis is complete. Thus we consider all possible ordered pairs of 12 individuals, *i.e.* 132 pairs, from which we can subtract 12 intraspecific pairs, since in this case <a,b> is equivalent to <b,a>. Thus altogether we should consider 120 ordered pairs. The work is reduced if we realise that in this particular case all 3 animal species act in much the same way. Clearly, however, the complete analysis of a complex community will require computer assistance. Work towards this goal is already under way, with a study of the use of the specification language Object Z for animal communities, following on the use of Z for animal environment (Abel and Niven 1989). The final result for Boyd's example is that the community is a second-order one, in the habitat specified.

### *7.4 Second Example of an Observed Community*

Strong *et al.* (1984) describe a community consisting of *Spartina alterniflora*, a common grass of saltmarshes, and its associated insects. They list 3 leaf-feeders, 5 stem-borers and 4 saprovores. Larvae of 9 parasitoids attack the leaf-feeders, larval parasitoids of 10 spp,. attack the stem-borers and larval parasitoids of 2 spp. attack the saprovores.

We start the mathematical analysis by choosing the habitat. Let the habitat B be a bounded (fenced, say) saltmarsh on the Gulf coast of North America. B extends upwards for a height of, say, 10m and down into the marsh to a depth of, say, 3 m. The plants, animals and modules, p say, in the community to be analysed are all such that B Hab p. Let us choose as our time constraint some particular interval of time, say one day during a period when all plants and animals under study are active.

Now consider an individual tiller of *S. alterniflora* as the subject. The 3 leaf-feeders, 5 stem-borers and 4 saprovores are all predators, or first-order modifiers (competitors) of predators. Now if we choose an individual animal from this set as the subject then the tiller is a resource and the other animals are all first-order modifiers. To make this clear we write down the semi-formal sentences for the tiller, an individual leaf-feeder and one other animal, which is a leaf-feeder, a stem-borer or a saprovore. First, the leaf-feeder is a predator of the tiller:

G(tiller) is decreased and H(leaf-feeder) is increased | ξ (leaf-feeder)(tiller).

The other animal is a negative first-order modifier in the environment of the tiller:

(∃ leaf-feeder)[(leaf-feeder)Pred(tiller) | ~ξ(other animal)(tiller) &

~(leaf-feeder)Pred(tiller) | ξ(other animal)(tiller)].

Now take the leaf-feeder as the subject. Then the tiller is a resource, since:

H(leaf-feeder) is increased and G(tiller) is decreased | ξ(tiller)(leaf-feeder).

The other animal is a negative first-order modifier, since:

(∃ tiller)[(tiller)Res(leaf-feeder) | ~ξ(other animal)(tiller) & ~(tiller)Res(leaf-feeder) | ξ(other animal)(tiller)].

Thus we have:

Mod$^0$:leaf-feeder→tiller,

Mod$^1$:other animal→tiller,

Mod$^0$:tiller→leaf-feeder, and

Mod$^1$:other animal→leaf-feeder.

Similarly,

Mod$^0$:tiller→other animal, and
Mod$^1$:leaf-feeder→other animal.

We have written down all 6 of the morphisms which occur when we consider 3 individuals.

A parasitoid acts as a second-order modifier in the environment of a subject tiller. Now consider as subject a larval parasitoid of a saprovore. The saprovore is a resource in the environment of the parasitoid. The tiller, a resource of a resource, is a first-order modifier. A stem-borer, which is a predator of a resource of a resource, is a second-order modifier and finally a parasitoid which attacks the stem-borer is a predator of a predator of a resource of a resource of the subject larval parasitoid; it is a third-order modifier. Thus:

Mod$^3$:stem-borer parasitoid→saprovore parasitoid.

Another stem-borer parasitoid modifies the action of the first stem-borer; it is a fourth-order modifier in the environment of the subject saprovore parasitoid. Thus:

Mod$^4$:other stem-borer parasitoid→saprovore parasitoid.

Clearly the listing of all possible functional relations between the ordered pairs of the 34 species in this example is a task for a computer analysis. There are 68x67-34=4522 ordered pairs which should be considered to complete the analysis and classify the community. From the analysis given above this is a fouth-order community in the designated habitat. A complete analysis awaits the advent of computer software.

## 8. Discussion

Southwood (1980) in his article entitled 'Ecology - a mixture of pattern and probabilism' wrote that ecology may be defined as "the study of living organisms at the level of the population and community". In this paper I have presented a probabilistic pattern extending from individual plant to plant community which is intended to serve as a mathematical basis for plant ecology. The system I have developed is stochastic in two ways. First, at a fundamental semantic level, the two primitive terms G, for plants, and H, for animals, both contain probabilistic ideas. G (or H) is incorporated in all definitions, explicitly in the five definitions of the direct environment and implicitly in the infinite set of definitions of the indirect environment. It is also the case that the definition of co-reproducer ('mate' in the animal equivalent) contains a probabilistic sentence. The system is also totally interactive, via the directed-interaction primitive. It is time-dependent; provision is made for the environment of an individual plant, or a community of plants, to change from instant to instant. All definitions are functional; it is the functional relations among plants (or animals) which provide both the structure of the environment and the structure of a community. By excluding the primitive term Hab (for habitat) from the definition of environment I have made the concept of environment habitat-indepenent. This enables us, for example, to include the blight *Endothia parasitica* among the predators of a chestnut tree, even in the case that the tree is growing in an area far removed from the place in which the observation was made.

In the first paper on the corresponding environment definition for animals (Niven 1980) the terms 'direct environment' and 'indirect environment' were used, as in this paper. However, Andrewartha and Birch (1984) preferred to rename these two sets of objects the 'Centrum' and the 'Web' respectively. It is for experienced plant biologists to decide whether the terms 'Centrum' and 'Web' should be used for the plant system. (To a mathematician, modifiers of order 0,1,2,3,... would seem more natural). All animal studies published by Niven and colleagues since 1984 have incorporated the names Centrum and Web.

The explication of G has been deliberately left rather vague. It is a number which expresses the general well-being of the subject plant. In this connection Harper (1977) writes "A large part of the study of mechanisms of plant interaction has concentrated on gross measurements such as life or death, or weight. The more successful attempts to understand interference have involved studying symptoms. Often the effects of a toxin or a nutrient deficiency are very specific: leaf tip blackening in *Grevillea*, potassium deficiency symptoms in *Desmodium*, sudden wilt... change in leaf area/weight ratio..." The mathematical definitions containing G are not dependent on the precise explication of G; should the explication be changed slightly, as experience in using the system is acquired, the formal definitions should remain unchanged.

In this paper I have attempted to strike a sensible balance between the amount of symbolism and explanation in ordinary English, where this can be done without losing too much precision. For example the notions that resources, co-reproducers and malentities may be both non-plant and non-animal, whereas it is obligatory that predators and associates be either plant or animal could be symbolized and added to the symbolic definitions. This seems to me to be unnecessary and I have been content to use natural language only.

The existence of the set I have called 'associates' came as a surprise to me, since the animal equivalent does not seem to exist in real life, although of course it is easy enough to write down the corresponding definition (in which the H of both subject and object animal increases). The example given by Harper (1977) is one of a fungus associate of a grass in the case that the fungus prevents seed formation, the result being a 'forced' vegetative growth by the plant. Liddle (1975) reports that trampling by humans may have the same effect and Liddle (pers. comm.) adds that the destruction of a plant's reproductive mechanism in order to stimulate its vegetative growth is not uncommon in horticulture. In these cases the human would be classified as a resource since:

G(plant) is increased and H(human) is unchanged $| \xi$ (human)(plant).

The choice of habitat, an essential item for the classification of a community, is of critical importance. Harper (1977) writes "The diversity of microsites within the habitat may permit different species to occupy specialized microenvironments within the community. Often this underlying heterogeneity is difficult to define..." Harper continues with a detailed example then "A statement about the floristic richness of such a pasture as a whole has no real meaning in relation to the chances of interspecific encounter." If when undertaking a mathematical analysis we find that a number of, say, non-overlapping fourth-order communities appear to exist in the same habitat, this would seem a pointer towards splitting the original habitat into several subunits.

The explication of the primitive term 'Off' (offspring) says nothing at all about whether the new separate individual is the same species as the parent, or parents. The assumption in the general system of formalized ecology, of which this paper gives a part, is that the idea of Paterson (1985) of the recognition concept of a species, is relevant. Paterson's semantic definition of species has been formalized in Niven (1989), for animals. It is confidently expected that the result will also apply to dioecious plants.

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