FOUNDATIONS OF AGRO-ZOOCOENOLOGY

Gusztáv Szelényi

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Gusztáv Szelényi Memorial Foundation
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http:/www.harmattan.fr
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FOREWORD

First published more than 60 years ago, this work by Gusztáv Szelényi has just recently been translated into English and its historical significance can now be appreciated by non-Hungarian speakers. Szelényi was concerned with identifying animal “communities.” While presently we consider a community to be an assemblage of species that occur in a specific place at a specific time, Szelényi was concerned about how to identify animal “communities” as a holistic concept without reference to a specific place or time. This is a terribly challenging problematic, as first of all, it is not entirely clear that an animal “community” exists with characteristics that are more than the sum of the parts, and second of all, as we and Szelényi recognize, these “communities” vary both in space and time.

His solution to this problematic was to define a community to be one that is tied together by the trophic relations of its member populations. In this way, he distinguished his approach from faunistics, which is merely a list of the species (and sometimes their relative abundances) that occur in a place and time. From a modern perspective, I believe that he developed Elton’s (1927) niche concept (the role of a species in its community). He suggested that the “community” is the composite of these roles, focusing primarily on the trophic interactions among the populations in the “community”. This shift in perspective from a view that the role is a species property (in the Eltonian niche) to the view that the roles are the whole community was necessary to justify that the “community” was more than just the assemblage of species occurring in the same place at the same time. Specifically, in his view, trophic interactions are relational, and depend on the other populations that are available to be eaten or to eat. That is, they are not a property of the species but a property of the population that depends on the other populations present.

His focus on trophic interactions with applications to cultivated habitats led him to foreshadow the development of several modern concepts associated with communities and food webs (Layman et al. 2015).

Unlike the phytosociologists, who suggested that there were plant “societies”, such as the beech-maple forest, the short-grass prairie, etc, Szelényi did not believe that animal “communities” converged to the same species composition and relative abundances, but that animal "communities" were highly contingent on what we now recognize as the species pool. In his view, communities come into being via temporal development and evolution though the processes of colonization and accommodation. Thus, Szelényi focused on what we now call species assembly rules for communities rather than a static concept of "societies".

He explained that the central questions of animal "community" ecology are why are the populations together and how do they coexist? This led to his focus on the accommodations necessary for coexistence of predators and prey (herbivores and plants) and of populations using the same resource. In his view the answer to the second problem was competitive coexistence, although nowadays we know that other processes may be involved. His simplistic view is probably related to the ideological dominance of Gause's competitive exclusion principle at that time.

Be that as if may, Szelényi pointed out that all animal "communities" are dependent on plants (and other primary producers) because all of the energy used by animals originates from plants. However, as their communities are not bound to the plant community (because of movement behavior and rapid reproduction), there is no simple association between plant societies and animal "communities". Regarding the herbivore-plant interaction, he stated "It is a generally accepted fact that the plant-based energy resources are, at all times, in abundance relative to the animals consuming them." From this, he deduced that natural enemies are critical components of a "community" by "controlling" populations of herbivores. These conclusions preceded an identical argument in the much more famous "the world is green" hypotheses developed by Hairston et al. (1960).

His investigations developed several other significant points. For example, he framed trophic interactions around life-history stages, which has been recently called for in modern trophic interactions. In this way, he suggested that trophic interactions are individual- and stage-specific, rather than species properties. A conclusion he reached from these ideas is that polyphagous species may be functionally monophagous or oligophagous in actual "communities," again highlighting the contingent nature of animal "communities." He preceded the concept of ecosystem engineers when he described animal activities that mirrored the creation of human settlements and agriculture. In passing, he concluded that there were no empty niches in a "community" as did Whitaker et al. (1973) and suggested that animal communities comprised a number of components that were tied together as did Root (1973).

Much of the work is devoted to distinguishing the idea of "animal community" (which he calls zoocoenosis) from other concepts (e.g., biome, biotope, ecotope, merotope, oecus, habitat, phytocoenosis, ecosystem, biogeocoenosis, etc) and developing a rather complex set of terms in an attempt to clarify these differences. The extended discussion about what is and what is not an animal "community" will be of historic interest, as it reflects similar discussions about plant societies that were prevalent at the time. Some of this discussion helps to understand how we arrived at our present community concepts. Regarding the complex terminology, I personally found it to be a barrier to understanding his ideas. For example, he uses the term "semaphoront" to refer to a specific life stage of a species that occurs in a population of interest ("life stage" would have sufficed).

A significant logical flaw this work is his assumption that a holistic community concept is real. Whitaker's (1956) very important work on the vegetation of the Smoky Mountains National Park in the US resulted in overthrowing the plant sociology movement and replacing these community concepts with the "individualistic species concept". This idea is that the populations of each species in a community assemblage reacts individually to the environment and to other species, so that species do not have constant associations with each other. Whitaker's work suggests that there is no clear way to delineate the boundaries of a plant society, so such "plant societies" do not really exist.

Szelényi clearly understands that this boundary problem is central to the identification and reality of an animal "community", and he devotes a substantial part of this work to address this issue and the related but equally thorny issue of temporal variation and stability.

He tries, and in my view, fails to establish spatial boundaries for an animal "community", but in the process recognizes some important issues related to the structure of trophic webs. His approach is to first consider a plant, a single specialist herbivore and the specialized predators (parasites/parasitoids) associated with the herbivore. He calls each of these *catenaria*, which we would now call specialized food chains. He then recognizes populations that feed on populations in more than one specialized food chain. These include polyphagous herbivores as well as polyphagous predators. The food webs that are associated with these multiple specialized food chains tied together by polyphagous populations are called *presocia*. Without the terminology, this is what we now consider to be a food web. What I found interesting is that he divided polyphagous species into large and small ones, with the large ones being vertebrates. These species typically have a much greater home range than the populations of small species, which were mostly arthropoda. The vertebrates link together several of the *presocia* into spatially larger units, which he called *supersocia*. Now I believe that the distinctions among these three levels of organization are not clear cut at all, but the idea of considering the scaling of predator size on spatial extent of a food web deserves greater attention. Most of the published food webs are from lakes and ponds, where the spatial extent of the lake or pond create a boundary, but for terrestrial food webs, the issue of spatial scale is paramount and difficult to resolve.

He recognized several factors leading to dynamical change in an animal “community” and discussed each. These are diurnal changes, seasonal changes, and successional changes. All of these discussions relate to temporal persistence of populations and “stability” of the trophic web. He notes that in practice, temporal persistence can be difficult to determine because populations may be present below the detection threshold of the sampling method, and because their life history may require their periodic disappearance (diapause, hibernation, torpor, stage-specific alternation of habitats). He considers “communities” to be dynamic and ever-changing and suggests that it is more important to consider how and why they change than to consider the stability of any single observed “community”. This contrasts sharply with the food web research program stimulated by May (1972) of investigating the stability of model food webs. I suppose the key difference underlying Szelényi’s perspective is that he recognized the tremendous difficulties to describe an animal “community” and the dynamic nature of these communities.

A key weakness in Szelényi’s approach is that it requires *a priori* life history knowledge on all the life stages of the species in a sample. It is from this information that he can construct the trophic connections among the populations. Identifying trophic interactions remains an active area of research today, with cutting edge molecular methods being used now to produce a third-generation of ecological food webs with greater accuracy. Thus, much of Szelényi’s thinking was before his time, and some of his ideas can only be addressed as these third-generation food webs are compiled.

Most of Szelényi’s ideas are of historical interest and it is interesting to see that many of his ideas are reflected in the subsequent history of food web ecology. It makes me wonder how our present ideas would have developed had his work been more widely known and appreciated. In any event, his work represents a total commitment to understanding real food webs as they exist in nature and his efforts to tackle the problems that arise provide fuel for thought even today.

David A. Andow
Distinguished McKnight University Professor
Fellow of the Entomological Society of America
Brasília, Brazil, 24 November 2021

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I. THE AIM AND POSITION OF ZOOCOENOLOGY IN THE SYSTEM OF BIOLOGICAL SCIENCES

Zoocoenology is the study of the laws of animal assemblages. Using this definition, zoocoenology is a strictly synbiological discipline and can only consider a species if simultaneously evaluating its connections with other species (Szelényi, 1955). The close relationship between zoocoenology and autecology underpins the frequent intrusion of autecological concepts into the zoocoenological framework. This continues to occur whilst coenologists persist with the incorrect viewpoint that coenology deals with "species". Due to this stance, faunistics also appears in a potentially confusing proximity.

§ FAUNA AND ZOOCOENOSIS

Therefore, we must examine, firstly, the difference between fauna and zoocoenosis, because we are convinced that we frequently present a faunal list instead of a zoocoenosis. Maybe recently, instead of an area delimited by political boundaries, we produce faunal lists of one or more association, i.e. of a natural unit.

The fauna is the totality of species to be found in a delimited area, while the zoocoenosis is the totality of populations that are existentially linked, at least in one direction.

Faunistics, over and above taxonomic aspects, extends its horizons towards evolution and zoogeography, and refers to, for example, boreal or Mediterranean faunal elements, or relict species. Zoocoenology, exploring more deeply in a vertical direction, uncovers food chains, and by considering connections between such food chains, also extends in a horizontal direction. The fauna is always linked to a territory, often with artificially sharp boundaries (for example, the fauna of a county, or a country), and the goal of faunistics is to study the occurrence of animal species in the most detail possible. Its results are enumeration-like; publishing lists of taxonomic groups, detecting new occurrences, and establishing how many species live in the area under study, and analysing them according to their distribution. This approach is unaltered when faunistical studies, as recently seen, have synecological overtones and are focused towards a physiognomically uniform area (a swamp, a grassland, forest, etc.).

The zoocoenosis, instead, represents internal links, difficult to delimit by area, and only relating to an area because it must link to some point in the biosphere. The base unit of faunistics is the species, while that of zoocoenology is the population Dudich, 1932; Park, 1949; Allee et al., 1949; Balogh, 1953; Glen, 1954; Giljarov, 1954). In practice, both work with individuals, thus they meet at the representation of the individuum, the semaphoront.

The semaphoront (Hennig, 1950) is a concept that is narrower than the individuum, and serves to indicate the changes (i.e. life stages) of the individuum. The semaphoront is the smallest element of any biological system. The individuum itself is in constant change, therefore when it is studied at a given time; it only represents a state, different from the previous one, and will change again later. The captured or observed "individuum" is thus a representation of a part of an individual life (morphological, ecological, ethological, etc.) – this is the semaphoront. The totality of semaphoronts provides the full picture of an individuum, and through this, of the population and concomitantly, of the species. *Faunistics places the semaphoront into a taxonomic category, the zoocoenology into a role which it fulfils in the community.*

Consequently, we are carrying out faunistics even when following exact methods in our sampling, if the identified material is only grouped by quantitative characteristics, even if this material was collected from an area with sharp physiognomic boundaries. The results obtained will hardly be more than a fragmentary picture of the fauna of the area; the fewer faunal samples gathered, and the more that are collected from only one developmental stage, for example the adults, the more fragmentary the results will be. If our analysis relies on only a single sampling, the result is no more than the picture of one aspect of the coenosis, representing solely the fauna (Kontkanen, 1937).

Faunistic research can concentrate on a single group. No objection can be raised against this, but what we referred to in connection with the total fauna is even more valid for "coenological" studies carried out on a single taxonomic group. If we represent the totality of the zoocoenosis with a circle, in which the constituent taxonomic groups are represented by smaller or bigger slices, then removing one of these will cut all the links that connects the studied group to the others. The zoocoenosis is not composed of taxonomic groups, but structural elements that make the coenosis a whole. Such studies, nonetheless, can have coenological aspects. If material collected from an area by exact methods is subjected to a standard coenological analysis, studies that reveal repeatedly occurring species combinations, and their quantitative characteristics, can indicate directions for further zoocoenological research. It is also the case, though, that such studies can only generate uncertainties and confusion; we are not able to see far into the complicated labyrinth of the biocoenosis.

If we want to order the collected material of an area using coenological characteristics, taxonomy will be the least suitable approach, and we cannot be satisfied with establishing the quantitative characteristics, because we need not only this facet, but to decide what roles the individual populations perform in the community. In other words: we arrange the collected population groups according to their roles in the zoocoenosis, as we attempt to do below.

§ THE SYSTEM OF BIOLOGICAL SCIENCES

We have seen that, from a cognitive point of view, the smallest unit of all biological systems is the semaphoront, and practically all scientific research relates to its representation as an individuum. According to our view, this is the unit where all biological disciplines meet; at the two component parts of bio-ontology, idiobiology and synbiology (Dudich, 1938). These are constructed by two views of the semaphoront: a) as part of an individual organism (species), and; b) as a member of a group of organisms (population). From these standpoints, directions of study, research methods, and aims are formed.

The unavoidable condition of the undisturbed development of community biology is that it be free of idiobiological considerations. We can only avoid this if we consistently view the semaphoront not as a species but as a member of the community, and frame all our research questions accordingly.

Both the individual and the community approach meet at three points, with consequent additional divisions for both the idio- and the synbiology. All semaphoronts are material realities, taking a given form, and this material reality relates to space, time and the semaphoront itself in some way. The same holds for communities, which are also material entities, of a given form, and, again, relate to space, time and the communities themselves. These three "dimensions" correspond to the individual disciplines for both idio- and synbiology, which are, naturally, not sharply separated. The name of the individual discipline means that the problems of the given discipline center around questions reflected in that name, but they have bordering areas where these problems are in contact, may overlap, and, also link semaphoront and community more fully (Plate I). On Plate I, the appropriate arrows symbolise these interdependencies.

We should not forget that the material-form relationship is intimately linked, and cannot be separated from each other, and this means that the research emphasis shifts in one or the other direction. Therefore, it is natural that the fields of science with such a research emphasis form a uniform whole, and are manifested as idio- or synbiology.

When the semaphoront is treated as an individual, or as a member of a species, we cultivate idiobiology. When the research direction aims to clarify relationships of form and shape, this branch of research should be called morphology (structural studies, biontostatics (which has, as components, promorphology, eidonomy, and anatomy)). From morphological conclusions, it is easy to delineate groups that have uniform morphology and, historically, this lead to the development of taxonomy.

The individual as living material presents problems that are of material nature, as it relates to the functioning of the living material. When the individuum is viewed as material, by necessity, we are lead to the next branch, functional studies (biontodynamics, composed of physiology and psychology). Material is not only functioning, but also has a spatial extension, so the individual is the species, which, being a specific material, is manifested in innumerable individuals. Therefore, the distribution of individuals must be viewed as the material relation of the semaphoront and, from examining this, distribution science (biontogeography) is born.

The relationship of the individual and the species to itself, and its living and non-living environment, presents ethological and ecological problems, and the study of these relationships, hypotagology, (comprising autecology and ethology) is born.

The central branch of idiobiology, developmental studies (biogenetics, with ontogenetics, phylogenetics, genetics and ethology as its fields), relates to all three dimensions, and plays a role of ever-increasing importance in the modern view of life. Life itself is morphing and evolving in space as in time; the material and relationships develop equally and, therefore, the developmental studies have the strictest link to all disciplines mentioned so far. Taxonomy, which originally started with a morphological basis, is now wholly imbued with an evolutionary world view (thus it is logical that, in Dudich's (1938) system, it appears among the genetic sciences), and the same starting point governs the solution to the main problems of distributional studies. A very tight, bidirectional link also exists between autecology and development, as all kinds of relationships of animals to anything else are related to heredity, although the path of development is also influenced by autecological factors.

The other group of sciences, synbiology, is formed when we view the semaphoront as a member of a community, thus we never consider it in itself but, at least, as a member of a population that relates to another population or community. The problems surfacing from this view must always be addressed: how does this focal population relate to other populations, and what are the relational (assemblage) needs that influence its positon?

The semaphoront, thus viewed correctly as a group of semaphoronts, can also be studied from the perspectives of morphology, material and relationships.

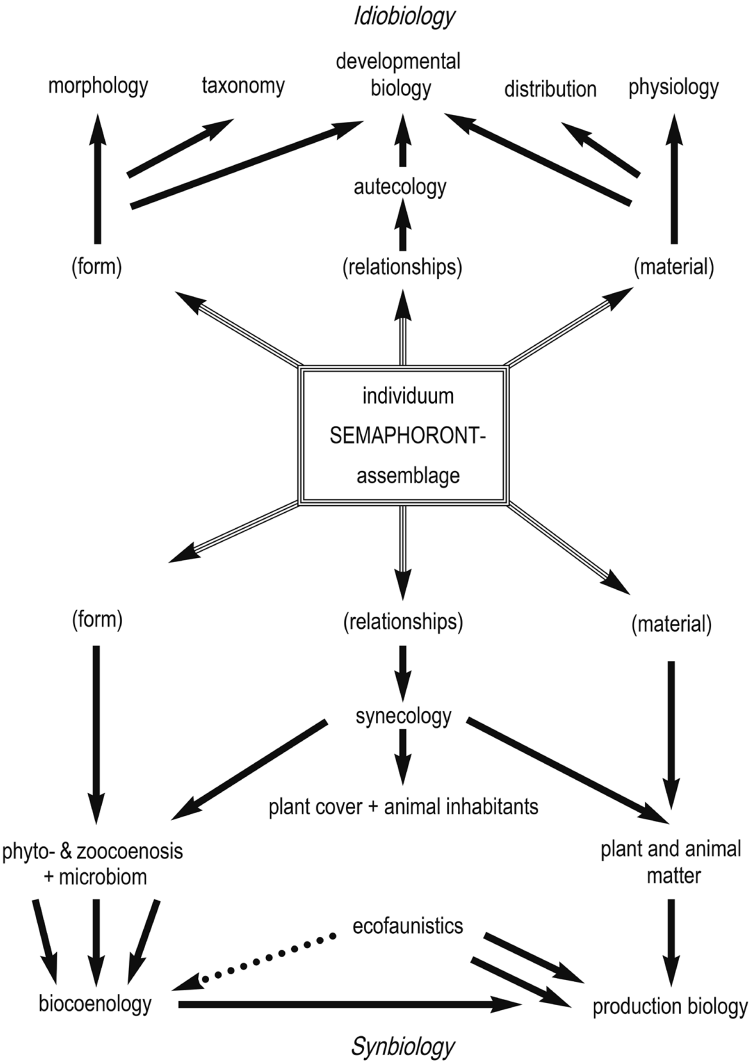
According to morphology, the groups of organisms can be divided into two major units, plant and animal associations. In addition to the morphological separation, there are also feeding lifestyles so profoundly different that allow the separate consideration of these two groups of morphs. Thus, are born the twin fields of plant sociology and zoocoenology. Biocoenology, the branch of science uniting these two, is the consequence of the intimate relationship, and the continuous interrelations, of the two groups of organisms, plants and animals.

Plant sociology, as well as zoocoenology, includes a series of sub-fields of research. These are: synphysiology, the physiological links of the groups of organisms, and, based on these relationships; syngenetics, the formation and developmental history of associations; and synmorphology, the structure, composition, and organisation. On this basis, syntaxonomy represents the system of associational categories. Given this understanding, synchorology deals with the distribution of these associations and, finally, synchronology examines the history of the associations.

In the system presented, we followed Dudich (1938), except that synecology is missing; synecology is removed from its subordinate position and, due to being the "problem" discipline of these relationships, is now placed above all other branches of synbiology (see Plate I). We were forced to do this because, according to our vision, the first fundamental question we meet when identifying an association is a synecological one. Whilst we can study either morphological, or material aspects, it is unavoidable that we start our work with an *a priori* synecological view; because all coexistence is a synecological problem, and we can only establish the categorical rank of the unity from the realised morphological and material realities.

As soon as we consider the semaphoront as the basis of a community that, by necessity, belongs to a given community, we unavoidably meet the united reality of the plant cover + animal community (the animal "fillers"; "Tierfuellung", Schwenke, 1953).

Plate I
The system of biological sciences



In recent decades, almost in front of our eyes, a new science has developed that aims to uncover the reciprocities that these two facets of the living world hide. All that zoologists cultivate today, under the names of zoocoenology or biocoenology, is none other than the quantitative and qualitative analysis of the "associated animals" of the plant cover and, by common agreement, this equates to biocoenology itself. If, however, we examine our subject from the theory of knowledge, we inevitably realise that, by this process, the whole flow of research has somehow been channelled into that blind alley. As soon as we accept that the organism and a community of organisms are two, radically different units (du Ritz, 1921; Schwenk, 1953),their study, likewise will give rise to two disciplines, different by methods and structure: idiobiology and synbiology. We must also realise that, as we turn from an individual organism (species) to groups of organisms (groups of populations), we face the living universe. As we are unable to understand this in its full complexity, we are forced to restrict our efforts towards smaller parts, which is also a logical step, given that the living world itself is organised into identifiable units. In these units, the plant cover and its animal "content" are evident, and, to extricate them, we have three paths:

a) we can study the co-occurring plant and animal associations, determined by identifiable rules;

b) we can also study the animals occurring in certain plant associations, without considering their interactions; and

c) we can also study the qualitative and quantitative changes of the produced plant and animal organic matter.

Thus, are born the three subdisciplines of synbiology; biocoenology, ecological faunistics, and production biology. It is not a new discovery that these three are related to each other, by various links, but we remain of the considered opinion that these three subdisciplines exist, and they may support each other, but it is undesirable that this support turns into a dominance over the "supported" subdiscipline.

It is perhaps daring and new to separate biocoenology and ecological faunistics, but we are forced to do it for the following reasons.

The two big realms of the living world, plants and animals, are deeply different and, from this recognition, it follows that they have completely different associational needs. From this, even though a physiognomically identified part of the plant cover can be classified into one associational unit, the same cannot be said of the animals occurring there, because the criterion of an animal community is not merely spatial co-occurrence. What we see here is a plant association and its animal "filling". When this group of animals is not analysed by zoocoenological methods, but only through establishing species identity and densities, we practice not zoocoenology but ecological faunistics; in which case, the plant association is no more than the instantaneous site of residence of the animal assemblage. Within the plant cover, populations of various animal communities are mixed, and their identification is only possible by using special methods. The bionomics of plants and animals are too different to declare that their co-occurrence can automatically pronounce them as communities (see Tansley, 1935: "to lump animals and plants together as members of a community is to put on an equal footing things which in their whole nature and behaviour are too different").

Among the coexisting animals, only a smaller or larger subset lives in coexistence with each other and the plant cover and, consequently, all animal assemblages contain two groups; one that interacts with the others, and thus forms a real community, and another group whose members are merely co-occurring due to their similar autecological needs.

The biocoenosis, though, is not merely an assemblage of individuals that, due to their similar living conditions, occur together, but a higher unit, in which the organisms are bound together (Thienemann, 1939). Therefore, we have to separate the research approach that fulfils its objectives by identifying and counting animals found in a certain plant association, from the other branch of science that, by studying correlations, uncovers the inner relationships (Keve-Kleiner, 1943).

The plant cover + its animal "filling" is called a biome (Clements, 1916: "plant matrix with the total number of included animals"). This is not a higher unit of a community, but – similarly to Schimper's formation – a biogeographical term (Tischler, 1950). Biome and biocoenosis are therefore basic units of two totally different biological disciplines. The biome (for example, a desert, tundra, prairie, alpine meadow, subalpine pines forest, etc.) can be a starting unit of biogeographical studies, but this is not a higher unit above biocoenosis, even though it contains several biocoenoses and, similarly, its animal filling is not a zoocoenosis, even though it is composed of several zoocoenoses. The term biome includes plants and animals; its plant component is a climatically determined formation, and its animal component is the animal assemblage, termed *zoon* by Tischler.

The zoon is thus the animal assemblage present in a certain plant association. In reality, Tischler uses this name for the fauna of a higher unit of biotope, called a bioregion, while the animal component of a biotope is called a zoocoenosis. We cannot adhere to this, because the concept "zoon" does not depend at all on whether, by this, we mean the animal assemblages of a smaller or bigger area. The animals filling an association is a zoon, just as it is of a larger category. The animal assemblage of the two areas, even if of different species composition, is essentially not different because, by definition, they are the same: an unsorted assemblage of animals in a given space. The animal assemblage of a biotope is not *the* zoocoenosis, but a zoon, as several zoocoenoses can live within one biotope (see Tansley, 1935: "Animal ecologists […] constantly find it necessary to speak of different animal communities living in or on a given plant community"; Glen, 1954: "a complex of smaller, interlocking, dynamic systems"). Consequently, the animal inhabitants of a plant association can, collectively, only be called a zoon, and this concept cannot be used for anything else. If we consider the biome as a biogeographical concept, its animal components cannot be anything else but a concept of zoogeography. Indeed, this is what a zoon is and, thus, it cannot be considered a sum of zoocoenoses, as the biome is not a sum of biocoenoses. The biome (plant + animal), zoon (only animals), and climatic formation (only plants) are biogeographical units, while the biocoenosis, phytocoenosis, and zoocoenosis are concepts of communities, and they do not mix.

The qualitative and quantitative study of a zoon should be viewed as a new branch of faunistics, called ecofaunistics, and we do not think of it as biocoenology, *sensu stricto*. Ecological faunistics, however, working with masses, and studies of the relationship of these masses (and not of individuals) to space, is to be viewed as a branch of synbiology. Still, we must call it faunistics, because it studies the relationship between species (or species representations) and space, and cannot be called biocoenology or zoocoenology, which aims to clarify the relationships between populations to their associated populations. Method-wise, ecological faunistics is related to biocoenology, but they are not identical and, considering its aims, it shows a closest link with production biology.

From the above, it follows that the groups stemming from the semaphoront, the idio- and synbiology are not mirror images of each other, which shows that organism and assemblage are not of similar value. Above the three subfields of synbiology, we must put synecology; be our interest material, morphological or interactions, synbiology is inseparable from the research of correlations. This study of interactions is so much the core of this science that Schwenke (1953) declares this the central principle of this discipline, and it is not synbiology but correlation research that he places diagonally to autecology. According to his perception, ecology is an idiobiological field, and synbiology (in his view, identical to biocoenology) cannot be pursued using the same methods as in the former. Even though making interaction studies the core of synbiological research is a remarkable advance, we opt for keeping the old terminology, for two reasons: a) autecology itself is intricately interwoven with interaction problems, and; b) the word synecology is a better indication that we are dealing with the relationship of assemblages to other, bigger assemblages. We can add that – as stated in connection to biomes and biocoenoses – the assemblages are not necessarily bound by interactions; they always contain intrinsic elements due to behavioural requirements and, as these can be represented by populations with many individuals, they unavoidably become objects of synbiological study. Consequently, autecology always contributes to the formation of animal communities, and occasionally becomes a synecological factor, even without correlations.

Biocoenology, ecological faunistics and production biology, however, are classified under synbiology, not synecology. This we must do, because the former has a wider, more comprehensive meaning. In each three of subdisciplines, there are elements that are biological rather than ecological. The three fields are not on the same plane: for example, it is the precondition of all production biological research that the operational representations are first described by biocoenological or eco-faunistic methods. Consequently, precisely to comply with production biological aims, the constant and dominant populations receive attention, which is unsurprising, and this sharpens the difference between the aims of production biology and biocoenology. Hence, production biological studies nearly always rely on ecofaunistical analysis, and omit the finer analysis of the biocenosis and, possibly, this dominance of production biology is the reason for the practice that, under the theme of biocoenology, there is only analysis of the fauna of various phytocoenoses.

The subject of production biology is the organic mass generated by plants and animals. Generally, both are mentioned as production, their sum is considered biomass. In theory, we cannot fault this, because it includes all the organic matter produced or transformed by living beings. Less acceptable is the extension of the term production to include organic matter produced by both plants and animals, because the two are substantially different in generation as well as chemical composition. If we call producent organisms only those that produce organic material from inorganic material (mainly by photosynthesis), then only the realised biomass can be called production. Animal biomass cannot exist without these producents, so animals use "ready-made" production to produce further animal protein, in which case these cannot properly share the same label. What is "produced" by animals is not equivalent to plant-produced biomass, but a dependent, and importantly – *transformed production*, which can be better called "transformatum". Production, in theory, is independent of transformatum, while the pre-existence of the former is indispensable for the latter. Between these two categories, we find the heterotrophic organisms, and these show similarities (for example, the presence of chitin in fungi) to animal biomass not only in their nutrient needs but also chemical composition. Production by such organisms (for example, fungi parasitic on animals) could be called "recuperated production". The volume of production and recuperated production, in all cases, much exceeds the amount of transformatum, as the plant biomass is a multiple of animal biomass, and this relationship is an elementary condition of the existence of any biocoenosis (Heikertinger, 1951).

Thus, the branches of synbiology discussed above can be defined as follows: synecology deals with assemblages of living beings, their relationships with each other and with their abiotic environment; according to whether the focus of interest is the close interactions among them, their coexistence due to ecological factors, or flows of materials and energy, synecology can lead towards biocoenology, ecofaunistics, or production biology. The starting unit is the ecosystem, or the biome.

The aim of biocoenology is the description of the organic unity of plant and animal associations, their interactions, and connections to the microbiome. In practice, it has three branches: phytocoenology, zoocoenology, and microbiology. Its basic unit is the biocoenosis.

The aim of ecofaunistics is to study, qualitatively and quantitatively, the animal component of a given biome, without considering their interactions, or only taking these into account in their effect on structure. Its basic unit is the animal assemblage (zoon).

Production biology aims to examine the flows of material and energy through assemblages and communities of living beings, and to establish qualitative and quantitative changes. Its main unit is the sum of the constant and/or dominant populations, either by density or by biomass.

One remaining question is: what, then, is agrozoocoenology? Agrozoocoenology is the sub-division of zoocoenology that considers the totality of animal assemblages that live on cultivated areas, and its link to areas less disturbed by humans, although they are connected to it by mutual influences. Plant protection entomology is, in essence, agrozoocoenology ("biozoenotische Entomologia", Schwenke, 1953). We cannot consider it as a separate branch of science, as its methods are identical to those of other zoological sciences and, even if its subject matter is connected to agriculture, this does not make it a separate science, only a link in the chain of universal science that connects practice and science.

In the recent past, Peus (1954) dealt with, in his deeply thoughtful article, the problems of biocoenology, and concluded that autecology, with its ecological methods, can approach all the important problems, because all key questions in an assemblage are problems of autecology. According to him, biotope and biocoenosis, with all their features, are products of human imagination, meaning fictions ("Gebilde des menschlichen Verstellungsvermögens") and, consequently, there is no such science as biocoenology ("die Biozoenologie als Wissenschaft hat keinen real Grund", p. 200).

In response to this surprising conclusion, we can only state that the otherwise excellent author went too far following his interesting emphasis on autecological studies. In all assemblages, there are reciprocities that exist only because, *eo ipso*, of the existence of this assemblage. In all assemblages of living things, there exist these exchanges that can only be perceived because the assemblage in question exits there and then and, without these features, could not exist. If we consider an assemblage as a coexisting unit, it presents special problems that only exist because of the existence of this unit, and this – in our opinion – goes beyond the framework of autecology. We imagine a completely different mental picture when we pronounce "*Festuca sulcata*" than when using "*Festucetum sulcatae*". In the first case, we picture a single plant, and think of its specific needs, while in the latter case, we picture a plant association, with all the complicated interdependencies that are formed precisely due to the association. The difference between the two is like the difference between autecology and synecology, or biocoenology. Such a science can, therefore, certainly be cultivated, and we can modify Peus' arguments so that autecology is indispensable for a successful pursuit of this branch of science.

The standpoint taken by Poljakov and Sumakov (1940, 1954) is similar in many respects but not so drastic; they also negate the right to existence of biocoenology, although they accept the concept of the biocoenosis as a unit of coexistence. As it transpires from their publications, these authors object to the methodological procedure that relies only on density relations when defining or analysing a biocoenosis. They oppose Beklemishev (1931), who wrote that a biocoenosis is more than the sum of its species, and displays phenomena that cannot be explained solely by the autecology of the constituent species. These authors instead declare that any problem of biocoenology can only be approached through autecological methods; consequently, we carry out autecological research even when we study the phenomena displayed by communities.

We can only partially agree with this viewpoint. We also emphasise that biocoenology cannot be studied without autecological knowledge about the constituent populations, and that the questions “what lives together” and “in what proportions” are not the defining, major questions of biocoenology – instead, these are the “why are they together” and “how do they coexist” enquiries. However, if we accept the objective existence of biocoenoses, the branch of science that studies the regularities of this unit as a unit of coexistence, is more suitably called biocoenology than autecology; in short, there should exist a branch of science that views the environment not from the viewpoint of individual species, but through analyses of a whole community as a unit. It is true that during biocoenological research, we reveal several fragments of autecological information; among them, knowledge that is related to phenomena that could not have been manifested without the existence of the coenosis. This is the reason why we cannot fully reject Beklemishev’s viewpoint, because certain autecological knowledge can only be obtained if the studied population becomes a member of a community containing another population(s). Using an example to illustrate this phenomenon that is a property of autecology but manifests itself on the plane of biocoenology, the following picture can be presented. When, on a strongly aphid-infested tree, there is high ant activity, this can greatly disturb the activities of populations of aphid-feeding species. The ants only disturb them because the aphid feeders are associated with the aphids, and these aphid-feeding populations clash with ants on a common energy source. It is evident that this activity is a manifestation of ant autecology, which exists only because of the association with these other species. The same ants are, probably, totally indifferent to the same species on parts of the tree that are not aphid-infested or, if the aphid feeders are prey for the ants, ant predation on them will have less impact on aphid density (and the zoocoenosis formed), than when they form a coenosis around high-density aphid patches. When the ants are missing from the tree, a qualitatively and quantitatively different coenosis will be formed, and the preceding phenomenon will not appear. How a given species behaves in its environment, and how this environment influences the species, are questions of autecology. But the question of why different populations of this same species behave differently can only be answered by the prevailing conditions of the specific environment where this population occurs. If there are populations of other living species coexisting under these conditions, the research must extend to more than one species/population, and a study of the interaction that considers not one but more species/populations will no longer be autecology but biocoenology. Such studies are frequently restricted to the autecology of one or the other species, but they can also diverge towards taxonomy. All this, however, does not constitute a reason for doubting the justification to study the regularities of a biocoenosis through this lens.

II. BIOCOENOSIS AND ZOOCOENOSIS

§ THE CONCEPT OF BIOCOENOSIS

The word biocoenosis has a very wide range of interpretations by different authors. The main reason for this is that the term has two meanings: it is used to express a relationship (living in a biocoenosis) and, also, to denote an assemblage (community) that this relationship brings together. In other words, the expression biocoenosis is used to denote the process of coexistence, as well as to name the resulting entity. In all likelihood, this double meaning is the reason that authors, in some cases, use the term for organisms living in very small spatial units, while others use the same term only for very large assemblages (Szelényi, 1955). To clarify our viewpoint, and clearly identify our interpretation of the term, we state the following.

Henceforth, we will not use "community" as a synonym for biocoenosis, because we are not referring to the assemblage, but to the relationships that make an assemblage an ecological community. For example, insects and bacteria living on a carcass comprise a community but they do not constitute a biocoenosis. Therefore, the term community indicates that a relationship exists: community infers a network of interactions that bring groups of organisms into coexistence. The biocoenosis is not visible nor tangible, its existence can only be deduced from certain causal relationships and is represented by all the living things that are held together by these interrelationships. The community is a visible and tangible entity, even if the constituent relationships can only partially registered.

The term biocoenosis is interpreted as an association of living beings, never limited to either plants or animals; on the contrary, a biocoenosis always incorporates all organisms in each space, if these organisms form an interacting community. Only then, can these species be considered a community. This means that the constituent organisms must be members of groups of living organisms that mutually presume each other's presence, that are mutually interdependent and, consequently, they influence each other.

Therefore, a biocoenosis, in our perception, is a total community, where any, and all, species are included, from bacteria through hetero- and autotrophic plants to animals, where they are in a state of association, i.e. they form an ecological community. Henceforth, I will avoid expressions like "the biocoenosis of a forest" because the forest, (if we understand a forest as only trees and undergrowth), is not a biocoenosis in the same way that the animals living in the forest are not yet a biocoenosis, nor is the sum of these two a biocoenosis, but both are members of a biocoenosis that also includes fungi and bacteria living there.

The biocoenosis is consequently an association of living beings, whose members are in functional relationships with each other, forming a very complex unit of living organisms, and its complete, real-time perception is nearly impossible.

The members of a biocoenosis, more correctly its living members, are usually classified into three groups: producing, consuming and reducing elements (Thienemann, 1939). If, however, we define a biocoenosis as the whole association of living beings, this theoretically correct three-way classification is insufficient. The plant kingdom does not only comprise photosynthesising green plants, but also organisms that are unable to assimilate CO_2, and ones that are dependent on already-synthesised organic materials. The producing organisms therefore produce organic material not only for animals, but also for certain plants, so the consumers are not exclusively animals; they include certain organisms classified as plants.

So, after all, what organisms constitute a biocoenosis? Firstly, living things able to produce organic compounds from inorganic ones (producers). To these are added organisms that need already-synthesised organic material, and these can be either plants or animals. Some of these rely on plants, others on living animals (corrumpents and obstants), while still others utilise organic materials in a non-living state (intercalary elements). There are living organisms that sustain others (sustinents) and, finally, organisms that convert organic materials into inorganic matter (reducents).

Consequently, we recognise the following groups when we want to unearth the structural elements of a biocoenosis:

1) Producents include plants that synthesise organic compounds, either by photo- or chemosynthesis, and which are the basis of all other life forms. Without them, no biocoenosis can be formed.

2) Corrumpents are the plants or animals that utilise other living plants (producents or intercalary element).

3) Intercalary elements (recuperants, *sensu* Woynarovich 1954) are plants or animals that are dependent on existing organic compounds, but assimilate them in their non-living form.

4) Obstants are plants or animals that live at the expense of other living organisms (plants or animals) as parasites or predators.

5) Sustinents are plants or animals that contribute to the survival of others, either as symbionts or as agents of reproduction, thus fulfilling a vital function in their survival.

6) Reducents are plants that decompose organic material into inorganic compounds.

Links among these structural elements elucidate the community relationship that unites these organisms as a biocoenosis. Irrespective of considering the traditional triad, or the above-detailed elementary categories, as the essence of a biocoenosis, it is certain that the concept must refer to an overarching unit, expressing some sort of totality that is also physically recognisable. Observing the development of the concept of biocoenosis, we can clearly see that a large majority of authors aim to express something similarly extensive and, apparently, want to avoid its use for a small segment of a habitat. By excluding the "community" interpretation of the biocoenosis, we squarely fall into this camp ourselves.

Delimiting a biocoenosis is, however, not an easy task, and from the desire that this concept be restricted to a larger, physiognomically recognisable unit, it follows that the additional concepts of biological equilibrium and its consequent homeostasis became included in most definitions. These will be dealt with in a separate chapter; at this stage, only the following needs to be acknowledged.

As only the producent organisms can generate organic material, it is without doubt that the basis of all biocoenoses can only be formed by producents. The essential point of a biocoenosis is not being, or not being, in equilibrium, but whether it contains producent organisms; in their absence, a biocoenosis cannot be formed nor sustained. Additionally, as with life itself, the biocoenosis, as a form of life, has development potential, starts from a small beginning, and gradually expands. It follows from the principle of development, that all biocoenoses start when a producent appears in each space. Therefore, once a producent is present, we see the start of a biocoenosis that is gradually enriched by the other structural components, and will reach a climax state permitted by edaphic and climatic constraints, according to the rules of succession.

Definitions that emphasise the equilibrium criterion contain the basic error that they totally ignore the principles of development/evolution, and that such a definition can only refer to an advanced, complex, climax association, containing all the component structural elements. An island just emerged from the sea, or the bare soil of a fresh landslide, is gradually colonised by organisms. When can we name such an area an "independent" biocoenosis; when can we apply to them the concept of an equilibrium and the ability to self-regulate? There are no certain answers to these questions.

A biocoenosis is, therefore, an association of plants and animals that is gradually formed by various structural elements, but always around producent organisms, its components are in living interactions with each other, and it is formed in a definable space of the biosphere, as a physiognomically recognisable unit.

In theory, all biocoenoses start with the tiniest of producents that make the soil suitable for a richer community of organisms, but it also follows from the concept of the biosphere, that the influences from neighbouring, more advanced biocoenoses can speed this process up (e.g. the arrival of pioneer plants).

The formation of the biocoenosis is, therefore, also influenced by the environment, but the impact of the space that it occupies is also decisive. From the first minute, there is a tight interaction between the biocoenosis and its non-living environment, which only becomes more and more complex; Schwenke (1953) was right to notice that the biocoenosis is a manifestation of the abiotic-biotic factor complex that is inseparable from the biocoen, and which is characterised by the organisms present.

The complex relationships present in a biocoenosis pose a formidable problem for the researcher. The fact that the biocoenosis can be divided into structural elements, allows that we start the exploration of the biocoenosis with the analysis of one of these groups, especially the links that binds this group to the others. However, precious little attention has been afforded in this direction, because the living world appears to us in the form of two major groups, one being the macroflora, and the other the macrofauna. Naturally, biocoenological research started (and continues, practically, even today) on these easily defined groups.

It follows from the unity of the biocoenosis, that both the animal and plant associations are entirely embedded in it, cannot be separated from it, nor be removed, but occur as a regularly repeating, identifiable phenomenon that can be observed and analysed. During such study, one should not forget that the biocoenosis contains unbreakable bonds throughout the plant and animal associations; for example, the obstant elements within a zoocoenosis are represented not only by animals, but obstants of plant origin also find their way into animal bodies and that, without sustinents of plant origin (symbionts, the bacterial flora of digestive tracts, etc.), animal life is hardly imaginable. The tight integration of structural components is obvious, and manifests itself in the mixed plant and animal membership in the groups of corrumpents, obstants and sustinents.

Just as one can distinguish plant and animal associations that differ in structure, as well as in evolutionary origin, there also exist biocoenoses that are not merely the sum of those two, but include additional, microbiotic elements and, with them, form more complex associational units of higher order. This tiny world, whose membership includes producents, but is mostly composed of reducents, obstants and sustinents, has vital links to both the animals and the world of higher plants; they form as indispensable an element of communal life as do the producents represented by higher plants (see Sukatchev, 1950).

The biocoenosis is bound together effectively by these components, more so as life on earthalso started with such tiny organisms (Soó, 1953), and the rich tapestry of life, with its expanded morphological richness of higher plants and animals, has developed from them. It would be much more logical to define the units of association starting from these microorganisms, and only practical reasons force us to do the opposite. We start with the associations of higher organisms that are visually perceptible, and continue to move in directions that, along tangible associative links, lead us into the invisible world of microbial organisms. These organisms are no longer members of an animal or plant association, but members of the biocoenosis itself. For us, the phyto- or zoocoenosis ends where we start including the microorganisms in the associations of higher plants or animals, as partners of life importance, incorporated within the true biocoenosis, and biocoenology is only correctly cultivated if we include all the interactions that exist among animals, plants and microbes.

Consequently, the biocoenosis includes those living things that are not considered by either phyto- or by zoocoenology (Dudich, 1953) and are present, even if invisible (except as occasional macroscopic phenomena e.g. as the spots caused by microbial infections, rots, calcareous patches, soil formation), and yet can decisively influence the composition of the plant and animal association itself. Considering the relationship between soil organisms and soil nutritional resources, remarkable studies have attempted to classify the soils themselves by qualitatively and quantitatively analysing the former (Franz, 1950, 1951).

Nevertheless, phyto- and zoocoenology study the composition, the structure of phyto- and zoocoenoses, and their impact on each other, as if cutting the links that bind them to the totality of the biocoenosis. This, however, cannot be faulted on a theoretical basis, because it is unavoidable due to methodological constraints (Tansley, 1935, Pavlovsky and Novikov, 1950).

The composition of plant and animal associations can also be studied without considering their links to the microbiome; in fact, the role of the latter can be surmised from the structure of the former. The question of "why" will inevitably force the researcher to look beyond the basic composition of the plant or animal associations and investigate the wider horizons of the biocoenosis; thus, the research area of the "full" biocoenology will, besides the phyto- and zoocoenology, always include microbiology as well.

The chapter on the concept of biocoenosis cannot be concluded without trying to clarify its relationship towards similar, or similar-sounding ones appearing in the literature. The biome (Clements, 1916) was already mentioned; others encountered include the ecosystem (Tansley, 1935) and the biogeocoenosis (Sukhatchev, 1947, 1949, 1950). These three concepts only partially overlap but are not identical, and are also different from the biocoenosis. Firstly,we need to state that the biome and biogeocoenosis are biogeographical, while ecosystem and biocoenosis are biocoenological concepts; the four concepts can be separated when presented together.

The biome denotes the full spectrum of living beings in a region, that is in a large, physiognomically identifiable spatial unit. The concept of a biome therefore includes only living beings, and the abiotic factors influencing them are only present in their effects and the consequences of these effects. The various biomes have visually recognisable differences, and they also differ in their species composition. These differences emerge from the effects of factors outside the biome, the abiotic factors; an example of a biome is the tundra.

The biogeocoenosis is a concept above that of the biome that also includes all the abiotic factors that are outside the biome but are influencing factors, and are responsible for its appearance. The various biogeocoenoses differ from each other in their physiognomy and species composition that emerge due to the differences in climatic, edaphic, geographical and geological conditions. A biogeocoenosis, for example, is the tundra *and* the totality of the conditions that lead to its formation and the ones that sustain it.

The biocoenosis is a particular association of species that includes living beings connected by biotic links. The various biocoenoses differ not only in species composition but are also spatiallyseparated. The alpine meadow, as a biome, is the same in the Pyrenees and Carpathians but the two biocoenoses, in reality, are totally different entities that have no interaction with each other, and, possibly, even have different species compositions. All subalpine meadows, as a geographical formation, belong to the same biome, and can also be classified into the same biogeocoenosis and, as such, differ from the needle-leaved forest biome and biogeocoenosis. The biome is immutable and, if a certain biome is transformed, for example, a needle-leaved forest develops on the site formerly occupied by a subalpine meadow, then the relevant biome would no longer exist, because it has disappeared as a geographical formation. However, the biocoenosis is under constant change, yet remains a biocoenosis, because its core is not a certain formation or species complex, but the biotic connections between its plant and animal species. A biocoenosis is always a particular assemblage that is encountered at a given location, at a given time.

The ecosystem is a concept that is wider than the biocoenosis, and includes the abiotic factors that generate or sustain the biocoenosis. Therefore, an ecosystem is a product of the organisms associated with each other, and the factors generating this association, that are effective in a space at a particular time, that then function and coexist in that space and time. The ecosystem changes – as does the biocoenosis – because, with changing abiotic conditions (that may be caused by the biocoenosis itself), the biocoenosis will change and, with it,the ecosystem will also change. At the highest level, the ecosystem is under the influence of macroclimatic factors, within which edaphic factors are influential and, finally, it is also under the influence of the biocoenosis formed within its boundaries. Therefore, all existing ecosystems are different, but all of them are existing realities. The oak forests of the Buda Hills are ecosystems that are different from oak forests in the Matra Mountains, because they exist in different geographical locations. As a biogeographical concept, they belong to the same biome and the same biogeocoenosis but, as an outcome of the effects of factors influential at a particular location, and through associations emerging through their activity, they are different ecosystems and different biocoenoses.

Therefore, while therefore, the biome and the biogeocoenosis are constructed as collective concepts that encompass various formations on the surface of the Earth (and the factors operating there), the ecosystem and biocoenosis are physiognomic units fashioned by the abiocoen + the biocoen, and their similarity of conditions. The formation can be the same yet separated in space, but the biocoenosis and ecosystem will, *eo ipso,* be different, and the same formation can contain several biocoenoses and ecosystems that differ from each other.

By listing the above concepts, we have also declared a belief that the biocoenology is a strictly ecological field, and separated from biogeography. Biocoenology is threatened not only by idiobiological contamination but, also, that we view its problems from a biogeographical platform. Biogeography, of course, is not only a descriptive science, but it also strives to explain the generation of the formations that it uncovers, thus also conducting a search for causes. While doing this, it extends towards geology. The deciphering of the laws relevant for the ecosystem and the biocoenosis as defined here, is not the task of biogeography but that of biocoenology, whose objective is, therefore, in all cases the study of a given, existing assemblage.

§ PLANT AND ANIMAL ASSOCIATIONS

We can always distinguish plant and animal associations, but this does not also mean a separation; the plant cover and its fauna are inseparable, yet not identical – thus the distinction is also justified.

The plant cover has primacy because, without it, no animal assemblage is imaginable. Nonetheless, this plant cover is not independent of the animal world, as we can risk making the statement that without animals, it could not even exist in its current state because it relies so much on fertilisation via arthropods.

The plant cover is organised through the action of various natural laws, resulting in the formation of various plant associations. Due to the tight link of the animals with plant cover, we can also assume that there is a link between plant and animal associations; that a given plant association is supporting a given animal association. It is obvious, from our previous knowledge, that certain plant associations have their characteristic fauna.

This convenient parallelism lead Franz (1939, 1950) to suggest that the word "association" should also be applied to animal assemblages, so that zooassociation should denote animal assemblages, and phytoassociation should denote plant assemblages, while the simple "association" ought to be used for a combination of animal *and* plant assemblages. The acceptance of this suggestion is hardly possible, because the word association, without the "phyto" addition, is already in widely accepted in plant sociology, as the name of the base unit of an assemblage. The term is also acceptable for Friederichs

(1930: 30) for cases of the biocoenological context where the term denotes a plant and its associated phytophagous organisms. To avoid an excessive complication of terminology, Janos Balogh (1946) also suggests the provisional use of association; in addition, he thinks it is even permissible to use "association" for higher categories of plant sociology and continued the development of the zoocoenological terminology in this direction (Balogh, 1953). We, however, in agreement with several other authors (Hesse, 1924; Palmgren, 1928; Krogerus, 1932; Dudich, 1939; Lindberg, 1944, Schwenke, 1953), cannot accept this suggestion; they judge that this term ought to be reserved for use by plant sociology, and the first two authors, and especially Dudich, provide weighty arguments of general validity against a hasty synthesis. We also see substantial differences between plant and animal associations; above all, the difference in structure is very noticeable. The [plant] association, homogeneous from the point of view of nutritional biology, with its relatively constant composition and biomass can hardly be compared to the zoocoenosis, which includes semaphoronts of very different life histories, biology, and which undergoes continuous modification. The heterotroph animal world can utilise the organic material provided by the plants through a wide range of adaptations. These life forms extend from the scale insects, spending most of their life anchored to a single location, to the birds of high vagility – an astonishingly variable spectrum. This is sufficient for us to resist the suggestion that the plant societies can be mimicked by that of animals and, thus, to resist the application of the term association to zoocoenology.

All members of a plant association perform a substantially identical function. There is a smaller difference between a geophyte and a phanerophyte than, for example, the larval vs. adult stage of the same individual insect. Animal associations are formed by performing task-adapted activities to use the energy produced by plants. This process is not substantiallydifferent from that of the plants, as the absorption, transport and assimilation of nutrient via plant roots is not too dissimilar to ingestion of nutrients by animals by sucking, chewing, or by other means. However, these characteristic animal activities, that precede food processing, are a core feature of both animal associations and their constituent populations, and are manifested as an antagonistic relationship between associations of plants and animals. This antagonism is what underpins the formation and sustenance of animal associations, as well as their clear separation from plant associations.

The animal assemblages cannot be identical across comparable plant associations; their only common characteristic is that, in both, certain species combinations are regularly repeated, so much so that we can assume that they are not in coexistence through chance. However, an individual plant (not the species), during its ontogenetic development, cannot visit various associations, as is commonplace among animals and, indeed, essential for some species. The plant association, beyond representing a sociological unit, for the resident animals constitutes a space, within which there can be several distinct animal associations. Consider the beech tree, that is but one species in a *Fagetum silvaticae* association; for animals, it is a higher category, the living space for a rather complex animal association. The lowest category in the taxonomy of plant associations, at least for herbs, is the species but, in the case of animals, there is a further consideration; on a given plant species, there may exist an animal association; the taxonomy of the two does not fully overlap, and plant associations have one category fewer. In this respect, one should recall Dudich's (1939) arguments, especially that the plant cover has an important role as the generator of the life conditions of a biotope, while this cannot be said of the animals living there. Due to the preceding arguments, the word association will be used exclusively for plant societies while, for animals, the term zoocoenosis will be used.

After distinguishing the plant associations from zoocoenoses, let us examine whether there are factors linking zoocoenoses to plant associations? If we find such linkages, we can assume that there is a connection between plant associations and the qualitative composition of zoocoenoses. The plant component of the biocoenosis is, characteristically, rooted to a place, even to a degree that the plant cover can be used to characterise the biotope. The plant cover is present as the same association for long time periods, in the case of woody vegetation for decades; this association-forming plant cover is an essential source of energy for the animals. Hence, the factors sought are present: the relative constancy of the plant association, and its role as energy source. These two necessarily lead to the conclusion that a plant association of a given composition predicts a more-or-less well defined zoocoenosis.

Thus, the solution is almost self-evident, that the associational relationships of a zoocoenosis are projected onto the relevant plant association, as its solid foundation.

The idea that the zoocoenoses should be linked to plant associations is not new. While Shelford and Tower (1925) suggest that the study of zoocoenoses ought to start from the animal communities themselves, and these are delimited by the area where the dominant species remains dominant, Palmgren (1928, 1930), Krogerus (1932), Rabeler (1937, 1952), Brundin (1934) and Franz (1939) are adamant that the limits of a zoocoenosis, at least in terrestrial habitats, ought to be made considering the plant associations. This is also the standpoint of Hungarian researchers (Balogh and Loksa, 1948; Nagy, 1944, 1947, 1950; Balogh, 1953). All these authors consider the plant associations as the basis for the area occupied by a zoocoenosis, and describe the zoocoenosis by its dominance relations.

Theoretically, we are in accordance, but the association-based construction is not elucidated by copying the framework of plant sociology, but in trying to get to the root of the question: what is the causal basis that underlies a given plant association harbours a zoocoenosis of a given species combination?

In the light of this precise question, the association or, more generally, the plant cover, loses its taxonomically-tainted guise, and becomes something more tangible: the energy source for animals, and a determinant of factors that provide living conditions (see Dudich, 1939; Nagy, 1944, 1947, 1950; Park, in Alee et al., 1949).

What we cannot agree with, in the current practice of zoocoenology, is that – irrespective of starting from plant or animal associations, and focusing on dominance relations – it is always only the fauna that is analysed, and that co-occurrence is deemed a sufficient condition for declaring a community. Hence, not even posing the question of other community criteria; copying the approach of plant sociology, the co-occurrence is considered sufficient to declare a zoocoenosis.

There is no doubt that there is a tight relationship between plant cover and the fauna, which is categorically important for the latter, although it can be positive for plants, too, and for a group of plants, essential. If the plants are essential for the animal world as an indispensable energy source, at least one layer must be directly based on plants, thus providing the possibility of the existence of further trophic levels. Given that plants rarely exist in isolation, and form associations, the smallest category of zoocoenoses must have links with plant associations and, in many cases, the existence of a plant association cannot be envisaged in the absence of an insect assemblage.

Plant sociology has intimate links with zoocoenology only through this intersection; the plant cover that provides food anchors the producent trophic level, the animal world secures the subsequent consument levels. The existence of plant associations necessitates the formation of animal associations, too. In this relationship, however, the host plant is the primary factor, not the association.

§ THE CONCEPT OF ANIMAL ASSOCIATION

To correctly interpret the concept of animal association in relation to an animal assemblage, we need to scrutinise the concept of the former – what is the criterion hat entitles us to declare that the collected animals, even if numerous, constitute not a random assemblage, but that they are held together by certain rules, that allows us to call it an association?

We can only answer this question correctly if we view these assemblages not as static ones, but examine their formation and development, i.e. analyse their dynamics. The question that we need to pose in all cases is: what does, in the study area, underpin the dominance of the population in question among the other coexisting populations? The literature indicates that this question can be answered by establishing the degree of dominance; from a coenological viewpoint, only the most populous populations merit attention. This reply, however, even if some populations are indeed dominant in certain associations, cannot be satisfactory (Smith 1928; Kuehnelt 1951) because the factor that binds the population in question to the association may be something totally different, and unrelated to dominance. The role of a population may be the same at low vs. high dominance situations. From the perspective of the end result of an association, events during the low-density state of a given population are the really important ones for the eventual fate of the association (Thalenhorst, 1951; Schwerdtfeger, 1953).

It is obvious that two factors can force animals to form associations: a) trophic links, that organises populations in a hierarchical order, i.e. vertically, and b) the exploitation of a common resource, that orders them horizontally, sometimes even along an extended chain.

The animal association is, therefore, the frequency of coexisting animals that co-occur to utilise a common energy resource, while they are in mutual dependency via a food chain (BejBienko, in Shegloev 1951, p. 101; Kuehnelet, 1951; Park in Allee et al., 1949. p. 437: "… organisms would tend to form natural groups of foods and feeders – in other words, would form communities").

In a vertical orientation, the animal association is reliant on the producent elements of the biocoenosis, generally meaning the plants, and the closer a population is to this producent level, the closer its relationship is to the immediate environment, together with the associated parasitic and episitic elements relying on the same plant energy source.

We can, therefore, define animal association any animal assemblage that fulfils the above criteria. Subsequently, we will use the term in this sense, while we shall consider other terms of association within this category at a later stage (see p. 70).

It follows from this, however, that not all animal assemblages can be considered animal associations, and we need to distinguish between animals living in a certain area (the faunal representation) and the existing animal associations in the same area (Szelényi, 1955). The substantial difference between plant and animal associations is most clearly manifested here.

It is an intrinsic feature of any plant association that it strives to cover most of the area available. Under a closed plant cover, however, weaker species cannot survive; the plant cover necessarily becomes a plant association, in which only species that have a similar set of vital optimum conditions can survive (Cajander, 1909). Such a plant association is relatively stable, bound to an area, and occurs where the influence of the dominant species on the others is obvious.

In a plant association, therefore, competition has a determining role. The plant associations, apart from providing an energy resource, create other environmental conditions, depending on the associations' own structural complexity, and this represents a set of life conditions, second only in importance to the energy source (food). In the animal association, however, the effect of competition for space is of less importance; an animal association is not formed because the spatial relations force the constituent animals to coexist. In an animal association, there is no equivalent for canopy closure – but its exact opposite: populations disperse, and more so as spatial competition intensifies. Vagility in animals is not only an obvious indicator of the difference between plants and animals, but has consequences that magnify the difference between the essence of plant vs. animal associations. This vagility produces an effect in two directions: a) for animals, it enables the avoidance of unfavourable conditions by moving, or they occupy the space to allow their existence under optimal conditions, and b) for animal life to flourish, a certain level of free movement is necessary. Consequently, individual populations mix, because it is impossible that the movements of populations of an animal association (groups of semaphoronts), representing different life forms, occur in the same direction and plane; hence, an animal association always, continuously, and of necessity covers the same area. Certain elements of the association may, of necessity, leave, and their place is taken by other, foreign elements. This phenomenon is clearly pointed out by certain coenologists, who remark that, after some time, species sometimes just disappear from the association (i.e. Balogh, 1953). The full discussion of this phenomenon goes beyond the current topic (see apparent and latent populations, p. 141) but its manifestation, unequivocally, indicates that certain populations can, indeed, leave the space where the association in question is under study, and – obviously move to other, foreign areas.

From this, it certainly follows that the animal assemblage of a given space (plant association) represents only the fauna; this immediate animal assemblage is dependent upon the relations of energy and environmental conditions, and these can be characteristic of the plant association in question. However, the assemblage is not identical, *in toto,* with *one* ecosystem, as – apart from groups of populations that rightly qualify for animal association status – it contains foreign elements, accidentally present as transient populations. For this reason, such an animal assemblage cannot be analysed using coenological parameters, because they are not members of *one* zoocoenosis. The semaphoronts found together share the same space, but this does not mean that they form a coexisting community. With regard to the dominant population in such an animal assemblage, one cannot say, justifiably, that it fulfils the most important role in the "coenosis", as this animal assemblage is not a zoocoenosis, and the dominant population will only affect those elements that are tightly linked to it along the trophic chain. Indeed, there can exist populations that occupy the same space, and for those, the presence or absence of this dominant population is totally indifferent. The more complex the plant composition, the more likely it is that various animal populations occur independently of each other in this plant community of great vertical complexity, varied plant-based energy sources, and special environmental conditions.

The fauna will be rich, and the number of animal associations can also be high, but the dominance of any population can only manifest itself within such an associative frame; it is inconceivable that it will influence the other animal populations of the association to the degree that a dominant plant would influence the other plants in the same association (see Schwenke, 1953).

The terms fauna, the animal assemblage (which is the instantaneous representation of that fauna) and zoocoenosis cannot be identical, as using two names for the same entity would be meaningless. The fauna is an abstraction, drawn from the study of many animal assemblages, but these assemblages are existing realities, representing the fauna of the area at that time. The sum of these assemblages is not the fauna, but the animal world of the area or spatial unit in question. The formation of this animal world is not caused by coexistence mechanisms alone; several other factors (life history, physiography, climatic, etc.) would influence it. The animal world, precisely because it is related to space, in essence, is not different from the animal assemblage of the smallest relevant spatial unit, and is none other than the sum of these, i.e. a bigger animal assemblage. The sum of plant associations is the plant cover, yet the animal world is not merely the sum of animal assemblages; additionally, it also contains populations that live in the same space but have no links and, thus, are indifferent to the members of the assemblages. While the sum of animal assemblages is a bigger animal assemblage (depending on the established borders), the sum of zoocoenoses is not necessarily a bigger zoocoenosis, and its limits are never the limits of an animal assemblage; the member populations of a zoocoenosis have functional relationships with each other, and their relationship with space is secondary.

Currently, zoocoenological practice considers the fauna as zoocoenosis, and the only criterion required to do this is a quantitative census, and analysis using coenological characteristics. This is an unacceptable approach, because it only changes the study method and does not touch upon the essence of the zoocoenosis assuming no change in the coexisting animal assemblage. Therefore, a zoocoenosis must be recognised and delimited, with non-relevant elements excluded, before its analysis can start; this is only possible by unearthing its trophic chains.

A zoocoenosis is, in all likelihood, constructed following some rules, built from elements arranged with some regularity; otherwise, it would be impossible to find repeated species combinations that describe the groups of coexisting populations.

It is natural that the starting point of zoocoenological studies is a plant association, thus, at the first step, we are faced with an animal assemblage. This assemblage must be analysed from a coenological point of view, meaning the constituent populations must be grouped into structural elements, according to their role in the zoocoenosis (i.e. their coexistence needs), to unearth their links to each other and to the plant association.

§ THE STRUCTURAL ELEMENTS OF THE ANIMAL ASSEMBLAGE

The semaphoronts found in a plant association can be grouped into seven coenological groups, there are:

1.) Corrumpent elements that are tightly linked to living plants, feeding on them.

2.) Obstant elements, feeding on other living animals.

3.) Sustinent elements that play a role in plant fertilisation.

4.) Intercalary elements that live on animal or plant excreta (Balogh 1953).

5.) Hospitants that feed on honeydew or nectar.

6.) Temporal (pro tempore) elements that, for some reason, live in extended contact with a member of the association, yet have no trophic relation to them.

7.) Peregrinant elements that are transients, with no relationship to any member of the association or zoocoenosis; they are en route to somewhere else, and only temporarily resident within the zoocoenosis.

The herbivorous semaphoronts in a zoocoenosis fill the role of corrumpent (detrimental) elements, because their activity can cost the life of a host plant (in the case of root feeders), or can result in an inability to produce seeds. Consequently, certain plant species can disappear from a plant association, together with all herbivores, parasites and episites that are linked to the plant species. As a result, the association is in a state of slow change, termed succession by plant sociologists. One cannot deny that, in some cases, succession can be caused by herbivores; unfortunately, there is a lack of rigorous studies on this topic[1]. Corrumpent elements can, however, have a transforming impact without causing succession; there are numerous examples in the field of plant protection. *Lymantria dispar*, defoliating an oak forest, will certainly influence all trophic chains starting from leaf miners; these chains cannot be formed in the absence of the initial food source for the leaf miners. *Anthonomus pomorum*, attacking apple trees during bud burst, can cause all flowers to perish in bud stage. On such trees, neither *Cydia pomonella*, nor *Hoplocampa testudinea*, or species of *Rhynchites* can colonise. We avoid calling this competition as, rationally, we cannot justify how competition could occur between *Anthonomus,* which is active in March, and *Cydia,* that will swarm in May? Similarly, can we find any kind of conflict in the phenomenon whereby mining insects will disappear from a zoocoenosis because, due to the activity of caterpillars, there are no leaves left for them? In our opinion, there is no justification for attaching the phenomenon of competition into these events. The underlying cause is no more than the system of interactions that make a zoocoenosis itself; intense demographic

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[1] From our own experience, we can cite an event of grave damage, seen at Tahitotfalu, on 18 April 1935, where 3.62 ha of the village green was so badly damaged by *Rhizotrogus* larvae that the infested areas were all reddish brown, covered by dried-out grasses, without a single live plant; they could be pulled easily from the ground, as their roots were completely chewed away.

events in one population will reverberate throughout the whole network, sometimes, also, in distant and seemingly independent elements.

Therefore, one cannot deny that the herbivorous semaphoronts have the potential to transform an association; this capacity of semaphoronts is the reason that we consider them zoocoenologically distinct from other elements of the coenosis.

One should not see a homocentrism in the term "corrumpent" – it is not identical with "pest"; we only want to emphasize the key position that herbivores occupy between plants and the other components of animal associations. From this point of view, one cannot consider the death of a plant solely in terms of the activity of corrumpents, because this will result in life conditions for a series of intercalary populations. On the other hand, the previously existing animal assemblage and, what is more, the biocoenosis itself, must fall apart. This is why they are called corrumpents!

It is another matter that, because of agricultural cultivation, all corrumpent populations living on cultivated plants are classified as pests. This term relates to an economic category, restricted to the interest of one species and a pest is neither unnatural nor extraordinary. This standpoint continues when considering the biocoenosis. There is no doubt that, from the point of view of the codling moth, the *Anthonomus,* by destroying the buds, is harmful just as the colding moth is a pest from the human point of view. A biocoenosis, however, serves the interest of no species; it exists precisely because of the often-contradictory interests of the component species and a complicated network of living organisms develops that enables the sustained existence of the coenosis.

Zoophagous populations form the obstant (counterweight) elements of the zoocoenosis, because, at least, some of them directly hunt the herbivores, or parasitise them, therefore influencing their population densities, preventing their gradation, and, thus, blocking their threat to the existence of the association. Obstant elements are also predators, preying on hyperparaites or episites that, despite relying on consuming insectivores that prey on herbivores (thus limiting their effect), means their role culminates in limiting the impact of primary parasites or predators, thus preventing the herbivores from becoming extinct in the area. Ultimately, this would result in the elimination of the first consumer level in the trophic chain, the herbivores, that would cause the collapse of the whole community.

A characteristic example of the importance of obstant elements is the role of the parasitoid *Trichgramma evanescens*, in keeping the herbivore *Mamestra (Barathra) brassicae* in check on poppies. This lepidopteran, annually, lays many eggs on the underside of poppy leaves. Judging from the number of eggs laid, the entire emerging caterpillar population would be fatal to the poppies but, with the same regularity, they fall victim to this parasitic wasp to the degree that only a fraction of eggs produce a caterpillar. In our experience, there was only one occasion, at the end of the 1930s in Biharnagybajom, when, obviously due to the absence of *Trichogramma*, the caterpillars completely destroyed a small field of poppies. This damage peaked after flowering, thus destroying the whole insect community of the poppies as well. The limiting role of *Trissolcus (Microphanurus) semistriatus* and many predatory insects (Treml and Batkina, 1951) on population densities of *Eurygaster maura* and *Eurygaster austriaca* is also well known.

Obstant elements are, therefore, all the semaphoronts that live on other populations, and their role is to reduce densities of other populations, irrespective of the role of those populations. Thus, a semaphoront living on another obstant population is also, itself, an obstant. The deeper importance of obstancy for the community is shown in the phenomenon that, in their absence, the otherwise corrumpent population itself gives rise to such elements, as a part of them starts to behave as obstant populations. Cannibalism is no doubt an obstant activity, and the result is the decline of the abundance of the corrumpent population. An excellent example is the case of *Tribolium confusum* (Chapman, 1931) where, at high densities, more and more of the semaphoronts start to consume eggs and pupae, with the consequence of a reduction in densities, whereupon cannibalism declines, and the "balance" between food and densities is restored.

The sustinents merit their category because of their important role in sustaining the association by mediating plant reproduction. By this, they assure not only the survival of certain plants in the association, but contribute to yield, through which the formation of further trophic chains (seed feeders) occurs. Membership is not gained by lifestyle (feeding on nectar, pollen, honeydew) but by playing a role in fertilisation without causing damage to the plant itself (e.g. as *Meligethes aeneus* does, see Friederichs, 1921).

The intercalary elements (decomposers) live on dead material, and are important members of the biocoenosis because they decompose material. Their importance is especially notable subterraneously, and can be divided into three groups: a) some of them live directly on dead and decomposing plants; b) the food of the next group is excreta of herbivores, and thus are indirectly linked to plants as a resource. Plant material is important in this case, clearly indicated by the rich insect assemblages on such excreta, while that of carnivores is less frequented (Kuehnelt, 1950). The third group lives on carcasses or other resources that are shed by animals (recuperants, *sensu* Woynarovich, 1954). Their characteristic position does not represent the last step of the trophic chain, as they can be linked to any contributor.

From the point of energy transfer, the first two groups are unequivocal, as belonging to the plant-feeding, biophagous group the populations in the third group, however, are intermediate members of a trophic chain starting with herbivores.

The feeding biology of intercalary element, in many respects, is still to be established. We know little of their food specialisation. They constitute elements that provide horizontal links between populations, and their numbers increase as the animal association becomes more and more rich. They constitute a layer that reduces the animal material flowing towards the reducents, thus it remains bound at the animal level (Balogh, 1953; Woynarovich, 1954).

How the intercalary element fit is often *ad hoc* and opportunistic. From a theoretical point, they are not needed for a continuous flow of energy (and material), as the reducents can themselves assure this. Their role, nonetheless, must be declared essential, because they contribute substantially to soil formation (Giljarov, 1949; Franz, 1950; Juehnelt, 1950; Dudich, Balogh and Loksa, 1952; Feher et al., 1954), and their absence leads to grave problems for the soil-based communities (Schaerffenberg, 1953) that provide soil quality feedbacks and can induce changes in plant cover.

The intercalary elements have the most important role in the soil and the layer immediately above, which is composed of litter and other organic debris; these two biotopes cannot be separated because, due to intercalary activity, they are in a constant, vertical relationship (Jahn, 1951). In the layers above ground, however, their presence is entirely occasional (see connexus, Balogh, 1953). Here, most of them are probably show strong dispersion over large areas. Consequently, they cannot be considered peregrinants, as wherever where there are living organisms, they can find a connection point.

The hospitant elements ("guests") are populations that feed on plant products, nectar, pollen or animal excreta (honeydew, sweat, etc.) without causing any harm to the plant or animal in question, or exerting a positive or negative influence on any member of the biocoenosis. Hospitant elements include many insects that regularly visit flowers but do not take part in pollination. Ants visiting aphids, for example, are not hospitants, because they induce them to feed more intensively and, also, protect them to a certain extent. In such a role, they are conventional corrumpent semaphoronts. This group is identical with Tischler's (1949) "hospites" group, with the restriction that populations that move to a place only to hide or overwinter do not belong in this category, because their role is only passive. These belong to the next group.

The "pro tempore" (temporary) elements only share the space with one or more zoocoenoses. They mix with other populations only because they seek sites for pupation, egg laying, perhaps overwintering, or hiding. Characteristic examples include the egg clusters of *Hysteropterum grylloides* on trunks of fruit trees, the soil-pupating caterpillars of *Operophtera brumata* or *Erannis (Hibernia) defoliaria,* or the individuals of *Eurygaster maura* that hide and overwinter in the litter at forest edges.

These temporary elements are, therefore, populations that have extended residence in a foreign environment, yet they do not have any positive connection to the plant-based resources of the site, and the association has no need for them; it will continue to exist without them. However, they can be followed by parasitic or episitic elements that will interact with the members of the association, and themselves can fall victim to obstant elements that are active there. Such temporary elements can only be distinguished following a spatially explicit approach, where they constitute obvious examples of movement between these temporary elements and zoocoenoses. They well illustrate the main reason why a zoocoenosis is not a topographic unit, in contrast to a plant association. Temporal elements are members of a zoocoenosis and they signal its presence, nearby or more distant; their characteristic is that they have emigrated from the space that contains their primary energy source, and now reside in a foreign space. Such spatial change is a regular phenomenon in several populations.

The role of the peregrinant (vagrant) elements requires little explanation. A characteristic example is the presence of a pea curculionid on an apple tree in June, or the wood borers (Ipidae) in an open herb association (Thalenhorst, 1951). Such peregrinants ("tourists") perhaps include a significant portion of insects present in any association that are considered tourist only due to our scant knowledge; not being aware of their links to a member of the association, or to the resident zoocoenosis.

This classification does not completely overlap with Tischler's (1947, 1950) four classes, and is also different because the latter is based on a relationship to habitats; it considers the spatially delimited zoocoenosis from the point of view of species, therefore the zoon, the animal assemblage, is suitable for analysis. His indigenae group includes our corrumpents, obstants, and intercalary element; the hospites group was already mentioned, while the groups vicini and alieni are, perhaps, similar to peregrinants, forming two subgroups, considering whether they arrived from nearby or from afar.

Such a grouping is legitimate in the analysis of a given spatial unit or plant association, but this is the field of ecofaunistics that had to be separated from coenology *sensu stricto*, using concepts liberated from a spatial view. Therefore, Tischler's *eucoen – tychcoen, acoen* and *xenocoen* terms cannot be used in coenology; they refer to sharing the same space rather than forming a trophic association.

We do not see the need to keep this framework in coenology, as this will not change the status of semaphoronts foreign to the association. The example mentioned by Tischler (turnip sawfly at field edges) points to a sustinent rather than peregrinant.

The seven groups are, clearly, not of equal importance when we consider the foundation of a zoocoenosis. They cannot be, because these groups include animals collected without considering their ecological connections, and we have already declared that they can be considered to belong to the fauna of the given area, but this does not necessarily overlap with a coenosis.

§ THE STRUCTURAL ELEMENTS OF A ZOOCOENOSIS

Therefore, amongst these groups, what are the structural elements of a zoocoenosis?

Given that the most important task for every animal is to secure the energy necessary for its life functions, the sought-for structural elements can only be feeding-based life forms that are essential to build a zoocoenosis.

There are multiple classifications of life forms, and animal ecologists have, so far, been unable to reach an accepted order. Consequently, the life form that we will follow needs a clear and unequivocal definition. This definition refers to a trophic-based assessment from a coenological viewpoint, and can be phrased as follows: a life form is any feeding mode (hence, a means of energy transfer) that is necessary to create a zoocoenosis. It follows from this that a life form can only be considered a coenologically important trophic life form if, from the perspective of a zoocoenosis, the given life form is *essential*. What are these essential life forms?

Such life forms can only be higher-level categories, such as corrumpent elements whose feeding activities liberate the plant-bound energy; the way in which this happens is irrelevant, the emphasis is on the end result. Examining the seven groups from this point of view, we can conclude the following. Above all else, the corrumpent elements, directly linked to the primary energy sources, are necessary for an animal association to form, because they are the initial transmitters of the energy flow into the animal realm. The continued existence of the plant cover, assuring the survival of the corrumpent elements, depends, in many respects, on animal activity, thus we must recognise that sustinents are also necessary structural elements. Obstants can only exist in a community if at least one of the previous elements are already present. They bring in a new life form into the zoocoenosis, which makes them real and essential structural elements. The organic debris produced by the total biocoenosis contains recoverable energy, allowing hilophages, forming intercalary elements, to link the others, and they constitute the fourth structural element of zoocoenoses.

Therefore, the four life forms discussed above, corrumpent, sustinent, obstant and intercalary semaphoront groups represent the structural elements of zoocoenoses. These groups, whose necessity cannot be doubted for the reasons explained above, are separated from the seven groups of animal assemblages, and are grouped under a discrete term, coetus, meaning the structural elements of zoocoenoses.

Coeti are trophic-based life form groups that are essential for any zoocoenosis, and are adapted to exploit certain energy sources (niche, Elton, 1927; life style type, Remane, 1943; *sensu lato* a collective life form, Balogh, 1953).

Semaphoront groups, rather than species, are members of coeti that are coenologically equivalent. During its life, the same individuum can belong to various coeti, by being active in various life forms, even within the same zoocoenosis. Expressions like "predatory species" or "herbivorous species" are not precise enough, and cannot be used as coenological categories. Larvae of Lepidoptera are indeed herbivores, but the adults can hardly be classified as herbivores in the same sense, even if in the form of nectar, they also consume plant "material" (while some do not feed at all). A certain larva may be strictly linked to a given coenosis, meaning it is a member of a certain coetus, while the imago flies from flower to flower, possibly ranging far. Adults of several parasitoids can be sustinents, but the same individuals become obstant semaphoronts as soon as they attack a lepidopteran pupa; not only laying eggs, but also feeding on the haemolymph seeping out of the pierced pupa (Bischoff, 1927). The piercing itself can also be lethal, even in the absence of egg laying, as in *Psychophagus omnivorus* (Nagy, 1952).

Without doubt, populations exist that fit into more than one coetus. The *Odynerus* wasps live on nectar, but prey on caterpillars that they feed to their progeny. The *Aclypea (Blitophaga) poaca* is a scavenger, but also feeds on plants. The activity of birds is obviously multi-faceted (Turcek, 1951), and one population can not only be obstant or corrumpent, but also, sometimes simultaneously, sustinent. This phenomenon can be expressed as populations with one, two or three coetus values. One can assume that populations with multiple coetus values are less dependent on any spatially-fixed energy source and, if they exert corrumpent activities, they are not dependent on another corrumpent element, because they can also directly connect to the primary energy source. it is correct to proceed by assigning such multi-coetus value populations to corrumpents, because this is the life form that is directly linked to the producent elements of a biocoenosis and, thus, makes energy available for other organisms.

These structural elements, though, are not identical with the basic life forms (syntrophium, Balogh, 1946, 1953), that are autecological groups; while the coeti are synmorphological units, in which populations with different life forms can be grouped together. When establishing these groupings, our aim was to unearth the structure necessary for the survival of the community, starting from a zoocoenosis and identifying the real roles of semaphoront groups, rather than trying to project the structure onto the coenosis, starting from the behaviour of the species.

This is the only way to frame our understanding when investigating the structure and conditions that ensure the "stability" of an animal association, to the degree that we can talk about regularly recurring species combinations.

Syntrophia (for example, spiders hunting with webs or by running or jumping; Balogh and Loksa, 1948) are groups that are smaller than, and belong within, coeti, as elementary life forms can only be interpreted within such frames. Within the obstant coetus, for example, such elemental life forms can be predation and parasitism, together with special ethological adaptations to this mode of life. Elementary life forms, therefore, cannot be structural elements. From the foundation of a coenosis, only the existence of a corrumpent element is decisive. The nature of the actual elementary life forms within which the semaphoronts are active is not fixed; they can feed by sap sucking, leaf chewing, can form galls, etc. The obstant coetus should be considered the same way, whereby it does not matter if the semaphoronts are predators or parasites. Therefore, one cannot conceive an *essential* structural element that is smaller than the coetus. The role of the syntrophium is to diversify the coetus; this role only modifies the qualitative composition of the zoocoenosis, but does not change its structure.

By using these seven groups, we can fully characterise the animal association of an area (for example, an association of a crop plant). The collected animal sample has to be analysed using these seven groups, to exclude the elements that do not belong to the coenosis. The zoocoenosis itself is composed of a maximum of four structural elements, the coeti of corrumpents, sustinents, obstants and intercalary elements. The protempore or hospitant elements do not form a coetus; they contain semaphoronts that can originate from any of the four coeti, and can be distinguished by their spatial relationships. Both are, however, members of the fauna of that area, can, themselves, also be energy sources, and can cause the appearance, and insertion into the coenosis, of otherwise foreign elements. An example of a protempore element is *Cydia pomonella* that pupates in the stem of an *Artemisia* plant, and which can attract one of its parasitoids, which has no link whatsoever with the *Artemisia*, yet they share the same space.[2]

Populations can only be part of the same animal association if they belong to at least one of its trophic chains, and this link is permanent; thus, they find their living conditions at that trophic level. Therefore, peregrinant elements, that cross the association at a horizontal level, do not belong to it. They cannot become members even if, en route, they occasionally prey on a member of the association, or take a bite from one of its plants, or themselves become accidental prey to one of the association's predators. Their impact on the quantitative composition of that association is insignificant, precisely because they are peregrinants, and have their permanent home elsewhere; an animal can only be a peregrinant if its role is unimportant, and their feeding is no more than accidental.

From the argument above, the following emerges; if the zoocoenosis is composed of the above structural elements, and if all animals belong to a zoocoenosis, they must also belong to a coetus. However, if a zoocoenosis is composed of coeti, then *eo ipso*, it cannot contain peregrinants, hospitants or protempore elements, because these represent semaphoronts that are foreign elements in the zoocoenosis. All of them are members of some coetus, and they can be classified into one of the three groups only because of their

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[2] Such a case was observed repeatedly at Dolinapuszta, near Pomaz, in the overwintering caterpillar populations of the codling moth, in 1952. The stems of *Artemisia* examined were about 20 m from the next sample tree.

relationship to space. From this, it also follows that, if we look at an animal assemblage from the viewpoint of a coenologist, the animals found there can only be classified from the perspective of the four coeti; only ecofaunistics can use distinctions like peregrinant, hospitant or protempore, because these reflect the occurrence of certain species, and not their associative needs. Therefore, any analysis that distinguishes these elements has, by necessity, lapsed into a faunistical viewpoint, and cannot be considered zoocoenology.

Zoocoenology, thus, must be careful not to fall under the influence of space, because this will alter the direction of research: instead of unearthing the relationships of populations to each other, it will focus on the relationships of populations to space. The latter is a question of distribution, i.e. faunistics, and it does not matter that it examines the distribution of more than one species; for example, instead of describing "lepidopteran fauna", it uses the term "lepidopteran association".

Zoocoenology is concerned with space only to the degree that it relates to the zoocoenosis. Its first question is not "what species live at the study site?" but: which are the corrumpents or, more generally, the elements that depend on plant material (also including sustinent and intercalary ones)? The next question is not about their distribution either, but: how are these primary transformants linked to populations representing the other structural elements?

The question of distribution of some species can only be of zoocoenological interest when the populations of the species in question inhabit a wide area, in associations with different species spectra. This area can be rather large (e.g. a species can occur over the whole of the Palearctic region), but the zoocoenosis is more than a matter of occurrence and can be established unequivocally, supported by numerous examples; within this continuous area, the populations of the focal species will associate with sets of populations comprising different species. The presence of a species does not form a coenosis, and even a newly-introduced corrumpent or obstant element is "only there" when it arrives, and is not yet "associated" with that coenosis. It must, however, become associated – it can only survive in this new home if its associative needs can be fulfilled, and if the existing biocoenosis can provide these needs. This illustrates why a zoocoenosis is more than co-occurrence.

For the sake of simplicity, we will only mention insects when identifying the elements of a zoocoenosis. This structural decomposition needs to be tested using other animal groups, for example game, domesticated animals, or birds.

When we consider these other groups of animals, the structure discussed above does not need to change; they can easily be fitted into the same framework and, for this reason, we believe we see the structure of zoocoenoses as a reality.

There is no doubt that the large herbivorous "game" in a zoocoenosis fulfils the role of corrumpents, and the importance of this role is positively related to animal size. It is sufficient to point to what wild boar or deer can do in an arvideserta; the corrumpent role of domesticated animals can be noticed immediately on any grazed area. A flock of sheep does not sustain certain characteristic desert formations, but can prevent the formation of a biocoenosis characteristic of that biotope. Carnivorous mammals, on the other hand, are obstant elements. The role of birds is very interesting: their obstant activity is the reason for the development of bird protection for economic reasons, albeit their populations often belong to more coeti; being not only corrumpents but, importantly, sustinents in the life of a forest, as convincingly illustrated by Turcek's (1951) fascinating observations. Finally, not to ignore humans, let us conclude that we belong to populations that are fully active in all directions: corrumpent when building a city, obstant when protecting plants and nature, intercalary in hygiene, sustinent with crop cultivation, hospitants, or protempore, in the depth of primeval forests, and peregrinant all over the uninhabited areas of the Earth.

§ THE QUESTION OF BALANCE IN THE BIOCOENOSIS

There is no doubt that multi-faceted human activities, wherever they meet nature, will profoundly influence the life and composition of biocoenoses. The longer this connection lasts, the more decisive human influence will be, and several authors (e.g. Tansley, 1935; Bejbienko and Mistchenko, 1951; Scsegolev, 1951) distinguish anthropogenic factors from abiotic and biotic ones. In this respect, let us only state that anthropogenic influence, from transient disturbance to sustained and long-lasting impact, is manifest to all degrees.

This fact, when we link it to the concept of biocoenosis, takes on theoretical importance, because since Resvoy (1924), most authors designate balance as one of the criteria of a biocoenosis, and only associations able to self-regulate – and thus be "in equilibrium" – qualify as biocoenoses. The first appearance of this consideration, in almost identical phrasing, occurs in Bronn's (1843, cit. Schwenke, 1953) long-forgotten discourses. Following this principle will logically lead to a conclusion that, in associations with sustained human influence, self-regulation will cease to operate, the equilibrium is lost, and what remains in the area in question can no longer be a biocoenosis, but an inferior replacement. This is where Schwenke (1953) concurred, excluding the areas under human agriculture from a biocoenosis, and calling it a merocoenosis. Rammer's (1953) standpoint is even more extreme.

We cannot agree with this position, because it does not separate the concepts of biotope and biocoenosis, and because it forces such an undefinable criterion as the equilibrium into the concept of biocoenosis and, excluding the developmental potential of an association, it forces – without proof – some kind of stability onto a biocoenosis.

We shall deal with the concept of biotope in the next section. Here, we only note that it is the biotope that is primarily changed due to human activity, and remains in a continuously disturbed state; consequently, the biocoenosis necessarily changes.

From statements relating to the structure of the biocoenosis, it follows that human activity will block succession. When interfering with a biotope, an association is destroyed that was in a phase that was moving towards a climax. On the steppe (grassland) of cultural origin thus created, a succession would restart if the agricultural activities did not repeatedly block the process. Human activity, with its cultivation of crop plants, forces foreign producents into the biotope, creating a "plant association"; however, this new association conceals a further association of ruderal and segetal plant species, and these would start the succession, in the absence of more human intervention (Ubrizsy, 1954).

In considering the structural elements outlined above, or the older, three-level classification, there is no doubt that the agrobiocoenoses contain all constituents. The producents are put there by humans, the consuments arrive by themselves (necessitating the birth of plant protection), and reducents must also be present, otherwise soil fertility would drastically be reduced; without all these elements, crop cultivation, that is already demanding, would be impossible. Human influence is immeasurable: the plant cover is transformed, its fauna changed and, in the soil, the fauna and reducent organisms are exposed to incessant disturbance. Nonetheless, the three life elements are present. The fact that in the soil, which, in our opinion, is the most important component in the life of the biocoenosis, only the species spectrum, andabundance relationships change, as confirmed by only a relative change reported in the results of coenological studies in agricultural soils (Franz, 1950; Scharffenberg, 1951; Jahn, 1951). Consequently, we cannot accept why would one consider a biological association living on a site under agricultural cultivation as structurally, i.e. *essentially,* different from biocoenoses present at relatively less disturbed (because we cannot consider them undisturbed) habitats.

This type of human activity is not as unnatural as many believe. It is certain that humans cause changes to the natural world that, at least to a degree, did not exist before the arrival of humans (Tschegolev, 1951); it cannot be doubted that, even under undisturbed natural conditions, there are transformative effects on nature that are the equivalent to human interventions. Essentially, an anthill does not differ from a human settlement: only things that are tolerated by the ant population remain in the vicinity and, within the hill, only what is useful or indifferent for ant activity is accepted. Fungi-farming ants or scolitid beetles are, essentially, "plant growers", and the dependence of the farmed fungi on these animals is very like the dependence of domesticated plants on humans as a result of plant breeding. The turning over of soil by a family of wild boar is the same as ploughing, and grazing domesticated animals cause the same changes as the activity of corrumpent elements such as grasshoppers, or a herd of bison, as both select plants that cannot tolerate repeated heavy grazing or increased nitrogen load.

Who doubts, however, that the background of such animal activity is the biocoenosis? Who claims that the plant cover that is transformed by animal activities was not "in equilibrium", or was no longer a biocoenosis? From the criteria listed, humans should be considered a natural phenomenon, as any other population, and their exclusion from the biocoenosis is not reasonable (Glen, 1954).

Is it justified to insert the criterion of equilibrium in the concept of biocoenosis? According to a clear majority of authors, yes. Bertalanffy (1949) shows that open systems (and every biocoenosis must be considered such) cannot achieve an equilibrium *sensu stricto*, and he uses the term "Fliessgleischgewicht" (lit. "flow balance") to characterise their stationary state. Poljakov and Sumakov (1940), Pavlovszky and Novikov (1950), as well as Jermy (1955), deny the link between biocoenosis and equilibrium. We agree with them. The biocoenosis does not come into being from the existence of a never-before-defined, and to-be-verified equilibrium, but is a correlative unity of its structural elements. It is undeniable, though, that in the life of a biocoenosis, there is something that creates the impression of order, some sort of harmonic cooperation between the structural elements, with some form of hidden organising principle. The existence of this underlying influence is noticed when something goes awry in the life of a biocoenosis, and the usual order is upset (Dudich 1939).

What can this organising principle be that, from the authors' perspective, creates the mirage of an equilibrium? If there is such an order, it can only manifest itself by showing, at every level, a gain in relation to the level above. There has to be an excess of producent elements, otherwise the consuments cannot fit in, nor survive, in the long term, and both must produce a surplus to accommodate intercalary and reducent elements into the coenosis. However, the existence of the producents, with increased demand of resources, is inconceivable without the activity of the soil-living organisms. Plants that evolved on humus-rich soils cannot live on rock faces where there is room only for lichens.

The organising or evolutionary principle, therefore, depends on the interaction of the members, and it is manifested so that, once a member is in place, it not only makes possible the addition of the next member, but also exerts an influence on the previous one. The first corrumpent, intercalary and reducent elements assume the pre-existence of the first producent, but they, in turn, generate further changes to life conditions because, in relation to each other, they introduce new environmental factors (Schwenke, 1953). The enriched life conditions allow the insertion of new producents, with the result of further differentiation in the complexity of conditions, preparing for the arrival of further elements. This is how the biocoenosis develops and gradually becomes more and more complex, the association more and more species-rich, and the relationships more and more interwoven. We do not see why this phenomenon would be a matter of equilibrium; this is nothing else but the impacts of the environment that all living organisms need and receive, and that all living organisms also generate, and which in the end, become interactions. The ever more complex interactions can unfold without disturbance, but can also be interrupted by factors that cut across the threads of these complex interactions. Lightning can strike a tree in a centuries-old forest, and the forest can become victim of a fire. Does this cause a disequilibrium in the biocoenosis?

According to the argument above, nothing of the sort has occurred and only the interaction threads were cut; one group of separate structural elements (the trees, representing the producents) were removed and, with them, the life conditions that this group provided for many other organisms were also altered, leading to their disappearance from the forest. In the space, however, new possibilities for life open and different environmental conditions develop, that could not have operated earlier because of the presence of the forest.

The biocoenosis did not lose its equilibrium, but the level of development that had been reached before the catastrophe occurred; the biocoenosis merely returned to an earlier state and everything starts again. We cannot tell the difference between the event just described, and the clearing of the forest by fire that was practiced by humans in the Age of Migrations, or forest clearance by modern humans using machinery. The result is the same in all three cases: an open grassland is created where there was previously a forest. In this scenario, however, a biocoenosis will appear that will have essentially the same structure as earlier; the remaining or colonising producents will attract appropriate consumers (the reducents), dominated by those that are best suited for the newly-generated environmental conditions.

If we could relate that to sources of energy, the consumers will be proportional; if the structural elements, measured by their role in energy flows, display a standard, unchanged ratio, we could speak of an equilibrium, but we could only declare this a criterion of the biocoenosis if this was a necessary condition for its continued existence. The events in a biocoenosis are not directed by a central organising principle, as with the organism (Schmid, 1941); consequently, its aim cannot be to create an equilibrium (Jermy, 1956). The biocoenosis is not an organism, although it has a certain recognisable organisation ("quasi-organism", Tansley, 1935). One can hardly attribute an "aim" to the biocoenosis; its components can have an "aim", and these aims cause them to associate. The biocoenosis thus formed, continues to develop; its structure, from its most primitive form, is determined by rules and, although there is no aim to exist in this form, it cannot exist otherwise. The biocoenosis is not the result of an aim but a condition, in which the associated organisms must live, fulfilling the aims of other organisms, and resulting in increasing complexity of the coenosis.

The equilibrium of the structural elements can only be conceived if the biocoenosis becomes permanent, and the producent level, once formed, does not change, either qualitatively, or quantitatively. Such a permanency is made impossible by the succession. Therefore, the concept of equilibrium can only be accepted if we consider it a fixed process, with a start and an end. Reaching the sea is not the aim of the river it must run due to the forces of physics, and the farther it flows, the more likely is that it will unite with other rivers, and increase in size. The end status of the plant cover is the climax; in this state, it will reach the stage at which, permitted by conditions of climate and soil, its production of biomass will reach a maximum. If this state becomes permanent, the consequence would be that the production of plant biomass would be largely unchanged. However, the composition and production of the climax plant cover certainly undergo considerable between-year changes (Tansley, 1935; Ramaley, 1939; Talbot et al., 1939; Costello and Turner, 1944; Scharff, 1954). On one side of the balance, there are the climatic and soil conditions and, on the other, the vegetation determined by them. Can this be called an equilibrium? Seemingly, yes, but it is much more appropriate if we talk about the adaptedness of the plant cover to the conditions. This becomes even more appropriate when we consider that this is not merely the impact of abiotic conditions on the plant cover, but also due to allelopathy; the individual plants (species) also influence each other, and must adapt to conditions created by each other.

The cornerstone of the system of interactions in a biocoenosis, however, rests on the producents. Any external impact that disrupts this group will, unavoidably, disturb the interactions and, if this destroys the producents, the biocoenosis will disappear, because it cannot survive in the same form with the loss of those producents.

Undisturbed interactions can, undeniably produce a balance-like state, illustrated by natural examples. For example, on the Kaibab Plateau of Arizona, there were 4000 deer. After humans exterminated the cougars and wolves that hunted them, forcefully breaking the existing interactive links, deer numbers increased so greatly that they consumed the food base necessary for overwintering, and the population, from its peak of 100 000, fell to 40,000 by 1925, and to 20,000 by 1931 (Leopold, 1943). Looking at the bare figures, instead of the original 4,000, today, the number of deer are around 20,000, whilst the numbers that primary production in the area can support is around 30,000. Is this a matter of balance? Even if one unwillingly believes this with some scepticism, we can only talk about the nature of the interaction, because a certain amount of primary production is suitable to support a limited number of transforming animals. If, however, primary production can support 20,000 deer, why was the deer population at a lower level when exposed to the undisturbed predatory activity of obstant elements? There is only one answer: the number of predators was so high that the deer population could not grow beyond 4,000, despite of the existence of surplus food base. An equilibrium situation is only conceivable if the corrumpent population is appropriate for the existing food bases, and there is an obstant population that is proportional to the existing corrumpent population. In the situation used as an example, the interaction was stronger from the direction of the obstants. Why would we call the relationship between these two populations equilibrium, when it was obviously the outcome of an interaction, and it was not the deer population that kept the associated obstant populations "in balance", but the latter that limited the former to the degree that they could not utilise the otherwise available food biomass? It is also possible that the plant cover has changed, and now can support more deer. This is again a matter of interaction, and we cannot see why we should use the word equilibrium instead, when the relative abundances are formed by the existing interactions.

It is a generally accepted fact that the plant-based energy resources are, always, in abundance in relation to the animals consuming them (Heikertinger 1951), and the animals, in most cases, do not utilise the food available.

An interesting case of the relationship within the interaction system is observed between grassland-grazing cattle and insects (grasshoppers and cicadas) (Wolcott, 1937). Where few cattle were grazing, most of the plant production was consumed by insects but, where the number of cattle was so high that they grazed the meadow low, the major part of plant production was consumed by them, because the defenceless insects were, in part, excluded and, in part, the open habitat attracted crows that decimated them. In this situation, it is impossible to see an equilibrium; this is the outcome of interactions.

There are more obvious signs of a disturbed interaction. Such as, for example, when a corrumpent grazes the forest canopy bare; does this phenomenon indicate a loss of an equilibrium?

When the oak forest is defoliated by *Erannis (Hibernia) defoliaria* or *Tortrix viridana*, the only event was that one of the interacting partners became too strong. If the energy source could limit its user, how could the equilibrium be upset? The equilibrium is, therefore, a fiction that we impose on the biocoenosis; there only exist interactions, that can take place so that the food base far exceeds the needs of the consumers, but can also occur in the opposite direction. Even if equilibrium were the essence of the biocoenosis, we could only speak of a disequlibrium if all oak trees perished due to this trauma and, consequently, also the herb layer in the semi-shaded understory. We do not know of such a case; on the contrary, the trees sprout again, and the usual state is restored. What had really happened? Nothing more than a temporary disturbance to the usual order. However, there are no rigorous studies support this image of "usual order"; how, then, could we claim that what we are accustomed to seeing is the equilibrium of the biocoenosis, and the essence of all biocoenoses? Only one thing is certain; that the producent level (and only a part of it) was, temporarily, during the period of a vegetative cycle, over-utilised by corrumpent elements. Consequently, one can assume that other corrumpents (e.g. gall wasps, leaf miners) were removed, or, at least, their abundance drastically decreased. These phenomena can be easily explained by the workings of the interaction network. Why would we complicate the explanation by forcibly drawing up this mysterious equilibrium, when the process affected only a part of the biocoenosis and, although the consequences are obvious, it could not have affected those populations that do not use oak leaves as their energy source?

The view that the biological equilibrium is manifested by the sustenance of a population around its mean abundance, and this balanced "iron minimum" is maintained by intraspecific competition for food (Nicholson, 1933), is contradicted by the fact that there are large between-generation changes in population densities (Solomon, 1949; Thalenhorst, 1950; Schwedtfeger, 1951). The mean is only a theoretical value, obtained by considering several factors, and it does not reflect the real conditions at all; the competition for food is not a universal phenomenon, either, because the biotic factors that influence populations operate in concert with abiotic ones, and in turn will be prominent as the main regulator of density (Glen, 1954).

What several authors call biological equilibrium, based on current knowledge, cannot be more than an interplay among the components of the biocoenosis, i.e. interactions. These interactions occur because no animal is a completely self-dependent organism; it consumes energy which it must acquire externally, thus any animal can satisfy its trophic needs only in the presence of other living things.

This need will generate synphysiological relationships and, does it follow from this, that satisfying these needs involves a fixed relationship in densities? The arguments mentioned above indicate that we cannot speak of a balanced, stable density. The view that, due to "environmental resistance", nearly 100% of every generation must perish (Thomson, 1929) is theoretically plausible, and occasionally occurs (*Diaspidiotus pyri [Aspidiotus piri]* – Szelényi, 1935), but projected onto the biocoenosis, it does not follow that the abundance of the populations and their ratio would be constant.

Widely fluctuating numbers entail that sequential generations always have different starting conditions, and it matters whether, at times with favourable conditions, their numbers are low or high. This may determine whether the starting generation will reach gradational densities, or only a high density that does not threaten the sustenance of the energy source. Density fluctuations can be caused by many factors and, even if in some cases one can establish a causal relationship between fluctuations in food plant densities and those of corrumpent populations relying on them (*Melanoplus mexicanus*, Scharff, 1954), in most cases, we do not see clear causes of fluctuations in abundance. The importance of a given regulating factor is not equal in space and time, and it is not indifferent which ontopopulation it will affect; therefore, it will never act in isolation but in combination with other factors (Glen 1954).

These cross-directional interactions will generate the incessant fluctuations in the biocoenosis that creates a perception of a form of balance, because our macroscopic impression is that the association is stable, without noticeable changes. Therefore, a complete defoliation, due to its highly visible consequences, creates an impression that something out of the ordinary happened and, to explain this, it seems logical to assume a disturbance of a balance.

The gradating population, though, does not drop out of the biocoenosis, and continues to be under the influence of its factors (Glen, 1954). The effect of biotic factors (e.g. parasites and predators) is greatest at high densities ("density dependent mortality factors", Smith 1935). The high activity of obstant elements during gradations of *Lymantria* or *Aporia* is very well known; several authors see this as a self-regulating ability of the biocoenosis, to maintain some sort of balance (Friederichs, 1930; Schwenke, 1953).

To this we respond as follows: the richer the biocoenosis, the more complicated are the interactions among its members, and more mortality factors are likely to decimate every member population. This can explain the inverse relationship between density fluctuations and the complexity of the biocoenosis (Solomon, 1949). This is also supported by the observation that there are more frequent gradations in agrobiocoenoses than in coenoses under lower human influence (Schimitschek, 1942). Is it correct to conclude from this that there is a lack of biological equilibrium in the former?

At first sight, it is attractive to explain the gradations of corrumpents in agrobiocoenoses through disturbances of the equilibrium (Friederichs, 1930). The writer himself interpreted insect pest damage this way (Szeényi, 1944), and he may still retain this opinion if: 1) he could define, precisely, the equilibrium, and; 2) his later studies, carried out in biocoenoses less influenced by humans, had not convinced him that gradations of corrumpent elements are no less frequent in such communities. Point 1 cannot be satisfied, because the studies mentioned under point 2 do not support the steady state of the biocoenosis, or any kind of balance. We illustrate this with two examples. One of them are the results for a gall fly, *Janetia (Arnoldia) cerris*, studied over 10 years in the same area that also exhibited gradations in this system, and where fly abundance can reach a level whereby their galls cause growth disorders on the host plant. Two years after the latest gradation (1955), the abundance became so low that only one *Janetia* gall was found per several hundred leaves. The second example is the *Rubus-Crataegus-Rosa* bushland on the southern slope of the Nagyszénás, above Nagykovacsi, that was censused over several years, and where, in 1953, without any previous signs, the abundance of *Cydia tenebrosana (Laspeyresia roseticolana)* reached extremely high levels, but hardly any were found in the subsequent year.

These biocoenoses are not studied by anyone, while the agrobiocoenoses are always under observation, and as their corrumpents are mostly economically damaging animals and their activity creates attention. We may ask whether we are misleading ourselves by believing that the number of gradations is higher in agrobiocoenoses than in natural ones? Even if it were so, we cannot conclude that this phenomenon can be explained by a disturbed balance, when it is obvious that fluctuations in population abundance do occur in other biocoenoses. Could this mean that the equilibrium can also be upset in these biocoenoses? If gradations and disequlibrium are equivalent, this suggests no less than that there is only a difference of degree between an agrobiocoenosis and a natural biocoenosis; thus, the criterion of equilibrium cannot be included in the definition of the biocoenosis, as its essence is not the presence or absence of equilibrium, but something else. This "something else" cannot be anything other than the interaction, necessarily present in every association, because this is what creates a coenosis from coexistence.

The interaction extends to abiotic factors as well and, the poorer the biocoenosis is in energy sources, and more uniform in ecological life conditions, the more gaps it will contain. For this reason, only populations with special capacities for adaptationcan survive there. The higher the influence of the macroclimate, the less the biocoenosis can dampen these effects, and the more obvious these gaps become. A field of maize has one plant energy base, the macroclimate is unimpeded; there is no canopy-generated shade nor water-storing litter as in the oak forest further away.

How could we expect the same conditions and interactions in these two biocoenoses? The result cannot be other than *Phyllotreta* beetles and beet curculionids will be present on the beet field, and corn borers in the maize as suitably adapted corrumpents, while several obstants that otherwise would feed on them, will not be present due to lack of appropriate adaptations. To explain these differences, why would it be necessary to invoke the fiction of equilibrium (Friederichs, 1930: "Das Gleichgewicht is […] bemüglich der Lebensgemeinschaft als eines Ganzen nur eine Fiktion, ein gedachter Zustand, von dem die Wirklichkeit immer sehr weit entfernt ist"), when they can be much more simply and incontrovertibly explained by species interactions?

The interactions are, without doubt, also present in agrobiocoenoses and explains why crop plant will attract corrumpents, and these their own obstant elements. The soil fauna is in interaction with what happens at above-ground levels, and will become impoverished not only due to less organic debris, but also because it is defenceless against macroclimatic extremes.

At the highest level, macroclimate determines the qualitative and quantitative composition of every biocoenosis. On the surface, it supports the fiction of equilibrium but, in reality, destroys it. It is an attractive view that whatever is in a biome, it is in equilibrium with the macroclimate. Essentially, the plants and animals living in a given area are adapted to the conditions provided by the ecosystem, and the macroclimate will be transformed and modified into an ecoclimate, that will affect the association in this form. In addition, the weather extremes of the macroclimate can devastate even living beings that have occupied the space continuously and are, apparently, well-adapted. This effect can have an impact on homeothermic as well as poikilothermic animals, sufficient to remember the effects of hard winters on birds.

How can we talk about equilibrium when a weather anomaly, in whatever direction, threatens the life of living things? Should we also classify this impact as disequilibrium? Why would we decide about the coenosis status of an association on this basis, when its essence is clearly not this unusual influence, but the interactions that bind it together? Even though a coenosis can be disturbed by irresistible forces, extreme temperature, storms, flood, fire and humans, it can be restored after every such disturbance. Restored, because the interactions are so much the essence of a biocoenosis that it has to appear wherever living beings are associated, as life itself is present.

In this respect, we have to seek the correct explanation of self-regulation, too. What constitutes the ability to self-regulate? We agree with all authors who claim that this is the process that recreates the disturbed order. We see the same in agrobiocoenoses, where this tendency is the only explanation for the phenomenon that agriculture must compete continuously with the pioneer weeds that try to occupy space; that specially adapted corrumpents break into monocultures, and devour everything that is foreign to the biotope, and; in areas where cultivation has stopped, succession continues after a few years. This ability to self-regulate is not changed by constant human interference. Therefore, we have to distinguish these from coenoses in which human influence is negligible, and this is why we call them agrobiocoenoses. No one can doubt that agrobiocoenoses are different from "natural" ones, but this difference is sufficiently indicated by a different name, although the forces regulating the community are identical in both.

The interactions can be disturbed by several factors, and our current knowledge indicates that such smaller or bigger disturbances are common in any biocoenosis, despite us noticing only the more obvious ones.

The interaction is undisturbed if; the producent level does not suffer from a catastrophic factor, other structural elements do not exhaust their energy bases, and due to their activities, the conditions in the biocoenosis become richer, and allow the insertion of new elements.

Disturbance in the interaction occurs when the producent level suffers a catastrophic factor, or other structural elements use their energy base to such an extent that conditions for life are restricted, and new elements can only insert themselves with difficulty, or not at all.

The survival of a biocoenosis is only threatened by interaction disturbances that endanger the existence of the most important producent elements. In the interactions of a biocoenosis, or its smaller constituent communities, such disturbance can only be caused by sudden catastrophic factors ("catastrophic mortality factor", Ullyett, 1947). Its cause can be extraordinary temperature, flood, fire, etc.; in zoocoenoses, it can also be the activity of obstant elements. The result is a new beginning; a new biocoenosis develops, or new elements become dominant in the biocoenosis. Catastrophic factors can sweep away a whole community from the space it occupied before, but a community can also be restricted leading to the transformation of its composition, or to depress the abundance of its members.

The seeming stability of a biocoenosis is caused by the rarity of any catastrophic effect on its main interaction system. The components of the biocoenosis are in permanent flux according to the working of their correlative links, and here, in the "depth" of the biocoenosis, interaction disturbances can occur but these are essentially like those along the "main" paths, thus there is no need to group them as "equilibrium". The flux in the biocoenosis is incessant, but without any two identical states (Kuehnelt, 1951:57). The changes are not only from season to season, but from year to year, and, following the laws of succession, may undergo long-wave transformation, too. This pendulum-like movement is not equilibrium, but the manifestation of an order that remains in effect during changes caused by interacting forces (Glen, 1954). This order means that a meadow remains a meadow, a forest a forest, and a reedbed transforms into a hygrophilous meadow, then a mesophilic grassland, then a forest. Just because our own lifespan is too short to see these changes as movement, there is no reason to declare a state of equilibrium that, itself, remains unaltered. The forces active in this situation are identical with the interactions, and operate in the most primitive biocoenoses, too. Their number and effect may increase but their essence remains the same. One triggers the other, and the system gradually becomes more complex. it is disputable that the climax is an end state because it is not only subject to wider effects such a climate, but can also degenerate and can undergo retrogression (Tansley, 1935; Soó, 1953).

The arguments above try to justify why do we not want to use the term equilibrium in the definition of the biocoenosis. The boundaries of a biocoenosis are the limits of the interaction network; there are differences between a forest, a meadow, a rock face or arvideserta, irrespective of whether they are in equilibrium or not. Disturbances within the interactions do not upset the foundation of a biocoenosis, only create obstacles in the path of succession. The autogenous succession is a process under the influence of plant cover, while the allogeneic succession is under the influence of outside factors (Tansley, 1929, 1935).

The disturbance in the interactions, in many cases, are of the second type, and it is unimportant whether this is caused by a herd of grazing bisons, termite mounds or human activity.

III. BIOTOPE AND ANIMAL ASSOCIATIONS

§ THE CONCEPT OF BIOTOPE

The animal association has been distinguished from the plant members of the biocoenosis, and their links were also pointed out. However, animal associations exist, without doubt, and can be classified into categories, because the repeating species combinations in well identified biotopes indicate, not only, that the animals filling a certain area (*ad hoc* faunal representation) are characteristically different from the surrounding ones, but also that these associations have limits. Every coenological study verifies their existence. Thus, we have to ask: how can we draw the borders of a zoocoenosis, and whether the drawing of such a line is possible at all?

This question of delimitation meets the problem of whether biocoenoses should be delimited structurally or spatially, and whether it is conceivable that these two factors would coincide.

Before answering, we must examine the spatial aspects of a zoocoenosis: how can we synthesise the structure, the characteristic species composition of an animal community with its spatial boundaries?

In this regard, we have to agree with Balogh (1946, 1953), who finds it unjustified that the question of the biotope is more important than that of the biocoenosis. Schwenke (1953) goes to the other extreme, considering the biotope as merely a spatial component of the biocoenosis, and declares that the two are identical on the basis that, without life, there is no biotope, and as the biotope is defined by its biocoenosis, there is no need for both terms.

This question remains undecided to this day. Several authors (Hesse, 1924; Friederichs, 1930; Palmgren, 1930; Krogerus,1932; Dudich, 1939; Nagy, 1944; Tischler, 1950; Bej-Bienko, see Scsegolev,1951; Rabeler, 1952) define and use the term "biotope" largely as we do below. For others, the biotope is not mentioned at all, or only in passing (Balogh, 1946, 1953), and is mixed with the biocoenosis; Schwenke (1953) consciously merges the two.

According to us, the question is not so simple, and the fact that the interaction of biotope and biocoenosis is very close is no justification that the two terms be considered identical.

The biotope is not determined by its biological association, as the latter only reflects the conditions in the former. The biological association is only the external, easily visible, sign of the set of conditions operating in the biotope and, if these conditions include elements of the biocoenosis, as correctly mentioned by Schwenke, there is no reason that we drop the dualism of biotope and biocoenosis; it is only a serious warning that we should not seek support in biocoenosis when trying to define the biotope. It is certain that underlying the biocoenosis, there is a hidden categorical factor that determines its creation and composition. Schwenke himself is obliged to use the term "biotope" later in his work, indicating that the two terms are not identical, and neither can be abandoned. No one can deny the existence of deep differences among the biocoenoses of a sandy grassland, a calcareous mountain, and the alpine region of a granite mountain, and, if we were to declare that these places are different because of the differences in their animal associations, we would commit the logical error of *idem per idem*.

What, therefore, can be considered a biotope? The biotope is a space that is suitable for the formation of a biocoenosis because, potentially, it has the energy sources necessary for its existence (Hesse, 1924; Dudich, 1939; Nagy, 1944).

In the biosphere, defined as the aquatic and terrestrial space suitable for life, innumerable biotopes can be distinguished. The condition that a biotope is a spatial unit suitable for the formation of a biocoenosis, unequivocally indicates a lower limit; the minimum necessary space to include a whole biocoenosis. The term biotope cannot indicate a smaller spatial unit than this.

The biotope is exposed to cosmic (e.g. radiation from the sun) and meteorological (precipitation, temperature, wind) factors which, themselves, can transform a space originally unsuitable for life, into one that can become a biotope. From this, it also follows that, at present, biotopes exist without life. A fresh lava flow, for example, is not suitable for animal or plant life, not only when hot but, for a while, even after cooled down and solidified; ultimately, atmospheric forces complete the chemical transformation that enables plant life to start and, by transforming the sun's energy, plants allow the formation of animal associations. The settlement of the first pioneers, however, depends on chance (consider the rock emerging from the sea) and, until this chance event occurs, the area in question can be equivalent to other biotopes, the only difference being the lack of life.

The first settlers of this "space-turned-into-new-biotope" are, by necessity, representatives of the plant kingdom. How a rock face, seemingly unsuitable to support life, turns into a biotope is nicely illustrated by Falger's studies (1914, 1922-23), according to which the first bacteria, algae and fungi are followed by the first animals; rhizopodes, ciliates, rotifers and nematodes. The next step is the settling of lichens and mosses and, at the same time, humus-forming animals also appear. Oosting and Anderson (1939), also studying the development of plant cover on rocky substrate, found regular, concentric zonation, the centre of which was always occupied by the most advanced association, while the hardiest pioneers were found at the periphery.

The vegetation, however, both in water and on land, will draw the bioptope into its sphere of influence and, with the advance of succession, more and more so. The stagnant water will gradually be silted up, the rupideserta becomes a closed grassland, then fruticeta, then lignosa. Hence, the biotope is exposed not only to cosmic and meteorological effects, but to a third one: the sum of impacts from the biocoenosis. Indeed, interrelationships and interactions start to become entwined, and it is very tempting to define the biotope by its biocoenosis. For simplicity, this may be acceptable when the biocoenosis reaches "maximum complexity": the biotope is still there, and has impacts. This is indicated, amongst other factors, by the conclusion of the process: the climax of the plant association. The climax, when fully developed, will be the one permitted by the cosmic, meteorological, and the edaphic factors, which are under the influence of the former abiotic inputs, plus the energy sources available – in other words, the features of the biotope. The alpine region above the tree line is not classified as such because of the absence of trees; the forest is absent because the biotope is unsuitable to support such a formation. A calcareous mountain, stripped of its oak forests may become karst, characterised by saxi- and rupideserta formations, but this will be different were the mountain originally covered by spruce forest, because these two formations are climax stages of different succession series, and are determined by what the biotope controls.

The above thoughts hopefully explain why we do think that the concept of the biotope is necessary, and why we do not want, by its abandonment, to "pull the rug" from under the biocoenosis. This would not be correct, because there is an inseparable interaction between living organisms and their environment, and the environmental requirements of the species have been formed during evolution, and are heritable (Bej-Bienko, see Tschegolev, 1951; Bej-Bienko and Mishtschenko, 1951). For this reason, the composition of an animal association can only be correctly perceived in the light of its environment, of its biotope. This is not to separate it but, to better grasp the conditions of life, the importance of the biotope needs to be better identified.

If the biotope is exposed to cosmic and meteorological forces, we can imagine that changes in these factors provide a way to separate different biotopes. However, the effect of the same microclimatic conditions differs according to the quality of soil, bedrock, slope, aspect, etc. We have also seen that, with the formation of the biocoenosis, there are also biotic effects, and it is also obvious that anthropogenic factors exert an increasingly important effect on the biotope. The biocoenosis that occupies the biotope, as an imprint of the conditions existing there, provides a good characterisation of these conditions (Cajander, 1916; Rabeler, 1952). Thus, if we now consider phytosociology, and use its concepts for a synthesis of the biotope of the zoocoenoses, we cannot be accused to defining the biotope using a living community. It cannot be disputed that, for plants, a biotope is an area that is, as yet, without life, but provides the conditions necessary for plant cover;

this cannot be said for animals, but the biotope becomes suitable for animal life as soon as plants colonise the area. The plant cover, for animals, represents space, an energy source and conditions for growth, whereas a biotope for animals is nothing other than the space that provides conditions for plants plus the plant cover.

The concept of the biotope is, therefore, not the same for plants and animals. The plant world needs fewer preconditions from the biotope than the animals because, for the latter, the plant cover is an essential component. A certain requirement for a biotope can be like this; for example, the herbal understory layer of a forest needs a more or less closed canopy as an essential condition.

From a zoocoenological point of view, such biotopes can be characterised by plant associations that include (after Soó, 1945): emersiherbosa (swamp vegetation), altoherbosa (tall shrub vegetation), sempervirentiherbosa (evergreen meadows), duriherbosa (dry grasslands), mobilideserta (sandy vegetation), rupideserta (rock vegetation), arvideserta (vegetation of cultivated areas), aciculilignosa (needle-leaved shrubbery or forests), aestifruticeta (deciduous shrubbery), and aestilignosa (deciduous forests).

Theoretically, this view agrees with Tischler's (1948) position, who also sees the biotope as various associative units of plant cover. He goes one step further, though, and uses the *ordo* (*-etalia*) level of Tuxen's plant sociological taxonomy. It is very likely that, at least in some cases, we have to go to this depth of classification, and the categories detailed above can be interpreted so that the formation group is the uppermost, and the *ordo* is the lowermost, limit for identifying the biotope.

The biotope of animal associations is also envisaged in the framework of plant associations by Nagy (1944, 1947), but he goes further by calling certain associations "biotope type", while identifying certain features (soil structure, slope, direction of slope, degree of vegetative cover, altitude) that relate to the structure of the biotope, and which can be decisive factors for shaping the ecoclimate.

Schwenke (1953) disagrees with Tischler, but only in the sense that he does not think that biotopes are suitable to delimit a zoocoenosis, which can only be made based on species composition; otherwise, he also sees the biotope as the dominant plant association (Schwenke, 1953).

Rabeler (1937, 1952) goes the furthest in this regard, and considers all associations as biotopes; accordingly, the 170 plant associations described from northern Germany allow him to distinguish an equal number of biotopes.

We have to mention that there are known biotopes that have drifted far from the theoretically essential plant cover. The zoocoenoses of deep sea do not have producent elements (Thienemann, 1939), and rely on resources drifting down from above. Caves also represent a very special biotope (Dudich, 1932) where, apart from chemosynthetic producents, the zoocoenosis also depends on organic material from outside.

Among the formation groups, the primary interest of agrozoocoenology is the arvideserta, which can be identified as all cultivated forbs and herbs. There are, however, trees among our cultivated plants, whose zoocoenoses are fundamentally different from those in the former, because they support animals colonising from herbosa and deserta formations; zoocoenoses inhabiting the cultivated tree stands (orchards) are related to lignosa formations. For this reason, it seems unavoidable to give these biotopes a different name and, without doubting the taxonomic logic of plant sociology, we will call these "agrilignosa". Therefore, the agrilignosa is not a separate category of plant sociology, but a cultural biotope whose zoocoenosis should be distinguished from the arvideserta, due to its different life conditions and energy sources.

In the above-mentioned biotopes, the zoocoenoses will be characteristically dissimilar due to the multitude of differences provided by the biotopes themselves; originally, under conditions undisturbed by humans[3], they will have had a distribution other than that of the present day. Suffice to say that the ancient biotopes are held back from returning by the arvideserta, because humans, by regulating rivers and maintaining dykes prevent the original emersiherbosa from replacing the cultivated land, or make the return of the original euriherbosa impossible through agricultural cultivation. The originally extensive forests of the Carpathian Basin have gradually been restricted and, today, only the highest crests are covered by continuous forest, andmost of those are managed by forestry. Today, the cutting down of forest is unimaginable without a subsequent replanting of forest trees that hastens the return of the climax stage, and almost totally prevents the natural process of succession. Today, the place of the forests that were exterminated in lowlands and hills is now occupied by arvideserta and agrilignosa. Also, we can assume that the dry grasslands covering the slopes of calcareous mountains, so characteristic today, have been created because of human influence: the cutting of the forest, and the appearance of karst after grazing created space for rupideserta. Also, it is to be noted that the replanting often introduces trees foreign to those biotopes. For example, the *Pinus nigra* plantations in the forests of the Danube Bend were not planted along with the characteristic plant species of the Scots pine forests of the Balkans, and the ground vegetation of the spruce plantations in the Mátra and Bükk Mountains is related to the autochthonous flora of those mountains, and not with the spruce forests of the Carpathians.

All this shows that the biotope determines, to a certain degree even countering human influence, the plant associations of a given space, and the two together, naturally, explain the zoocoenosis. Only in considering this role of the space is it understandable as to why the animal associations are

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[3] Even if we are far from having precise and comparative coenological data from the biotopes listed, the existing differences can be assumed from the results of the available faunistic studies.

different in two arvideserta at two different locations, where the same crop species is cultivated. Therefore, the space is a factor important enough for it not to be subsumed under the biocoenosis. It should not be placed above it, either, but it is possible to place it at the same level or, especially, below it, as a set of conditions, linked to space, that has a determining influence on the biocoenosis at every step of its development.

§ PARTS OF THE BIOTOPE

The reservations that are manifested in the use of the word biotope is no wonder, given the variety of uses conferred by various authors. The concept is used in connection from small to large spaces, which indicates that the concept itself is insufficient to indicate the spatial aspect of a biocoenosis. The populations living within the biotope are existentially bound to it, and we cannot use the term biotope to indicate that place, as it was already used to denote a more ample space.

If we recognise that the biotope is a synbiological concept, and we can mention it only in connection to a biocoenosis (Dudich, 1939; Bej-Bienko, 1954; Schwenke, 1953), we will not define its limits too strictly. Unfortunately, the within-biotope terms and definitions are disorganised and uneven, mostly because of the intrusion of idiobiological positions.

Before considering anything else, we must examine the nomenclature of the parts of the biotope.

Hesse (1924) is satisfied by objecting to the excessive restriction of the term biotope. Friederichs (1930, 1954) uses the word *habitat* for the small spaces (tree trunk, leaf, flowers for bees), and his phrasing is, without doubt, idiobiological. Dudich's (1932) view is entirely synbiological, when coining the term *oecus*, while Park's *habitat-niche* (see Allee et al., 1949) is idiobiological in one respect ("Rest and sleep, or their physiological equivalents, are consequently generally consummated within a more or less sheltered place. This is the habitat niche or home", p. 437.), but can also be interpreted as part of the biotope (p. 438: "In limited sense, each habitat is a microcosm, containing a biocenose"; p. 439: "The habitat may be a part of the physical environment […] or of the biological environment"). The most varied position is Tischler's treatment. Based on his examples (tree trunk, hazelnut bush, a cadaver), his *biochor* is the same as Friederichs' habitat, his *stratum* is a vegetation level, and the term "Strukturteile" (lit. structural parts) is used for plant parts (roots, flower, fruit) that can be considered parts of the biotope only through an idiobiological view, because they are parts of a bigger unit, the plant, without which they cannot exist. Tischler's habitat is identical with the site where a species lives, so it is also an idiobiological term.

Krogerus (1932) suggests *biochorion* instead of Friederichs' habitat, and uses it for what is, more or less, an association. Given that the term *biochor* was already used by Hesse (1924) to indicate units bigger than biotope, and this use seems general (Dudich, 1932; Bej-Bienko, see Tschegolev, 1951), we cannot use Krogerus' biochorion nor Tischler's biochor to denote a part of the biotope.

Russian entomologists (Bej-Bienko, see Tchegolev, 1951; Bej-Bienko and Mishtschenko, 1951)) use biotope in a strictly synbiological sense, but also use an idiobiological concept, "statio", as the life space unit of a species. This is not identical with the habitat, because it refers to the area occupied by one species, and is not identical with the biotope, either: it can be small or large.

To clarify the concept of the biotope, Vite (1951) discussed the spatial relations of animals at the individual and species level and, in this context, with the habitat, too, defining it as the space where the individual lives ("…ein charakteristischer Ort, der stats sufgesucht wird, da er seinem Bewohner […] den relativ grössten Schutz gegen [negative] Unwelteinflüsse gewährt"). To express the entire space needed by the individuum, Vite introduces the term oecotope, meaning the area in which the individuum, during its daily activities, will move between its habitat and food resources. An oecotope, therefore, is also an autecological term, but is not identical with the statio, because the author refers to mating, overwintering, etc. oecotopes, from which it is clear that he thinks of spatial needs of certain semaphoronts, and not of a species.

Thalenhorst (1951) divides the biotopes vertically, into biorophs. The bioroph is the same as Tischler's stratum but more acceptable, because it has a synbiological character. Schwenke (1953), as he considers the biotope as the space occupied by the biocoenosis, makes no further division and, because the concept of biocoenosis is linked to equilibrium, any smaller part, by necessity not being able to be in equilibrium, including all parts of the biotope, is called a merotope. Considering the concept of a merotope, a tree, a tree trunk, a field of wheat, a carcass, etc. will be at the same level, and these (including, for example, the cadaver of a single individuum of a zoocoenosis) are so heterogeneous that the term itself becomes unacceptable. Balogh's (1946, 1953) synusium is mostly a term of association, including the animal assemblage of a bioroph; hence, it is related to space occupied by living organisms, thus identical to bioroph. The term synusium cannot be accepted, because it has already been used in plant sociology, where it means something totally different. In addition, various authors ((Tischler, 1950; Franz, 1950; Kühnelt, 1951; Schwenke, 1953) interpret it very differently.

The question is: what are the arguments that justify the division of the biotope into smaller parts, and whether division is possible at all?

A subdivision of the biotope is necessary, because: 1) the biotope itself is stratified; 2.) within layers, it has a mosaic-like structure, and; 3) the number and composition of animal associations is linked to this stratification and structure.

Vertically, the biotope is stratified into levels, biorophs (ground, moss or grass, or litter, shrub and canopy layers). These are not equivalent: without a ground level, no biotope is imaginable, and the other layers gradually build up over this one; the fullest biotope contains all layers. This cannot develop everywhere. *The climax biotope is the biotope with the maximal vertical stratification that is possible under the given soil, climatic and cosmic factors.* Examples include the deciduous forest on central European hills, the dwarf pine in high mountains, the alpine meadow at higher altitude and, even higher, the vegetation of rock faces.

The associational importance of the biorophs is indicated by the fact that many authors consider the levels in biotopes of zoocoecnological importance. These are, however, neither frames for zoocoenoses, nor components of biotopes, but structural elements of the biotope (*sensu* Nagy, 1944, 1947; Tischler, 1950). It is also true, on the other hand, that every new bioroph, via their associated plants, leading to trophic specialization of animals and other ecological factors, brings further nuance and new frames of association into the biotope (*conf.* Park, see Allee et al., 1949).

The vertical stratification of a biotope is created by one or more plant species forming the vegetation cover, and the animal association is also shaped from this origin. Thus, the smallest units within a biotope, the structural frames within the biotope, must depend on individual plants. There cannot be a smaller unit than this, because a leaf, fruit, or litter, cannot exist without individual plants. If the biotope is identical with the plant cover, then its smallest units cannot be other than the plant individuals that, collectively, constitute the plant cover! And, as there is no vegetation without soil (even the epiphytes depend on this, indirectly), in the evaluation of plant individuals, we cannot ignore that the above-ground parts are integral with roots and with these, a certain segment of the soil. From this, it also follows that it is not the biorophs that are parts of the biotope, but individual plants. The vegetation layers are also composed of individual plants, and there is some artificiality in their separation. The soil in which a plant grows its roots is more a property of the plant than are the neighbouring plants of each other. The plant cover, through their roots, is also a member of the association of soil-living beings, and profoundly influences its zoocoenological relationships (see Giljarov, 1949; Franz, 1950; Kühnelt, 1950; Jahn, 1951; Dudich, Balogh and Loksa, 1952; Fehér et al., 1954), but this is also modified through the species composition of the plant cover, thus, ultimately, the individual plant also has an influence, and its animal association can be sharply different than that of a neighbouring plant that happens to be a different species. Even though a tree extends to all vertical levels, the animals living on it chiefly belong to the tree and, only additionally, often temporarily, to a certain bioroph. However, as the different individuals of the same species theoretically provide the same set of conditions, and thus the same reference frame, these obviously belong together and somehow form a part of the biotope.

Therefore, how, based on the discussion above and, in view of previous attempts in the literature, do we establish the nomenclature of the smallest units of the biotope? What is the lowest zoocoenological level within the biotope that we can accept, before we subside to an idiobiological view?

There is no doubt that, if only a zoocoenosis can have a biotope, the smallest unit of the biotope cannot be anything other than the spatial aspect of a subcategory of the zoocoenosis, and which mirrors a spatial need. The smallest space is but the point of the biotope where the idiobiological and synbiological concepts necessarily meet, because we can view this unit from the zoocoenosis and, also, from the perspective of a species that belongs to the zoocoenosis.

In considering the zoocoenosis, this space is identical with a spatial unit where there is a possibility that groups of populations meet and their interaction unfolds. For the species, the point in space is the location which provides the possibility for one of its populations to fit into an association with other populations. Without it, the zoocoenosis would be poorer by one species.

To name this smallest space we can choose from several published terms; all might be needed during zoocoenological studies and preserve clarity among synbiological terms, we list all of them here.

The *habitat* (Friederichs, 1930; habitat-niche, Allee et al., 1949) means the location where the semaphoront can be repeatedly found. It is identical with the (usual) place of residence of the species and the extent of its normal distribution area.

The *ecotope* (Vite, 1951) is the individual area of interest, used by a semaphoront during its daily routine.

The *statio* (Bej-Bienko, see Tschegolev, 1951) is the area of interest of the species, including all the habitats that are used by the various developmental stages, thus identical with the area that a species needs to fully flourish.

The *oecus* (Dudich, 1932) is a separate part of the biotope that contains a special association, a *microbiocoenosis*, a part of the total biocoenosis.

The *merotope* (Schwenke, 1953) is a structural part of the biotope (for example, leaf, fruit or gall) that cannot be formed independently, and includes the *merocoenosis* (Tischler, 1947), which is a part of the zoocoenosis.

The first three are clearly autecological terms, thus unsuitable for use in naming parts of the biotope. The merotope is too small to accommodate a whole zoocoenosis; it can contain only a fragment of it. The character of the merotope can be decided based on whether it can or cannot be a place to provide enough energy to support a zoocoenosis, independent of other sources of energy.

A leaf, gall, root or litter cannot exist without an appropriate plant and, thus, can only be considered a merotope. This statement may sound strange, given the existence of a litter layer in the forest, and its characteristic fauna. This fauna, though, interacts chiefly with the soil, and its composition is so dependent on it that the litter can only be considered a merotope, belonging to the soil, with which it constitutes an oecus. In the same way, the space under a rock is also a merotope, and it is not even an oecus, not to mention biotope, because it belongs to the soil.

A merotope does not include a full zoocoenosis, but this is not its criterion – those are detailed above. The fauna of a gall can develop as a special community, yet it cannot be an oecus, because it constitutes a microbiocoenosis only with its oak tree.

This appraisal of the merotope is different from Schwenke's (1953), who claims that a merotope is the spatial component of a merocoenosis, and it differs from a biocoenosis in its lack of equilibrium. In our opinion, fields of cultivated crops are not merotopes but oecuses, and these oecuses form a biotope, an arvideserta.

Consequently, the name of a unit that is smaller than a biotope but still independent can only be the oecus, the only term suggested for the smaller units of the biotope that clearly reflects a synbiological approach.

The oecus is a physically existing part of the biotope, formed by the locations used by different developmental stages of certain populations. A leaf, a head of wheat, a cadaver of a deer is not an oecus for the consumers/parasites feeding on them. And as the biotope is a space + its plant cover, this criterion should be held valid for the smallest part of the biotope, thus none of the above examples can be an oecus, even less a biotope. *The oecus is not a location where a semaphoront can be found, but the reproductive space of interdependent populations.* If we define a zoocoenosis as a coalition of populations, living in a biotope, then its smallest unit should be of sufficient size for whole populations. A single leaf cannot be an oecus, because it can support perhaps a few semaphoronts, thus a fraction of the population in question. A *single* poppy plant, or a lone apple tree is not necessarily an oecus, because the poppy or the apple tree is necessary to allow the colonisation of the biotope by a certain zoocoenosis. The oecus is therefore the totality, or at least a bigger group of these individual plants, on which groups of populations that require these plants can live, or where populations are dependent on them as their primary life condition. A single plant can be an oecus, if it stands alone (such as a single rose bush on the meadow).

Therefore, the division of a biotope into oecuses does not mean that it a convoluted patchwork, and there are not as many oecuses as there are individual plants. When studying *one* poppy plant or *one* oak tree, I do not study the oecus of populations linked to these plants, only a segment of the oecus. The more such segments I study, the more detailed will be my overall impression. The fact that the examination of the whole oecus may exceed our research resources does not change the validity of the above statement, but only attests the relative value of the results obtained.

In a plant association, therefore, the different oecuses intersperse in a multi-coloured kaleidoscope. The more homogeneous (by species spectrum) a plant association, the fewer are the oecuses, and its zoocoenosis will be more characteristic. The plant components belonging to an oecus should not be seen as individuals, but as sources of energy, to which specially adapted populations are linked.

The oecus is, therefore, the totality of plant-based energy resources of identical quality, in which special microclimatic conditions are also embedded.

In referring to "identical quality" plant-based energy resources, we always mean, here and elsewhere, plants belonging to the same species, with a minimum one whole individuum, and not, merely, a part of it because such parts would not be available to animals without the whole plant. All the oak trees in a mixed forest, or all of a forest's beech, hazelnut bushes, etc. constitute separate oecuses, because they constitute life conditions to which particular population groups are adapted, the component parts of a biotope. From the above, it also follows that the sum of oecuses is a biotope, as the biotope can be divided into various oecuses. A forest advancing in the direction of a meadow does not form a sizeable and discrete frontline, but individual trees appear first, advance scouts of the oecus, forming the first elements of the future lignosa biotope. The mosaic of herbosa-lignosa oecuses clearly shows that, here, we are faced with a mixed and not a homogeneous biotope. This solves the problem of shorelines and forest edges, too (Balogh's (1953) edge- and strip-biocoenoses). The latter, for example, could not exist without the forest, thus it is clearly a part of the lignosa, because it constitutes its special edge element, with distinctive plant association and is an oecus belonging to the forest, with its characteristic zoocoenosis. In the same manner, the shoreline zonations belong to the lake biotope, and its belts are nothing other than oeceuses, and these could only exist because of the presence of the extensive water body; thus, it is the lake which is the primer element, and not the meadow, into which the zonation gradually merges. Biotopes usually have contact with each other through transitional zones, and sharp boundaries are often created by anthropogenic factors (grazing, mowing, forest management, etc.).

The edges of biotopes are called ecotones in English (Park, see Allee et al,. 1949). This distinction seems correct, because existing studies detect dissimilar populations that strictly adhere to these edges, although missing from the two bordering biotopes.

We can pose the question whether we can speak of a biotope at all, if this is a mix of various reproductive sites. Our reply to this question must be affirmative because, if the plant association is developing towards the highest possible closure that local conditions permit, the plants, necessarily, form associations, and these will combine into characteristic plant cover, that is: recognisable biotopes.

The oecus is not only an energy source of high quality, but also the site of environmental conditions that attract many semaphoronts. An excellent example of this can be found in Nagy's (1944, 1947) studies on Saltatoria (grasshoppers) of the Hortobagy, that require pasture of a certain height with clearly manifesting constancy. The author, with acute sense, attributes this to "the structure of biotope" and, indeed, this can be explained by the structure of steppe biotopes. The animal associations are, thus, formed not only by trophic relations, but the divergent ecological factors following from the oecus-structure of the biotopes. Similar differences are reported by Kuehnelt (1950:251) who demonstrated microclimatic variances between neighbouring tree stumps, and whose zoocoenoses, consequently, reflected these differences. The oecus, above all, must be seen as an energy source of special quality, even though a manifestation of defined environmental conditions; the first characteristic may be of decisive importance for colonising populations. The same oecus can therefore harbour different zoocoenoses.

To complete our understanding, we have to examine one further circumstance. When several plant species form a characteristic plant association, this also results in groups of oecuses, showing structure-related features that influence the microclimate. Such a sub-biotope (see Varga, in Fehér et al., 1954) is the ecotone; in the arvideserta, the crop plus its weeds and in an agrilinosa, the fruit trees and the weeds growing among them. The structure of the biotope follows from the grouping of the oecus, and changes in the microclimatic relations that are influenced by this structure, while the essence of the energy source remains unchanged. The same oak species will represent the same energy source everywhere, but will be available under various microclimatic conditions in a gallery forest vs. a forest of closed canopy. The animals do not only need food, but a certain combination of macro- and microclimatic conditions and, only when these are available, can they utilise the food source. The influence of soil moisture can be illustrated well by the behaviour of *Nicrophorus (Necrophorus)* populations: on moist, clay forest soils, *N. humator*; on dry, sandy soils *N. vespilloides* and; on meadows, *N. vespillo* populations will live on the same food source (Pukowski, 1953).

A few more words on the concept of the statio, that is also needed in zoocoenology, because we separate the various animal populations by their species identity. To survive in a zoocoenosis, a population needs to find the conditions that it can tolerate as an inherited feature of its species. As a population of a species is a member of an animal association, so do all populations belong to a species. The statio is a spatial expression of the species-specific need concerning the living and non-living elements of its environment. This need can be modified by evolutionary adaptations, but such needs are always present. The realised zoocoenosis of a given biotope, or oecus, also depends on the statio needs of the populations of the species present. At this point, the syn- and idiobiological viewpoints must meet even though they must not be mixed, because the latter helps to better understand the formation of the association under study. With better description of animal associations and zoocoenoses, more light will be shed onto the ecological needs of the participating species, thus increasing our idiobiological knowledge about them. This illustrates why, in zoocoenology, we need to pay attention to the idiobiological concept of statio that mirrors the species-specific needs. The law of changing stadia (Bej-Bienko, see Tschegolev, 1951; Bej-Bienko and Mishtschenko, 1951; see also Elton, 1927; Kühnelt, 1943;

Nagy, 1947; Tischler, 1950), revealing that certain insects, due to their ecological needs, under different climates may live in different habitats, indicates that the species-specific factors that influence the composition of zoocoenoses in different biotopes and oecuses, should not be ignored.

We can accept the assumption of a tight connection between animal associations and biotopes, because the latter also brings particular life conditions, and we can also see that the requirement for area of interest does not make it possible to delimit the zoocoenoses based on space, declaring that an animal association is what coexists at a given site. We have reached the point where we can attempt to define the zoocoenosis.

IV. CATEGORIES OF ANIMAL ASSOCIATIONS

§ THEORETICAL BASIS OF THE CATEGORISATION

From the arguments we can see that the biocoenosis is an inseparable entity of coexisting plants and animals, that are different, yet mutually dependent on each other, termed (in Hungarian) a bioassociation; the community is used in a generalised sense to denote any link that is not based on a simple co-occurrence, but is created through trophic relationships, and has the importance of an essential life condition.

So far, only one sub-category of the biocoenosis was established, that of the microbiocoenosis, which is the community of an oecus. The totality of these groupings form the macrobiocoenosis, that is, the animal community of a biotope, or of an even larger space. The micro- and macro- modifiers should not be interpreted as in micro- and macrofauna, but through the lens of community biology; bigger-bodied individuals are also connected to smaller, or tiny organisms.

The concept of animal association was anchored on plant feeders that transform plant materials into animal material, thus making the stored energy within plants available to animals. The association is created by other levels becoming attached to this level, and these are held together by existential links.

Therefore, not all animal associations can be considered zoocoenoses, because animal associations can be formed by the most varied factors. In order to avoid any further misunderstanding, we define the concepts used in the categorisation of animal associations vs. zoocoenoses as follows:

A *semaphoront*, in all cases, means a part of the life of an individuum. When using the term semaphoront, we never mean the whole individuum.

A *semaphoront group* is composed of semaphoronts of several individuals that are zoocoenologically equivalent. The semaphoront group is, therefore, a group of animals but not a group of individuals; a semaphoront group represents parts of different individuals.

An *individuum* is the full series of semaphoront stages that an individuum passes through during its development. In this sense, an individuum is always an abstraction because, in any given moment, we never see it, only its momentarily representative semaphoront.

A *population* is the semaphoront representation of individuals that belong to the same species, i.e. a semaphoront group with the same species identity.

The population is, therefore, the representation of a species in a zoocoenosis. Of these species representations, we only ever meet semaphoronts, thus all equivalent populations, in reality, are semaphoront groups. The two concepts are not equivalent, though, because a studied zoocoenosis does not necessarily contain only one semaphoront group, but may contain a full semaphoront series; in which case, within a species population, there may be several semaphoront groups present. The population remains essentially the same, but the semaphoront groups will change. The population is restricted in space and time. The population is also an animal association.

A *population group* is the totality of populations of different species that live in the same space. Their grouping is possible from several angles, and the term can be used in ecofaunistics as well as in zoocoenology. The population group is also an animal association.

Under the term *animal association*, we understand the coexistence in space and time of two or more animals (semaphoronts), without considering their species identity or functional connections. The animal association is, therefore, the widest term to denote the coexistence of animal organisms somewhere, at a given time.

An *animal assemblage* is the realised form of the animal association that we find in each segment of space, and which space they share for various reasons, sometimes by chance, and only temporarily. The animal association expresses a relationship that exists between two or more animals through their coexistence; the animal association is the visible manifestation of the animal association at a certain time in a fixed segment of space.

The *animal contingent* is the animal assemblage of a given plant stand, but is not an identified stand, but the animal association that is always, necessarily present in the studied plant community.

The relationship of the last three terms is as follows: an animal association always exists whenever animals are together for a shorter or longer time. The form of the association that is characteristic for a certain plant community and, as a rule, is always present in it, is called its animal contingent. The reality of the animal contingent (*sensu stricto*) and of the animal association (*sensu lato*), the part coexisting in space and time and that we meet at the start of our investigation, is the animal assemblage.

The fauna of a given area, in precise space and time, is represented by such assemblages. The researchers of the fauna, on their collecting trips, do not meet the fauna; they find the assemblages that change from week to week, even in the same area. The sum of these assemblages constitutes, collectively, the fauna of the area, especially if these are listed just considering the species identities.

The animal associations can be divided into three kinds: colonies, groupings and "real" associations. Only this last one is a zoocoenological term, the other two have distinctly different meaning, and both can be members of associations. In the neighbourhood of a lone *Cydia pomonella*, there can be large colonies of the aphid *Aphis pomi*. The colony is not a zoocoenological term, but is a manifestation of an ethological feature of this species, which can obviously affect other populations of the zoocoenosis; all the other populations influence the coexisting populations, via their species-specific features. An ant hill is not, in itself, a zoocoenosis, but its different populations belong to a zoocoenosis.

The difference between colony and grouping is that, in a colony, individuals or at least semaphoront groups belonging to one or more species live together (for example aphids), without influencing their bionomics; the groupings are coexisting groups of the same species in which the semaphoront groups collaborate for the good of the community, following some sort of division of labour.

The above two social forms of animal associations were exhaustively categorised by Deegener (1918), distinguishing the two groups based on whether individuals become "tools" for others' interests or not. The terms used for the two are societas and associatio, corresponding to our two groups. The social categories defined do not correspond to any of the zoocoenological categories; therefore, we can only use them when we want to emphasise the ethological characteristics of one of the populations.

The zoocoenosis should be sought for within assemblages but, for the very reason that one is within the other, it cannot be identical with it. To associate, two or more populations must meet in space; consequently, coexistence, or more precisely coincidence (Thalenhorst, 1951), is the physical precondition of all associations, yet many populations co-occur but do not associate with each other. The animal assemblages are most importantly related to space and,therefore, are animal-geographical terms, and the seasonally changing animal assemblages are held together by occupying the same space. A zoocoenosis, on the other hand, is related to energy sources, and thus is a biocoenological unit; its seasonal manifestations are the aspects (see p. 138), and are held together by strict trophic links.

We have established earlier that animal associations can be formed by two explanations: they are connected by trophic links, either directly, or to a common energy source (by which we always mean plant food). The association created by these two causes is formed through time but is, necessarily, also fixed in space, but never with the stability of an aspect, and it is the space that is what can change with the highest frequency (change of oecus or biotope). This means that various, contemporaneously existing food chains can cut across each other in space, perhaps even with temporary interactions. The third criterion is, therefore, the sharing of the same space. What is the difference, though, between the simple coexistence and the associative coexistence? The latter has three criteria: a) the presence of whole populations, as opposed to single semaphoronts; b) durable coexistence, and; c) being linked to one or more food chains.

This statement does not contradict the coenological literature. All authors share a desire to link the results of zoocoenological studies with the composition of plant cover, and this clearly indicates their realisation that the qualitative composition of the plant cover is decisive in the formation of animal associations. Commonly, the importance of trophic links is emphasised by Hungarian authors (Dudich, 1932, 1939; Balogh, 1946, 1953).

The above three criteria are only valid collectively. The presence of whole populations in a space is no proof of an association, as it can be a temporary phenomenon, caused by, for example, the swarming of a species. The *de facto* association only happens when it becomes part of a food chain. The "whole population" criterion also means that the relationship of the population in question to the energy source is pivotal. A population of *Lymantria dispar* caterpillars disperses over a larger area than a *Curculio nucum* population. The basic unit of the categorisation, however, is the population (Dudich 1932), and an association can only be delineated if we consider the population that is directly related to the plant as an energy source. Here, we must take into account the area over which a "whole population" spreads, and how it is related to the given energy source. The winter moth, *Operophtera brumata* will be present in more oecuses than *Tortrix viridana* or *Mikiola fagi*, and the zoocoenoses around them will relate to space accordingly. So, if we start studying zoocoenoses in spaces greater than 10 m^2, there can be populations that are "whole", and others will be represented only by one or two semaphoronts. If this is not the consequence of extremely low abundance, this will indicate that these populations cannot be comprehended in their entirety, because they extend over a much wider area.

Hopefully, these examples illuminate the spatial aspects of the zoocoenosis. The continuing confusion in setting up and delimiting categories of animal associations is caused because, even if authors are aware that the plant cover (or at least a plant-based energy source) is essential for their formation, the categories are still either independent of the plant cover (synusium, Franz, 1951; faunula, Friederichs, 1930; connexus Balogh, 1953), or in contrast, they are taken to be the same; the plant sociological categories are considered identical with the zoocoenological ones (association, Rabeler, 1952; sociation, consociation, association, consocion, associon, Balogh, 1953).

We cannot agree with either. It is certain that any category in an animal association must be built on the plant cover, and this principle will be rigidly followed. Yet plant sociological categories cannot be identical with categories in zoocoenology, as the latter are formed in a totally different way (see p. 55). Neither can we agree with the solution that puts animals living on plant parts into a group (synusium, Balogh, 1946, 1953; stratocoenosis, choriocoenosis, Tischler, 1950; meroenosis, Schwenke, 1953), because these only exist exceptionally.

Some authors are against the spatial delimitation of animal associations, for example Shelford and Towler (1925: 29. "Communities must be determined by dominants rather than habitat; the limits of the dominants as such are the limits of the community…") and Franz (1950. 61.: "Tiergemeinschaften können deshalb stets nur durch ihren Tierbestand gekennzeichnet werden, nicht aber durch Vegetation Boden oder andere Standorts-faktoren”). This standpoint can easily spill over to the other extreme, separating the animal and the plant associations from each other. The greatest point of contention is due to authors who, without exception, use the characteristics of plant sociology to categorise animal associations, although these characteristics have a different importance.

So, we break new ground when we try to dissect animal associations by their structure, and as structural elements of all animal associations, we identified four coeti (corrumpent, sustinent, intercalary, and obstant elements); for these categories, only three published terms show similarity. One of these is Deegener’s (1918) heterosynphagium that he used to name animals of different species that congregate on the same food (coprophages, flower visitors). This term is too narrow for intercalary elements (as more than just coprophages belong in this category), but too wide for sustinents (not all flower visitors are sustinents). Another term is Balogh’s (1946, 1953) *syntrophium* that was discussed already. The third is Elton’s niche (1927) that is identical with the coetus, and can be considered its English translation. There are minor points of difference between the two: Elton does not distinguish sustinents, and does not restrict the term to populations; he refers to species and, therefore, the niche has an idiobiological overtone. Otherwise, though, Elton also considers the niche a structural element of all zoocoenoses, as we do with the coetus (p. 63. “…although the actual species of animals are different in different habitats, the ground plan of every animal community is much the same”. “It is therefore convenient to have some term to describe the status of an animal in its community, to indicate what it is doing and not merely what it looks like, and the term used is »niche«…”; p. 64.: “The importance of studying niches is partly that it enables us to see how very different animal communities may resemble each other in the essential organisation.”).

These clear thoughts were written in vain, because zoocoenologists continue to describe “zoocoenoses” based on “dominance”, without considering the coetus aspect of populations. A zoocoenosis can only appear if it contains at least two coeti, and the most populous zoocoenosis can only contain four of them. By stating this, we are in opposition to authors who built animal associations considering plant layers (Brundin, 1934; Balogh, 1946, 1953; Tischler, 1947, 1950). We strongly disagree that levels of vegetation have any role in the structure of animal associations. Biorophs, being energy sources of different quality, bring new associational opportunities, but the structure of the animal associations of different vegetation layers is identical. A space becomes richer in zoocoenoses, rather than the zoocoenosis of a space growing richer.

§ THE SMALLEST CATEGORY OF A ZOOCOENOSIS: THE CATENA

From the statement on the structural elements of animal associations, it follows, naturally, that their formation is gradual, small at initiation and then expanding as they develop. Where should we look for the smallest units of a zoocoenosis?

Given that the most important energy source is the plant cover, the simplest zoocoenoses should be sought here, at the meeting point of animals directly feeding on plants, and of zoophagous organisms. The more specialised a plant-transforming population is for its energy source, the more restricted will be the zoocoenosis forming around it, both in space and in its relation to energy sources.

This is the simplest unit of an association, the smallest unit of a zoocoenosis, the catena. A monophagous corrumpent, sustinent or intercalary population belongs to a catena, and its existentially dependent obstant, and possibly waste-consuming intercalary populations follow. The catena is, therefore, a trophic chain[4], in which the subsequent trophic levels are represented by the appropriate structural elements.

One should not view a catena through an idiobiological lens, and be baffled that the same species may be present in various catenae; this view considers the species, but a zoocoenosis can only be viewed through a community lens. Looking at the question with this approach, it becomes clear that an obstant population living in a given catena (even if its *species* is polyphagous) is really existing in this catena – this trophic chain – and it is not possible that it can be present at the same time in any other place. The circumstance that other populations belonging to the same species live in other catenae means nothing more than that it will appear in the species combination of those catenae as well. The same occurs when an episitic semaphoront, during its hunting trips, will take prey from several catenae; the moment when it effectively entered that catena, it became its full member.

This view is not only more correct coenologically, but is also of theoretical importance, because the various populations of the same species, when they are active in several catenae, form coenological links between these small zoocoenological categories. It is certain that several parasitic or episitic obstant elements that depend on several hosts can only remain in the zoocoenosis if these hosts are present there. These cannot be members of the same catena and, due to their intermediary host needs, can only fit into catena A if catenae B and C are also present. The relative obscurity of obstants, compared to the

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[4] For these links, we use this term instead of the food chain, which has a production biological "nuance", emphasising the distance kept from any production-biological approach or influence. By food chain we mean the path through which the energy-binding organic material progresses through the animal elements, while a trophic chain is the mutual dependence of populations that are forced into a zoocoenosis because of their trophic dependence. We believe such a sharp distinction is useful.

high abundance in arvideserta of corrumpent populations, can be *partially* attributed to this lack of intermediary hosts.

The endoparasite *Bracon* sp. is a parasite of the weevil *Neoglocianus (Ceutorrhynchus) maculaalba* (*macula-alba*) living in poppy heads. The species *Baryscapus (Tetrastichus) diaphantus (terminalis)* is a parasite of *Bracon*. All three are, therefore, members of a catena around the weevil, but the last one also appears in the catena linked to *Eurybia cardui* that lives in the flowerhead of *Centaurea sadleriana* and, moreover, also in the catena connected to the oak gall wasp *Biorrhiza pallida*. We know from our own studies that the adult *B. diaphantus* that is linked to the poppy head weevil appears in the middle of summer, while those active in the catenae around *Eurybia cardui* and *Biorrhiza pallida* emerge in spring. It is likely that this population could not insert itself into the catena around the poppy head weevil if the overwintering generation did not have the two other catenae at their disposal nearby.

Examining the role of constituent populations in a catena, we can distinguish two sharply different groups. It is obvious that we need to distinguish between the larval populations of *Cydia pomonella*, its parasite, *Perilampus laevifrons*, and its hyperparasite *Dibrachys microgastri (cavus)* and the great tit, for example. One or two semaphoronts of the latter may visit the orchard, and among other prey, may consume the pupae of the codling moth (with its parasite) and fly away, perhaps even the same day, not to be seen for several days. A different one would be a goshawk catching the tit, or a cat preying on its distant nest. Likewise, the larval populations of *Syrphus*, *Aphidius*, *Pachyneuron* spp. active in a colony of aphids must be considered differently from the *Coccinella septempunctata* adult that stays there for 1-2 hours, destroying a few aphids, and then moves to feed on scale insect nymphs on the next tree. This is not a matter of mono- or polyphagy, which would be an idiobiological and coenological view. The above mentioned larval populations of *Perilampus* and *Dibrachys*, or the *Syrphus*, *Aphidius* and *Pachyneuron* are permanent residents around the codling moth- or aphid-based catenae, while the other animals are not.

Therefore, all catenae have a core, that stays together for longer time scales, and cannot remove itself, and there are elements that are transients, temporarily contacting the core catena, but soon cutting their links to it. This casts a sharp light onto the dynamics of the zoocoenosis: the composition (and, also its species composition) can change from day to day, and even from hour to hour.

An overabundant *Agrotis segetum* infestation will have a rich larval population, and numerous obstant elements, parasitic flies and wasps, and episitic beetles will also be present. This catena can remain unchanged for a week, when a murmuration of starlings arrives, and for a few hours, will feed on the larvae of the moth. There is no doubt that, during these hours, the starlings will belong to the catena; yet they were not until they physically appeared, and will not belong there on the next day when they have flown far away, descending on the populations of Moroccan locusts on the salty grassland.

The trophic chain is more extensive in space, and will become more of a network, when the populations of more mobile and larger sized animals are considered (Elton's (1927) "pyramid of numbers").

We are less interested, though, in the flow of energy along the trophic chains and networks, than the associations forced together by such trophic relationships. From the examples above, it can be seen that the trophic chain contains a group of populations that stays together, forming a "real" association. Such populations are the *stable elements* of the catena, forming the catena *sensu stricto*, and we can always find these together. The members that are attached only rarely and temporarily are often represented by single semaphoronts but, until they are present, they are not real members of the catena, and if they are obstants, one cannot deny that they possibly play a decisive role in the fate of populations belonging to that catena. Due to their short activity, though, they cannot be permanent members of the catena; therefore, they constitute the *temporary elements* of the food chain. Such temporary elements are obstant or intercalary populations and, for them, the catena in question is not the sole energy source; they move far and wide, and form temporary associations now here, now there. We shall soon see that these populations, that are usually dispersed over a large area, belong to the next, bigger associational category, and this includes the example above of the starlings.

The stable elements of the catena are held together by a tight trophic chain-like connection. The catena is a real frame of an association, and its composition has to be unearthed using specific methods, and it is not identical to the species list of parasites and episites that make their appearance at the end of monographies devoted to pests as a list of natural enemies.

Populations of the same species are always the starting point of all catenae; we see no obstacle to use this in nomenclature, emphasising that, in this case, a species name denotes an animal association. This is also practical, as it simplifies the discussion, if – as will be seen soon – the catena can be referred to by a single species name. We can also be certain that the same catena, the trophic chains originating from populations of the same species, will, according to the landscape differences, show different species combinations. If the catena bears the same name, we can also refer to these species combinations using a few qualifiers (as in plant sociology: *Festucetum pseudovinae artemisetosum*), and this means that from no less than a single name, we can draw conclusions about the landscape, biotope, or the presence of other catenae, etc.

Therefore, we propose that, following the example of plant sociology, a special terminology is also introduced into zoocoenology, one that conforms to its needs, and promotes research as well as the better understanding of relationships.

To name a catena, we should always use the name of the corrumpent, sustinent or herbivorous intercalary element from which the catena in focus originates. This rank frame should be denoted by using the genitivus of the genus name and adding the end of the word catena to it; the species name is also in genitivus. The above-mentioned catena used as an example would, therefore, become: *Ceutorrhynchitena maculae-albae, Eurybiaetena cardui* and *Biorrhizaetena pallidae.* The use of these names covers all the populations included in the catena that are linked *as stable* elements to the corrumpent living in each place, biotope or oecus. The catena (never forgetting that we are dealing with populations, and not species) does not mean the circle of parasites, predators and detritivores linked to the progeny of a female corrumpent, but the whole population living in the given oecus or biotope. It is not a catena that lives on a single poppy plant but certain semaphoront groups; the whole catena is formed by the whole poppy seed head and weevil populations living on all the poppy plants of a poppy field, and the totality of detritivore and predator populations linked to these.

Therefore, a catena can include a huge mass of animals and the relationships of the structural elements and, within these, the individual populations can only be clarified by appropriate study methods. A catena, therefore, can extend to a whole oecus or biotope, although not necessarily. It can occur that, on a given portion of a poppy field of several hectares, certain obstant elements, that are not present elsewhere, associate themselves into the *Timaspiditena papveris* catena. Two *Timaspiditans* catenae will, therefore, be different, and will form two *facies* of the same catena. The same facies-difference may exist between the species combination of *Timaspiditena* in the Carpathian highlands and that of the Transdanubium.

Catenae can originate from three types of elements: corrumpents, sustinents, and intercalary elements living on plant debris. Obstants will, necessarily, be attached to all three elements (the only way the catena be formed), plus occasional intercalary elements living on animal food that are not always present. To form a catena, at least two operative elements have to meet. Between these two structural elements there is a tight interaction that is reflected in population dynamics: the host population allows the attachment of obstant elements, and its abundance will have a feedback effect on the other's dynamics, and the other element will also influence the density of the host population. The catena includes the obstant elements of the second and third levels. The catenae are, therefore, the most independent, and the most tightly interacting frames of the zoocoenoses. They are independent of each other and do not assume each other's existence (except in the case of syrmatophagous intercalary catenae that appear on plants killed by corrumpent elements), but can mutually influence each other's species spectra.

For example, in the wheat field oecus, there are no catena members of the C*ephitena pygmaei* that could also be involved in the *Oscinellaetena frit* or in the *Chloropiditena pumilionis* catena, even if these occupy the same oecus, and the *Toxopteraetena graminum* catena is also independent of the other three. The four catenae can develop independently of each other, without their respective pre-existence. Their coexistence will remain undisturbed, unless one of the corrumpents overexploits the plant energy source. (Due to this, all of them belong to a next – more extensive – associative frame)

The formation of the catenae starting from plant-feeding intercalary elements can be a consequence of plant mortality caused by the activity of corrumpent elements. Thus, an *Aspidiotitena perniciosi* catena can be followed by an *Eccoptogastritena rugulosi* catena.

Several authors have attempted the delineation of the smallest frames of zoocoenoses. The critical comments about the terms faunula, synusium, choriocoenosis, merocoenosis were presented earlier; given that all these are ecofaunistical terms, they cannot be used in an approach that considers the trophic chains as the backbone of zoocoenoses. Friederichs (1930) correctly noticed that animals linked to a certain plant have an associative position, but the term suggested by him, association, cannot be used without causing confusion, because of its pre-existing use in plant sociology. This type of zoocoenosis will be discussed in the next chapter.

The catena has a wider interpretation as well. Although we should consider the communities based on a monophagous herbivore as characteristic catenae, communities formed around polyphages can just as easily be identified, and these – as we shall see on p. 122 – will form a presocium. Leaving aside the presocium, and restricting our study to such a community (for example, the parasitoids and predators of *Lymantria dispar*), and especially if the corrumpent is monophagous at a given place and time – in this example, on oak trees we can consider this as a pure catena, and express this in its nomenclature, too. One condition, however, must always be met: a zoocoenosis has always to be identified as a trophic chain that starts from a plant. While taking this approach, zoocoenology can use methods that try to describe populations through their spatial distribution (e.g. quadrat, plant or plant part) but these populations cannot be seen as zoocoenological categories, as that would be an ecofaunistical perspective.

From the terms found in the literature, the *connex* (Friederichs, 1930) is the closest to that of the catena, and we could have adopted this, if only the author had not expanded its boundaries to such an extent (as in the *Anthonomus grandis* connex example) that it far exceeds the acceptability for a zoocoenological category. The term connex has continued to develop in the direction marked by Friederichs (Franz, 1950; Tischler, 1950, 1951) and, currently, it means a system of dependences from the plant through symbionts and parasitism, and the abiotic conditions of the biotope ("Abhagengingkeitsbeziehungen", Tischler, 1951) that creates a community out of a biocoenosis. The connex is, therefore, the organisational skeleton of a community of living beings. Schwenke (1953), disputing Tischler's (1951) idea, correctly states that, in such schemes, there is always an abstraction

("Es handelt sich also ein Schema von »Kann« Beziehungen und nicht von »Ist« Beziehungen", see Schwenke, 1953: 153) from which the study of interactions can only be of limited guidance.

Balogh's (1953: 22) interpretation is totally different; under this term he means "stands that do not have the characteristics of a hierarchical layer, and are sharply different smaller units". In the lights of his examples, Balogh's connex is identical with Friederichs's faunula, Tischler's choriocoenosis, and Schwenke's merocoenosis. Balogh's connex also differs from Friederichs's nomenclature because the former has double meaning, including not only a biocoenosis, but also the space that it occupies (the animal world of a group of trees or, a few bushes on a meadow, a heap of stones, a rock, a fallen, rotting tree, tree trunk or a carcass, a pile of dung). It seems to have some relationship with our concept of oecus. From our perspective, however, the listed entities are not "entirely foreign elements" or "disorganised spaced inclusions" within habitat levels, but its natural constituent parts (Park, in Allee et al., 1949:485). Further, we do not dare to claim that "they are present in the respective zoocoenoses only for a very short time"; instead, we think that they are constantly there, but are strictly bound to their respective oecus, or as with necrophagous organisms, concentrate on appropriate food source. These examples only prove that a biotope is indeed composed of oecuses, and that the macrobiocoenosis is a combination of microbiocoenoses.

The basic mistake of connex frameworks is that they relate in terms of species, thus their graphical representation becomes a labyrinthine set of arrows. Yet, if they were considered using populations, it would be obvious that a part of a population can only be at one place at one time, and that the independence and real existence of the simplest categories of animal associations is not influenced by the activity of other populations of the same species in other catenae.

§ THE FORMATION OF A CATENARIUM, A CHAIN OF CATENAE

How is a larger unit of animal associations born from the coming together of catenae?

The appearance of such a larger category can be observed repeatedly, even where crop rotation creates new conditions year by year but, also, where a stand remains for a longer time. The sown poppy is sought out by corrumpent elements that specialise on this plant and, in their wake, the relevant obstant elements also appear; as the catenae gradually develop, a society of catenae will also be formed that can be easily distinguished from the fauna of the neighbouring wheat field. The early spring-active *Stenocarus ruficornis (fuliginosus)* and *Ceutorhynchus (Ceutorrhynchus) denticulatus,* the adults of which are active on the above-ground plant parts, and whose larvae go for the roots, will soon be followed by the stem-living *Timaspiditena papaveria,* and a host of obstant elements (*Eupelmus [Eupelmella], Pteromalus [Habrocytus], Phaenecra*). On the underside of the leaves, *Doralitena fabae* appear and are active until mid-summer, bringing several obstant elements into the poppy field (*Syrphus*, *Chrysopa, Aphidius, Coccinella, Pachyneuron*, *Coruna [Pachycrepis]* etc.). In the bud stage, we find the *Ceutorrhynchitena maculae-albae,* followed by *Dasyneuraetena papaveris*; both are sources of a rich trophic chain (*Bracon, Chelonus [Chelonella], Tetrastichus, Eurytoma, Pediobius [Rhopalotus*], etc.).

All these catenae, for the reason of a shared energy source, necessarily belong together, and will form a bigger unit of animal association, here named the catenarium, a chain of catenae.

The catenae of the catenarium are kept together by the common food plant that also anchors them, even if temporarily, in an oecus. In this way, a quality energy source will keep together animal associations that are characteristic, at least to a certain degree. The catenae of the catenarium do not have as strong interrelationships as the members of an individual catena, because between them, apart from the common energy source and eventual multi-catenal obstant and intercalary populations, they have scarcely any horizontal link.

Without doubt, such catenaria exist. The catenae of the poppy field listed above are entirely different than the population groups of *Oscinellaetena frit, Chloropiditena pumilionis* and *Cephitena pygmaei* living in a wheat field. The catenaria of an oecus composed of oak or beech trees will be sharply different, as will be the catenaria of rose or hazelnut bushes.

Although the catenae forming a catenarium are independent, there is no doubt that their living side-by-side will, inevitably, stimulate interactions that will influence their development, population dynamics, and trophic needs. The interrelationships that are a criterion of all animal associations, therefore, doubtlessly exist in the catenarium. The intercalary elements living on animal debris will not join a single catena in such high numbers compared to a catenarium where there is much more debris, and of more varied quality. The activity of corrumpent elements can cause the death of plant parts, allowing the assimilation of syrmatophagous elements. The sustinents, by their nature, are temporary elements of any catenarium where the food plant requires insect pollination. The possible insertion of corrumpent elements that live on seeds or fruit also depends on their activity, as well as of the relevant catenae, but all these can be blocked by the activity of corrumpents specialised on flower buds. If the *Contarinia medicaginis* uses the flower buds of the lucerne, the sustinents will be absent from the oecus, and neither the *Tychiitena flavi* nor the *Bruchopagitena gibbi* can develop there. A single catena within a catenarium can, therefore, influence the density of certain population groups in the same way as within a catena; a given trophic level can influence the one below or above it.

The catenarium will directly connect with the plant cover in all directions (through all catenae). A carcass therefore cannot be a catenarium, whose hilophagous populations represent the intercalary elements of the catena to which the dead animal belonged. The fauna of a bird nest is not a catenarium, either, although there are obstant and intercalary elements that parasitise birds or live on debris produced by birds; there are also *pro tempore* and peregrine elements that were unwillingly carried there with the nest material, and have nothing to do with the bird or the oecus. From this, it also follows that we do not consider the animal association in the last two examples as a valid category, because these do not have an impact on the plant cover, without which there is no permanent zoocoenosis. Before their presence, there must be elements that create this link, and only with these can they form a complete zoocoenosis. On the other hand, there can be a catenarium in a rotting log or litter, where there can be active plant-based intercalary elements, attracting obstant and their additional intercalary elements, thus forming starting points of trophic chains or catenae. These catenae will constitute the catenarium of the oecus (rotting logs or trunks).

Catenaria can be named adding the -narium end to the genitivus of the genus name. The catenarium can logically be named after a genus of a plant-feeding population or species. Given that, in a catenarium, there can be several catenae, the name cannot be decided haphazardly, and only one way seems to be acceptable: to consider the role that the given population fulfils in the oecus. We shall return to this question during the discussion of the zoocoenological characteristics (see p. 119).

Catenaria can be horizontally linked by obstants needing an intermediary host (or prey), or by intercalary elements. Some of the corrumpent elements can occur on several host plants, i.e. in several oceuses. The larvae of *Agrotis segetum (segetis)* can attack several crop plants in the arvideserta; most of the grasshopper fauna of meadows and pastures cannot be forced into one catenarium, and; the larvae of *Aporia crategi* can damage nearly all kinds of orchard. All these populations point to the existence of a larger frame of animal associations. Such a frame will also be composed of trophic chains, but these will not be restricted to one oecus, but a group of those or whole biotopes, and the populations are accordingly dispersed. Their corrumpent elements are, consequently, polyphagous.

§ THE FORMATION OF THE PRESOCIUM, THE HABITAT ASSOCIATION

It is only when we view catenae starting from corrumpents that are mono- or oligophagous (such as those living on poppies, small grains, oilseed rape, mustard, cabbage, etc.) that the catenaria formed by them seem to be sharply identifiable. The catenarium of the oak trees is different from that of wild rose bushes or beech trees, and sugar beet has a catenarium different from that of lucerne or small grains. The moth *Lymantria dispar*, however, is present on all the trees of the forest, i.e. the whole biotope, and *Agrotis segetum (segetis)* is corrumpent on beets, lucerne and grains, as is the case for elaterid beetle larvae. The species *Opatrum sabulosum* meanders through all the arvideserta, and we find it in the most diverse oecuses, whilst *Operophthera brumata* is at home on all kinds of fruit trees of the agrilignosa. The populations following these corrumpents through the various coeti will also be present throughout the biotope, as will the episites that find their prey in a multitude of populations, as well as to the intercalary elements that find their food in different trophic chains. The food chains emerging from such corrumpents, therefore, need a rather extensive space. More precisely, the presocium emerges from the unification of these food chains: if these populations are projected onto an ample energy source, we notice that a community exists over a larger space, that is above catenae and catenaria, which, with their mixed populations represent an association that can only be recognised at this scale, the presocium.

The presocium is composed of populations that cannot fit any catenarium, because they are active over a much bigger area. These animals can enter a series of catenae without being affected themselves in return, and their trophic chains are also independent of each other. Thus, the presocium is an even looser assemblage than a catenarium; representing a category whose members are not tightly interdependent, where there are several independent catenaria, loosely linked by a few obstants with a need for intermediary hosts, and by a few intercalary elements.

Therefore, a presocium includes those populations that use several (or all) energy sources of a biotope or of several oecuses. Any one of these populations will absorb the energy made available by plants in several oecuses, or preys on populations belonging to several catenaria. All the populations that use more than one catenarium concurrently belong to the presocium; we can demonstrate this using an example.

In the arvideserta, the semaphoront groups living in the catenae *Ceutorrhynchitena maculae-albae, Timaspiditena papaveris* and *Stenocaritena fuliginosi* only occupy the oecus represented by the poppy, and together form one catenarium. The catenae *Subcoccinellaetena vigintiquatuor-punctatae, Phytodectaetena formicatae, Hyperaetena variabilis* form a catenarium in the lucerne oecus. *Oscinellaetena frit, Chloropiditena pumilionis* and *Cephitena pygmaei* are members of the catenarium on wheat fields. It is indisputable that the above catenaria belong to separate oecuses, and the obstant populations linked to the individual catenae, are only present in those. (A catena extends until the populations joining the trophic chain are clearly distinguishable elements; their entirety is the catenarium.)

However, the *Agrotiditena segetum* can be active in the whole arvideserta, spanning all three oecuses because, as a corrumpent, it is polyphagous, can appear in several oecuses, and attracts an obstant coetus as well. Despite this, the above named catenaria can exist; all that has materialised is that a broader category, with more extensive energy needs, occurs above them. This is the presocium. A presocium cannot exist if there were no species with more extensive stadia, which extend to all semaphoront groups. Their associated obstant and intercalary elements, by necessity, also extend to whole groups of oecuses or biotopes. Among the eucoen catenae and catenaria, there are semaphoronts that do not belong to any of them, yet neither are they peregrinant elements, because they have trophic connections to the plant cover as well as with similarly dispersed other populations. The presocium is the association composed of such populations. If they did not exist, the catenaria would continue to exist without them, which clearly indicates their status as independent categories. Yet such tichocoen or acoen elements are present, with their associated obstant and intercalary elements; they form a wider associational category above catenae and catenaria, the presocium.

For the tichocoen and acoen obstant elements, most of the catenaria of the biotope constitute energy sources and, without them, they could not persist. Thus, they are linked to several catenae; their fate depends on them but, at the same time, they also exert an influence on these catenae. Hence, the formation of the presocium, an associational category above the catenarium. Its foundation is formed by those sustinent, intercalary and corrumpent elements (see Elton's (1927) "key industries") that are present in the whole biotope, and are connected to obstant and intercalary populations of similarly wide distribution.

§ THE LIMITS OF ANIMAL COMMUNITIES. THE CONCEPT OF SUPERSOCION

The fact that the different semaphoront groups of the same species fit into various animal associations, and the different populations have contact with other different elements in these associations, creates exceedingly complex interrelationships (see Elton, 1927), that can be represented by using connection diagrams (Tischler, 1951); this makes conceptualising the limits of animal communities very difficult.

This leads to consideration of the question posed earlier (see p. 31): how can we draw the limits of animal associations?

Based on the discussion so far, one reply is evident: to delimit animal associations in space, in a manner as resolved for plant associations, is impossible. Neither the biotope levels, nor oecuses, nor the limits of the biotope can be perceived as if they were also borders of animal associations. We have seen that individual groups of semaphoronts can change bioroph, oecus or biotope, according to their ecological needs (Nagy 1944; Bej-Bienko, in Tschegolev, 1951; Tischler, 1950; Bej-Bienko and Mishtschenko, 1951). This fact is not changed by the existence of populations that occur only in certain biotopes, because every zoocoenosis is anchored somewhere in space, attached to the population that constitutes the first level of the food chain.

This uncertainty of the borders of animal associations should not be understood by viewing the populations of a zoocoenosis as dispersed, irrespective of the biocoenosis and oecus. There is not a dispersion – there is a mixing. Individual catenae can be zoocoenoses totally independent of each other, in the sense that their species spectrum will not overlap at all; the catenae will not be separate in space but mixed, as in the elements of a "mosaic". A little like a mixture of glass beads of different colour, where the ones of the same colour belong to the same population. The animal association is held together, not by spatial limitation but, by their tropic connections. This is, however, a totally different kind of connection than the ones that exist in plant associations, and this needs to be considered when analysing a zoocoenosis.

Structurally, every zoocoenosis is linked to plants, through the herbivorous population that provides the base of its existence. This population is, necessarily, spatially anchored either to one oecus (the case of *Neoglocianus [Ceutorrhynchus] macula-alba),* a sub-biotope (*Agrotis segetum [segetis]*), or a whole biotope (*Lymantria dispar*). Being linked to plants by a trophic connection, the population must also follow these plants in space; the caterpillars of the winter moth to the canopy, the pupae to the soil.

In the canopy, however, the obstant elements of the tortricid moths are also active; scale insects live on the twigs with their ecto- and endoparasites; the soil is also the site for pupation for weevils, and; the trunk is the site where obstant elements hunt for codling moth.

From this example, perhaps, it becomes clear what we mean in relation to the impossibility of identifying the borders of animal associations, if we aim to do this spatially. From this, two things follow:

1.) the trophic chains are the zoocoenological categories that can be most sharply identified (see Jermy, 1955, Park in Allee et al., 1949, p. 495: "These natural groups are relatively self-sufficient… ");

2.) the single ontopopulations are linked, more or less, to a spatial level (Park, in Allee et al., 1949: "… and the component species populations are spatially integrated and stratified").

From these two statements, a decisive question arises: should we view associational categories in the spatial levels, or in trophic chains, and the communities formed by them? As we established earlier, we can only agree with the latter option. If, however, only the populations coexisting in levels, oecuses and biotopes form assemblages, then it is, indeed, impossible toseparate the zoocoenoses spatially; because what we see together in space is, from the point of view of the best described categories – the catena and the catenarium – is merely co-occurrence.

How should we view the presocium, whose populations are related to whole biotopes, whereby viewing the animal association from this perspective, coexistence must occur within tighter borders? Do we not end up identifying the animal association of a given space with the presocium?

Coexistence is, indeed, relative, and the higher category we ascribe to coexistence, the hazier it becomes, though without doubt being a real occurrence. Every catena would coexist if there were no resource conflicts between catenaria, nor resource conflicts among presocia. Often, there is no direct link between populations in the different catenae. Between the populations of *Baryscapus (Tetrastichus) diaphantus (terminalis)* that belong to the *Ceutorrhynchitena maculae-albae* catena, and those of *Halticoptera aenea*, that is a member of the *Oscinellaetena frit* catena, there is only coexistence, even though they live alongside each other. Another population of *T. terminalis,* however, is an obstant element of the *Eurybiatena cardui* catena. Consequently, while *Eurybia cardui* and *C. macula-alba* populations can, at most, live in close spatial proximity, the adults of *B. diaphanthus* can form a community with both and, what is more, they also need this double connection, because during the second half of the summer, when both the poppies and wild poppies disappear, their winter larval cohort can only survive in the oecus provided by *Centaurea sadleriana* or *Cirsium arvense.* The adults of *T. terminalis* do not belong to either catena, and they are not obstants either but flower visitors, and probably sustinents. As such, they are members of the presocium!

The larval population of *Agrotis segetum (segetis)* belongs to a presocium, as it can fit into several oecuses. Populations of its parasite, the braconid *Periscepsia (Wagneria) carbonaria (migrans)*, can only have a coexistential relationship with any member of the *Oscinellaetena frit* catenarium, but the activity of *Agrotis segetum* can be fatal to populations of *Oscinella frit* and, if it destroys them, this action has a direct effect on all obstant elements of the *Oscinellaetena frit* catenarium. This link is, nonetheless, of a different nature to the case of *Baryscapus (Tetrastichus) diaphantus* (*terminalis*) shown above. In the former case, an obstant population changes into a presocium while, in the latter, a corrumpent element of a presocium clashes with a whole catena. Both are community relationships but at very different levels. Therefore we must distinguish the population interactions, and we can do this as follows:

A coenotic relationship can be of four types:

1.) *Bilateral, direct* coenotic relationships exist among populations that mutually influence each other's density, thus belonging to the same chain of energy exchange. Such a relationship exists between corrumpent (also sustinent, or herbivorous intercalary) and obstant elements of the same catenarium (compare Jermy's (1956) *connexulus*).

2.) *Unilateral, direct* coenotic relationships exist between populations that are connected by the same energy transfer chain, but the influence on population density is unilateral. Such connections exist between the intercalary elements feeding on animal waste and the other populations (Jermy's secunder *connexulus*).

3.) *Bilateral, indirect* coenotic connections exist between two or more animal associations in which one or more obstant populations belong to the same species. The population size of one is not indifferent to the changes in size of conspecifics linked to the other zoocoenosis (its fate, composition or dominance relationships); thus, indirectly, the two are linked.

4.) *Unilateral, indirect* coenotic connections exist among populations that may be totally independent of each other, yet they utilise the same energy source, or the same space, and the consequence of such overlap is that they influence each other's population size or density. Such links exist between the elements of catenaria, presocia and supersocia.

The closest link exists between populations that are in a bilateral, direct coenotic relationship; the intercalary elements connect to this "internal core" in a looser manner. Jermy (1956) correctly noticed the decisive difference that is manifested in their interaction. Hence, he suggested the term "secondary connexus " to distinguish the intercalary coetus in the chain, from the primary connexus, including populations with bilateral, direct connections. In our opinion, however, the former belongs to a separate associational category, the presocium, given that their energy source is not a single catena but a series of catenaria.

The various categories of animal associations can only be delimited if we do not lose sight of the fact that the populations form links with each other. A category, therefore, is valid until it links various populations. If intercalary elements were to be linked to one catena only, to one or several of its populations, then they would, indisputably, belong to that catena.

However, these intercalary or obstant elements that cross several catenae horizontally, obviously fit into a wider category of animal associations, due to their behaviour. Their populations are dispersed; not really populations, but 1-2 semaphoronts that belong to one catena, and even these may be only temporary. These would, indeed, deserve separate consideration. If we focus on populations, it is not possible to squeeze these elements, and the other strongly dispersed structural elements, into one catenarium, and the obvious category is a wider one, the presocium. While the individual semaphoronts of such populations, that are active as temporary elements in one catena, they become permanent members of presocia, because that includes all semaphoronts in their entirety.

The limit of the presocium is, therefore, where the constituent populations are single semaphoronts. In other words, precisely where the catenarium starts.

Only a few individuals of the imago semaphoront of *Coccinella septempunctata* will prey in gynopedia of *Aphis pomi*, others will hunt larvae of *Sphaerolecanium prunastri* on the neighbouring plum tree, and so on. In this example, an obstant coetus of a presocium links up to two different catenaria; here, the semaphoront group is only represented by a few semaphoronts that interact with uniform populations of corrumpents. These populations are members of catenae and, also, of catenaria, whose limits are semaphoronts that provide energy for the presocium.

The presocium, therefore, meets catenae and catenaria on a broad front; it does not include them but is built on them, and is above them.

There are many populations occupying the same space, but their needs are drastically different; it is impossible to lump them into one group. A red deer lives where the winter moth, the stag beetle and thousands of other populations are also present, yet they have very little to do with each other, apart from occupying the same location. How can we recognise the frames of an association among these populations, with manifold life histories, and sharply different sizes and feeding habits?

This thorny question of categorisation can be only solved by focusing on energy sources, because this is the sole factor that determines the size and boundaries of the association, and which organises them into such communities.

It has been established that the ultimate energy source is the vegetation, and we saw that this is present in stands of different biotopic value. From the structural point of view of the catenaria, it is indifferent whether these energy sources originate from a single oecus, a sub-biotope, or one or more biotopes. Accordingly, however, communities of very different sizes can be formed. A catena rooted in poppies, an oilseed rape plant or an oak tree is spatially more fixed than a presocium, to which elaterid and melolonthid beetle larvae belong.

If, however, we classified all zoocoenoses as presocia, whose energy source extends beyond a single oecus, then the mole, the field vole, soil-living mites, the winter moth, tits, grasshoppers, roe deer and the common viper would all belong to one group, this is a clear nonsense; if we did this, we would be classifying the set of animals living in a given space as a zoocoenosis. The most striking feature is the size differences: the deer, grazing on the meadow, and the leafhopper, sucking on the plants of the meadow, would belong in one group. The former appropriates quite a share of the available energy source, while the latter would hardly need much.

Based on the details articulated previously about the associations and their boundaries, the associative boundaries of these co-occurring populations can be recognised.

The catena and catenarium, as they are built on a single oecus, can only include animals of small size, from arthropods and molluscs downwards. The members of the presocium are also of small size, with the only difference being the wider relationship of these populations to the plant-based energy sources. Sometimes, the space occupied by a single population of a given presocium is surprisingly big; for example, the bees (Apoidea) range very much farther, relative to their size, than the field voles do. The latter, however, belong to a different, wider associative category. Evolutionary considerations justify that we consider another factor in the categorisation of animal associations, apart from the relationship to energy sources, because it is impossible that the highest level associative categories could exist without the presocia. Vertebrates belong to these highest categories, and constitute the zoocoenological unit of the supersocion.

This associative category can be distinguished from the others by the following criteria. Their corrumpent elements rely on extensive plant stands, and the relevant obstant and intercalary elements are also related to this factor. The large area influences the density of populations, although this is very variable; in the case of populations with high vagility (deer, hare, crows) density can be low, but in populations with low vagility (ground squirrel, field vole, etc.), it can reach very high values. Among the obstant and intercalary elements, there can be large vertebrates and tiny invertebrates; the density of the former is lower than that of corrumpent macro-members (fox), while the latter can be very high (ticks).

The catena in a supersocion cannot always be traced back to one corrumpent. The populations of the field vole, ground squirrel and hamster, being dependent on the same energy source, are members of the same supersocion; the mole, however, even though being obstant, is not associated with these, because its energy source is derived from numerous soil-living invertebrates. The mole, consequently, does not associate with one or more corrumpents, but to the whole presocium, in the same way as the hedgehog or the shrew. Therefore, these animals occupy a position above populations of smaller animals of high density, above presocia that are related to whole habitats, in a quasi-singular position, and even where one of their populations is dispersed over a large area.

This associational category, extending above a whole presocium, is the supersocion. This is not only a category for macrofauna, as both vertebrates and invertebrates appear in its food webs. Their separation is justified not only by their relationship to space and time, but also their different morphological and evolutionary features.

Considering these features, it is unimaginable that populations of deer, great tit or woodpecker could have appeared without the previous appearance of plant cover + invertebrate mesofauna, i.e. the formation of presocia. Likewise, it is impossible that space occupied by vertebrate populations would lack micro- and mesofauna. When these animal life forms appeared during the evolutionary process, presocia must have existed and, probably, also catenae and catenaria. If we consider specialisation as a higher degree of development (Heikertinger, 1951; Mazochin-Porsnjakov, 1954), then, at least, presocia must have existed before life forms displayed by terrestrial vertebrates, could have evolved. As the existence of supersocia presupposes the existence of presocia, the two contact along a broad front. The supersocion is a higher associative category, following from its evolutionary superiority; it does not unite presocia, but food chains that are attached to presocia "at the edges". For a supersocion, the energy source is represented by a whole biotope, with its plant and small animal associations, as well as the environmental conditions, the necessary micro- and macroclimate.

The red deer does not associate with the stag beetle, the hazelnut weevil, the beech tree and the lily-of-the-valley, but all that these represent, collectively, are necessary components of the deer's energy source; they are the first level of the food chain which also contains the deer.

This relationship with the presocium is direct in the case of all the insectivorous vertebrates and, also, the related catena and catenaria. The relationship is indirect for vertebrates that have a role of corrumpents, but the relationship, nevertheless holds, because – as we have proven earlier – the current condition of the plant cover would not have formed without the humus-forming and sustaining activities of the communities of smaller animals (as sustinent elements).

The four above-mentioned categories, even if each has a spatial aspect, reflect a non-spatial nature of the zoocoenosis. The borders of the zoocoenoses should, therefore, not be drawn by area, but through considering the stable and temporary populations constituting a food chain.

The factors holding an association together, among which there are spatial influences, also make it possible that we can largely delimit the four categories, albeit not without accepting transitional zones caused by the presence of temporary elements. These catenaria do not have a nested structure, the bigger ones including the smaller ones, but a bigger category intrudes into the smaller one to a certain degree; the presocium into the catenae or catenaria, the supersocion into the presocium. The sites of these intrusions are the transitional zones, where one category overlaps with another one, but, otherwise, all categories have non-overlapping domains, and these allow a sharp distinction between the various associative categories.

In the oak tree catenarium, a presocium formed by *Lymantria dispar* can intrude, but the zone of contact is limited largely to corrumpent elements, while most of the obstants are linked only to the populations of *Lymantria*, and not to other populations in the catenarium. Above a presocium formed around polyphagous, soil-living populations of insect larvae a supersocion can extend, represented by the vole *Microtus arvalis* where, again, only the corrumpent elements are involved.

§ THE NOMENCLATURE OF ANIMAL ASSOCIATIONS

Discussing the concepts of catena and catenarium, we presented how we conceptualise the nomenclature of communities. In the following pages, we provide examples of practical use and discuss the terms presocium and supersocion, as well as the general considerations concerning terminology.

We emphasise that only the term catena is unchangeable, as it follows from the fact that a catena is built around a single corrumpent, or other, monophagous population relying on plant-based energy. The catenarium can change, according to the dominance, or degree of corrumpency, of the constituent corrumpent populations.

The same holds for the presocium and supersocion. These two categories do not imply that the first would encompass all polyphagous herbivorous insects, nor the second all vertebrates living in an area; in doing that, we would end up with an ecofaunistical view. A given area does not support *one* pre- or supersocion, but several, occasionally many of them (especially of presocia).

We formulate the names of pre- and supersocia as in the categories discussed before: to the genitivus of the appropriate generic name, we add the -cium or -cion ending, with the species name also in genitivus. The delimitation of either category can only be made considering the contact through a shared energy source, and we illustrate this below.

Let us assume that, in the arvideserta biotope, three corrumpent populations play a decisive role: *Agriotes sputator, Melolontha melolontha,* and *Agrotis segetum (segetis).* All three utilise the same energy source, so they belong to the same presocium, with all their obstant and intercalary elements. The zoocoenosis is named after the corrumpent with the highest degree of corrumpency and, if in the arvideserta in question at that time, the role of the larvae of *A. segetum* is the largest, the name of the presocium is *Agrotidicium segetis.* It is possible that, at a distance from this area, the dominance of the larvae ceases, and it becomes a *Melolonthaecium melolonthae* or *Agrioticium sputatoris.* It is conceivable that a concentration of field voles appears in the field of alfalfa; in this case, the presocia present will be covered by an *Arvicolaecion arvalis* supersocion, but this can be of such a low density that it does not influence the formation of the presocia.

In an agrilinosa, the catenaria formed in spring on oecuses constituted by apple, plum and cherry trees can be covered by a strong *Operoptheraecium brumatae*, followed in the summer by a *Hyphantriaecium cuneae*. In a monospecific forest of oak, a *Lymantriaecium disparis* cannot be formed, because the larval populations of the gypsy moth can associate with it only by a catenarium. Therefore, what is formed there is a *Lymantriaenarium disparis.* Likewise, a fall webworm population, living on a mulberry tree hedge, can be a basis for a catena (*Hyphantriaetena cuneae*) or, at most, a catenarium (*Hyphantriaenarium cuneae*).

From the above, we can see that the actual names of catenaria, pre- and supersocia change according to – given the landscape and the year – the dominance of different populations, or their degree of corrumpency. This is not a defect of the concept but a consequence of us striving not to "straightjacket" reality into a rigid terminology. This peculiar change of the terminology follows from the essence of the zoocoenological concept. Why would a catenarium be named after a species whose population was dominant in the given location and year, when it is possible that it will play a minor role in the subsequent years? Following this path would distort the reality of the zoocoenosis, creating an impression of stability where none exists. The advantage of the changeable terminology is that it also mirrors the dynamism in zoocoenoses, that is reflected in the names.

The zoocoenosis named following the above scheme is an *existing reality*, both in space and time. The term *Hyphantriaetena cuneae* (Mezőtúr 1954) means that, in the given location and year, the gypsy moth population formed a catena, i.e. colonised only a single host plant. The use of the term is only justified if we have qualitative and quantitative data about the populations in question, meaning that we can ascertain the existence of the zoocoenosis. The term *Hyphantriaecium cuneae* (Dolinapuszta 1954) means that the same corrumpent is associated with other corrumpents in at least one sub-biotope, meaning that it colonised several host plant species, which it had to share with other corrumpents. Zoocoenoses exist independent of us, but a named zoocoenosis assumes that we carried out a census of its populations. This census is location- and time-specific, and maybe never encountered in the same way again.

We illustrate the coenologically correct analysis, and the practical application of the above associational categories, through the following example.

We complete a census in a wheat field of an arvideserta, using a sweep net. We catch many individuals of *Oscinella frit* and a few *Meromyza saltatrix*. These are corrumpents, and represent populations of catenaria of the studied oecus. We also catch several *Coelinus niger*, and we know these are parasitoids of the barley gout fly, an obstant of the catena *Chloropiditena pumilionis*. A few *Alticoptera aenea* indicates the formation of the catena *Oscinellaetena frit* and we also find a few *Cantharis fusca,* too. This predator can live on several species, and we classify it as an obstant element of the arvideserta's presocium. A captured *Pyrrhidium sanguineum* does obviously not belong to the oecus, and is a peregrinant. A few *Halictus* spp. and the honey bee, *Apis mellifera,* are sustinents, belonging to the presocium. The presence of several *Collyria calcitrator* (*calcitratrix*) and a few *Norbanus (Picroscytus) scabriculus* signals – even though no stem sawfly were captured – the formation, in the wheat stems, of the catena *Cephitena pygmaei*. The adults of ladybirds (*Coccinella*) and hover flies (*Syrphus*) are obviously attracted by the population of the aphid *Schizaphis (Toxoptera) graminum,* that is a corrumpent of the catenarium. The two predators, on the other hand, can range over the whole arvideserta; therefore, they are obstant, or sustinent elements of the presocium, while the few *Coccinella septempunctata* larvae are clearly obstant on the catena *Toxopteraetena graminum*, as well as the lone *Pachyneuron aphidis*. The adults of *Trissolcus (Microphanurus) semistriatus* are obstant in the presocium, while their larvae, living in the eggs of *Eurygaster maura* are obstants in the *Eurygastritena maurae* catena. The *Athalia roase* must have ventured here from another oecus far away, and would be a peregrinant, given that there is not a single oilseed rape plant in the wheat field, except that we observe it feeding on the flowers of *Lithospermum arvense*, and, therefore, it is a sustinent of the presocium.

We see a *Nicrophorus (Necrophorus) vespillo* walking on the soil surface among the wheat stems: an intercalary element of the supersocium, probably attracted here by the few vole nests whose entrance holes are visible among the cracks of the soil surface. We find a single *Trichogramma evanescens* in the bottom of the sweep net; we do not know where it came from and where it will go to. As it has several potential hosts, we classify it as an obstant of the presocium; here, it is at least a hospitant and not a peregrinant, because there may have been a few *Agrotis* eggs on the weeds, and it could have been en route to these when captured. We observe a robber fly that captures a stem fly – a sole representative of the obstant coetus of the presocium; a single semaphoront, that is a temporary element of the *Chloropiditena pumilionis* catena. It quickly flies away, and its next victim will be from a totally different catena.

The above is an example of how one can distinguish the various kinds of associations, and how the semaphoronts that belong to various associative categories may mix. The above list – and this must be considered an advantage "lives", and is dissimilar from species lists and their respective columns of numbers that tell nothing about the simple coenological questions: how does the animal in question associate with others, and what is its role in the coexistence. This is, however, not the endpoint but the start of the analysis of animal associations, and only the initial step was demonstrated above. The methods of coenological analysis will be dealt with in a separate chapter; first we have to discuss the dynamics of the zoocoenosis. These dynamics are so important in the coenological censuses that they need a separate chapter.

One question, though needs to be asked at the end of this chapter. The links in the above example also exist if we do not complicate the terminology with new terms; therefore, what sense is there in setting up these new frames? The reply is that these links are manifested within these associative frames and their clear-sighted recognition and observance leads us towards understanding relationships that profoundly influence pest densities, but these may remain hidden without clarifying the internal relationships of the associative categories. To do this, we need to know in which associative category the individual semaphoronts live, where we can find them, and what factors are they subject to? This is why need agrozoocoenology!

V. THE DYNAMICS OF THE ANIMAL COMMUNITIES

§ DYNAMIC PLANT COVER – DYNAMIC ANIMAL ASSEMBLAGES

The profound differences between plant and animal communities can be most clearly seen in phenomena triggered by dynamic changes in the biocoenoses.

Changes in plant cover are of two types: the appearance of the plant cover changes by season, relatively quickly and visibly (aspects), or undergoes a slowly progressing, relatively gradual change, which can only be recognised through long-term, continuous studies, and is independent of the seasons (succession).

The aspects do not influence the composition of the association; they show a characteristic sequence, visible by the changing seasons, and represented by different species groups. The succession, on the other hand, influences the composition of the association, causing the dropping out of certain species and the appearance of new ones; so this is the process of the formation of a new association.

It is obvious that the composition of animal associations must, in some form, follow both kinds of changes, because both directly impact the corrumpent elements. Apart from these, other changes, which have no parallel in the plant kingdom, can also occur in the zoocoenosis. These are due to the previously mentioned profound differences between plants and animals, and is the precise cause of the kaleidoscope-like variability that we attempt to conceptualise below.

§ THE ASPECTS

Changes in the seasons influence the animal communities, too, either by influencing their ontogeny (in poikilotherms) or behaviour (migrating birds, hibernation in mammals). Consequently, animal communities also have aspects.

The aspect is a periodically returning, season-dependent change in the same animal community, reflecting the concurrent seasonal changes in plant cover. All animal communities appear as a series of aspects, following each other in a regular manner and, generally, show the same species combinations from year to year. So far, there is little difference from the aspect used in phytocoenology.

The aspects are not associations linked by trophic connections, but the totality of populations, frequently belonging to different food chains, that are active at the same time and, thus, are animal communities that can be subject to the full force of competition. The aspect is a moving segment of an animal association, including the populations that display the most intense activity of the zoocoenosis. The aspect is a snapshot of the zoocoenosis because, in a part of the activity season, it represents less than the totality of the association, being restricted to the apparent populations that give the characteristic appearance of the aspect.

If two populations of an aspect specialise on the same food source, they can have a mutual relationship that seems competitive. Instead of this anthropocentric term, we would rather use "a clash of interests" that happens with all its – frequently grave – consequences, and without any elements of real "competition". Such a clash can occur between the flower-chewing Tortricidae and *Hoplocampa testudinea* on apple trees and, also, between Tortricidae + *Hoplocampa* and *Rynchites* spp. Both the *Rynchites bacchus* and *Tatianaerhynchites (Rhynchites) aequatus* lay their eggs in fertilised, developing fruit. It is not known if they tolerate each other in the same fruit, but it is very likely the two populations are not indifferent to each other.

The scale insects *Diaspidiotus (Aspidiotus) ostreaeformis* and *Epidiaspis leperii (betulae)* frequently form mixed gynopedia, especially on stone fruit. The same cannot be said of *Diaspidiotus (Aspidiotus) pyri (piri)* and *Diaspidiotus (Aspidiotus) perniciosus,* that exclude all other scale insects, plus the *D. perniciosus* even the *D. pyri.* Consequently, these always occur in pure stands, with the excluded species hardly present. It is also known that ant activity in aphid colonies disturbs the egg-laying parasitoids. The same phenomenon was observed on pines infested by wood borers, where *Formica* ants disturbed the activity of obstant elements (Wichmann, 1954).

If the aspects of animal communities are represented by characteristic species combinations, the reason for this is hidden in the ontogenesis of the species – developing through metamorphosis that, on the first level (herbivores), adapts to plant phenology, bringing different populations to the surface and making them noticeable. The aspects will, therefore, be represented by semaphoronts that are active within the zoocoenosis, whilst the inactive developmental stages, that are temporarily in a resting phase, will not be seen. Only the larval (+nymphal) and adult stages are active in the coenosis; the eggs and pupae, and the diapausing stages cannot take an active part in the life of the zoocoenosis.

The zoocoenosis, at any given time, has active and inactive populations; thus we distinguish apparent and latent components.

The apparent part of a zoocoenosis is composed of the populations that, through their activity, have a direct influence on the plant cover or the other populations of the zoocoenosis and, thus, are actively participating in the energy flow as active users of the energy sources.

The latent part of a zoocoenosis is composed of the populations that are not active, do not influence the plant cover and, temporarily, do not take part in the energy flow; they influence the other populations of the zoocoenosis only by being a potential energy source for them.

From the perspective of the zoocoenosis, the apparent element is composed of all animals that move, feed, take exercise of any sort, or carries out any element of sexual activity. The periods of rest, sleep and hiding (see later) are only temporary breaks in these otherwise continuous activities, characteristic of the ethology of the given semaphoronts, but do not change the apparent character of the semaphoront. Apparent members of a zoocoenosis include, for example, a larval population of *Operophthera brumata* at bud-breaking time, or its imagoes during leaf fall, or the imagoes of *Entomoscelis (Entomoscelia) adonidis (adonidia)* in spring and autumn.

In the latent part of a zoocoenosis are all the animals that stop moving, feeding, etc. for longer periods; they do not exercise any muscle, and enter a resting phase during which their life functions are supported by energy stores in their own bodies and, from the external world, they only use water and oxygen. Latent constituents are the insect eggs and pupae; larvae and adults if they enter diapause. Latent members of the zoocoenosis include the bird egg and the hibernating mammal. The latent populations have no effect on the plant cover, nor do they disturb the other populations. They continue, however, to influence the composition of the community; they remain potential members of the zoocoenosis, because their presence can attract predators and parasites, insectivorous birds and mammals into the zoocoenosis.

Looking at the populations of the zoocoenosis from the positive and negative phases of activity, we can state the following.

The zoocoenosis contains populations that remain active through the year; they are always apparent, e.g. the field vole, the thrush, etc. These are the *permanent populations* and it is obvious that the permanent populations are members of supersocia.

The activity of the next group is profoundly influenced by environmental temperature, and they become latent during the cold season, irrespective of our ethological or physiological definition. Such examples are all poikilotherms, including arthropods, reptiles, amphibians, but also a few homeotherms such as the hibernating ground squirrel, hamster, marmot, etc. These species are sub-permanent populations (predominant species, Shakleford, 1929)[5].

All sub-permanent populations are only active during the vegetation period, and their role can be different: either they remain active during the whole period, or are tightly bound to a certain part of it. The former comprise

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[5] We cannot use the term "predominant" because it can be misinterpreted; dominance means something different, and the permanent populations are not necessarily dominant.

the eurichron, the latter the stenochron populations (Dahl, 1921). Between them lie the mezochron populations (Balogh, 1953) that are active over a longer part of the vegetation period but not the whole.

In the arvideserta, *Neoglocianus (Ceutorrhynchus) macula-alba* is a stenochron, while its second-grade parasite, *Baryscapus (Tetrastichus) diaphanthus (terminalis)* is a eurichron. The imagoes of *Opertophtera brumata* and *Erannis defoliaria* are stenochrons, while their larvae are mezochrons. There are also populations that, when the temperature becomes unfavourable, respond by leaving the zoocoenosis and change biotope. Migrating birds, that leave in the autumn, or the ones that arrive at the onset of the winter, belong to this group, and among them, there are both steno- and mezochron populations.

The “species groups” of aspects represent populations that are active at the same time, and the different species groups are more divergent when their activity periods are more distant in time. Their characteristic is not only the species identity, but also their ontostadium (the winter moth, for example, is represented by larvae in spring, and by adults during the autumn).

Above we used “aspect” only in the associational sense, but there is no doubt that the animals living in an area also have seasonal changes. It would not be correct to call these aspects – they are nothing more than the fauna itself. This fauna is defined as all the animals that are present at a given site at a given time, from which we can screen out the associations using coenological characteristics. The criterion on which we declare that the animals in a plant community form a community does not change with the changing of the seasons: all our encounters with the animal kingdom brings contact with such concrete communities. We can recognise aspects in this community; they are not seasonal representations of the given community, but a sum of aspects of several communities, in no need of a separate name because it is not an associational term but a form of coexistence. It is something that is a study subject not of zoocoenology, but of ecofaunistics.

If, during a study of a wheat field at a given time, we find adults of *Chlorops pumilionis, Cephus pygmenus* and *Collyria coxator (calcitrator),* as well as larvae of *Lema cyanella,* among numerous other insects, it does not mean that these semaphoront groups represent an aspect of the wheat field, as this would be an ecofaunistical approach. We can only state that we are confronted by a *Chlorops* adult, a *Cephus-Collyria* adult, and a *Lema* larval aspect of the catenae *Chloropiditena pumilionis* and a *Cephitena pygmaei,* and *Lemaetena cyanellae.* The other individuals collected can only be sorted into aspects of zoocoenoses once we know their associative relations. Lacking this, the collected material remains a part of an animal community, that can be analysed faunistically, but not coenologically. Consequently, we cannot talk about aspects, either.

§ SEASONAL ASPECTS AND PLANT PHENOLOGY

It seems useful to attach the linkages of animal communities to plant phenological stages. This is desirable because the apparent populations of the catenae organised around corrumpents adapted to pterophytes often appear together for a short time; at least some populations are apparent for a short time only. After this, the corrumpents may enter a long diapause; the obstants, if they need intermediary hosts, move to another zoocoenosis.

The corrumpents, especially the monophagous ones, and among them the highly-specialised ones (such as spermophages), have adapted to their host plants very closely. The parasites of the *Neoglocianus (Ceutorrhynchus) maculaalba (macula-alba)* only have two weeks after flowering to find their hosts in the developing poppy head (Szelényi, 1935; Schroeder and Nolte, 1952). Our own studies on *Rhagoletis cerasi* during 1931-1943 on the same site (Budapest, Hűvösvölgy), showed that the adults emerged precisely when the earliest cherries started to show colour. Due to the extraordinarily warm spring of 1934, the cherries ripened almost a full month earlier than in 1933 or 1935, but the cherry fruit fly tracked the phenology of its host plant. *Contarinia medicaginis* or *C. lentis* cannot provide any care of its progeny before the flowering of the alfalfa or lentils, respectively. Coincidence (Thalenhorst, 1951) is therefore essential for the population to remain part of the zoocoenosis. The seasonal aspect of the zoocoenosis, by necessity, coincides with plant phenological stages.

The aspects can be delimited by the following plant phenological stages (not ignoring that these are not sharply differentiated): in the case of herbs, we distinguish; 1) seedling (until the formation of real leaves); 2) stem development; 3) flowering; 4) seed fertilisation, and; 5) seed maturation. On trees, or perennial plants, we can distinguish five phenological stages: 1) bud-break or sprouting; 2) flowering; 3) seed fertilisation; 4) seed maturation, and; 5) leaf fall. For the latter grouping, winter brings a 6th stage, while for the overwintering annuals (oilseed rape, winter cereals) this aspect is identical with the seedling stage. After harvest, herbs produce a fallow aspect, unless human activity prevents this, but this is a separate aspect only from the point of view of the phytocoenosis – but not for the animals living there. In this zoocoenosis, for example, on wheat fallow the *Cephitena pygmaei* is represented by the imago aspect of *Norbanus scabriusculus*, while the contemporary aspect of the *Chloropiditena pumilionis* catena is represented by the adults of *C. pumilionis – Coelinius niger*.

These aspects are easy to distinguish in crops, but attaching a zoocoenological aspect to a plant phenological stage is much more complicated in other biotopes. Our knowledge here is rather uncoordinated, and the way of naming these species spectra (prevernal, vernal, aestival, autumnal, hyemalis, Shakleford, 1929) merely indicates the seasonal changes of the animal assemblage, and is not identical with the above-detailed zoocoenological aspect.

§ DAILY ASPECTS

There are other within-aspect phenomena that characterise the incessant movements in an animal community, and that can cause temporary changes. Not all animals are continuously active, even during their periods of activity. Animals living above ground are influenced by the alternating days and nights, and while most of them are active at daytime, there exist crepuscular and night-active ones, too, and they are either hiding or not apparent during daytime. While the existence of aspects can enrich a zoocoenosis (for example, due to the swarming of an obstant element during a given period), the reaction to the daily periodicity of light does not cause a change in the composition of a zoocoenosis, but causes a dynamic in activity that needs to be considered during censuses. *The time-of-day assemblages include animals that are active in a given part of the day.* From this definition one can see that this is not a coenological term, and such a group can be recognised at the level of assemblage. It reflects the zoocoenosis only when one or another population is only active at certain times of the day. The day-active populations rest during night-time, and the night-active ones during the day, and often at places that are difficult to find, thus they remove themselves from the *visible* life of the biocoenosis. The larvae of *Gonioctena fornicata* withdraw to the base of alfalfa stems during the day, and chew on the top leaves only during the night (Manninger, 1949). The adults of *Tropinota hirta* disappears from the meadow during the night, and become active sometime after sunrise (Szelényi, 1934).

Weather events can, likewise, influence the activity of apparent populations, as it is known that cold, rainy days are bad for collecting. The weather influences even the soil-living populations (Jahn, 1951). It is also certain that the litter is populated by night-active animals during the day, and day-active ones during the night.

Although the composition of the zoocoenosis is not altered by it, daytime is relevant for the census methods used and, if one or more of the constituent populations are active at other times than when the census was made, the quantitative relationship of the zoocoenosis will be grossly distorted. Already, we can state here that a zoocoenological survey cannot be restricted to the sampling of adults (or larvae) during daytime. The daytime has no further impact on the life of a zoocoenosis; it has less influence than an aspect, even though that is not a structural part of a zoocoenosis, either – a community is not composed of aspects and one can compare them to spikes of a rotating wheel.

The relationship of the aspects and zoocoenological categories can be conceptualised so that, occasionally, among the permanent and sub-permanent populations, stenochron and mesochron elements appear, that will, after a shorter or longer period of activity, again return to a latent phase, giving space to other, similar populations. These changes are characteristics of the aspects, and not the permanent or sub-permanent elements. The changes throw light onto the movements in the zoocoenosis, and provide clues for the studies of interactions.

Finally, only an association has an aspect, the term is strictly a synbiological one, and thus it is unfortunate if used for species aspects (Balogh, 1953); the activity curves belong to idiobiology. Even if an aspect has the name of one species, this does not indicate its peak of adult activity (a larva can also be an aspect); it only means that in that period, among the numerous populations of a zoocoenosis, this is the species that is apparent, i.e. active.

§ THE IMPORTANCE OF SEASONAL ASPECT IN PLANT PROTECTION

Precise knowledge of the aspect is important for protection, because it indicates which pests co-occur at a certain time, and what combination of methods is necessary to affect all of them. It can also provide useful information about the obstants that ought to be spared, even if they belong to catenae whose corrumpents may, currently, be latent. For example, after the flight period of the adults, the tortricid population enters a latent phase while, at this time, the egg parasitoid *Trichogramma evanescens* can be highly active on apple trees, and in order not to disturb its obstant activity we should not use contact insecticides.

The corrumpent populations missing from the aspect had entered a latent period. The first question is: which of this latent phase, be that egg, pupa or another semaphoront group in diapause provides an opportunity for a precise census, which is a tricky methodological problem. From the relevant density (e.g. egg numbers), we can estimate the expected level of damage during the next apparent phase, and this helps pest forecasting. For this, however, we need a detailed knowledge of the aspects, as it can easily occur that an obstant element will start its activity, in full force, at a later stage than its host, as in the case of *Microgaster* spp. parasitising the caterpillars of *Aporia crategi.*

It is not surprising that the aspects do not always separate sharply, because all apparent phases have a wave-like shape, starting with a few early individuals, and ending with a few late ones, plateauing somewhere in between. This plateau characterises the aspect; plant protection measures are best implemented before this point.

§ THE QUESTION OF PERMANENT SPECIES REPRESENTATION

After seeing the various dynamic events, overlapping each other, and dependent on weather, time of day and season, we can rightfully ask: can we talk about stability at all, about communities of constant species composition?

There is no easy answer to this question. All coenological studies so far, as we have seen, analysed the fauna, and the results can only conclude that different physiognomic units have different animal communities. We hardly know of studies that lasted for several years in the same biotope or oecus, and followed the composition of the same zoocoenosis. The question, though, of whether a species combination first found remains unchanged during subsequent years, can only be answered by such studies.

Knowledge from plant protection offers few clues, because a negative conclusion only means that a corrumpent was not a pest, which is far from implying that it is not present in the zoocoenosis. Precise plant protection censuses only exist for a few pests, and the information only indicates a forceful fluctuation in the densities of certain corrumpents (Schwerdtfeger, 1951).

Due to theoretical speculations, we have to assume that characteristic species combinations are constant. It must be the case, because we cannot assume that a latent phase (Thalenhorst, 1951) of an animal would have disappeared from the area, and will colonise it again in an eruptive phase. More likely its density failed to reach the detection threshold.

The detection threshold is the relaxed state of a population dispersion, below which our current methods cannot detect is presence. We cannot exclude, though, that a species in the state of gradological latency, has indeed disappeared from a large area, and its presence is only “island-like”. The knowledge of catenae can provide certainty as to whether a member of a species combination, currently not detected, is still present. Species of concealed activity can be ascertained through members of its food chain. For example, the presence of *Tetramesa* spp. can be identified from the obstant *Homoporus*, or the root-living *Pseudococcus* from their encyrtid parasitoids.

Change in the population size of species is incessant; the density, the number of individuals per unit of space is, consequently, in constant flux. At the start of every generation, density reaches a peak, followed by gradual decline, reaching its nadir when the semaphoront performs the last step of species continuation, egg laying. This *intracyclic* fluctuation can be repeated once or several times a year, depending on the tocogenetic features (Hennig, 1950) of the species. Over and above the intracyclic fluctuation, there is another movement of bigger amplitude, extending over years, in which generations with small population size alternate with those of very high population sizes. This *hypercyclic* fluctuation appears because of the direction of movement of the intracyclic fluctuations. If this increases in several generations, the population size of the species will noticeably grow, and the lower the pre-reproductive within-generation mortality, the steeper this increase will be. The conspicuous peaks of these hypercyclic waves are called gradations. Their study fits in to gradology – from the point of zoocoenology this is relevant because this mechanisms creates strong dominance of certain populations, or at least increases their density above the detection threshold.

The gradation of the corrumpent elements can have serious influence on the composition of catenaria and presocia, and can substantially change them. These, however, are only hypotheses, in need of a proof.

The precise censusing of zoocoenoses depends not only on today's imperfect methods, but also on the distribution of the constituent populations that is, overwhelmingly, discontinuous (Thalenhorst, 1951): we face populations with island-like distributions. The unevenness of dispersion is not changed by increasing the survey area until the originally "unsuitable" dispersion will become more even (Balogh, 1953: 56). The resulting means do not reflect reality, because the dispersion of the populations remains clumped, irrespective of our calculations.

The degree of dispersion depends on the needs of the developmental stage of the species. The bigger the area necessary, the more dispersed the population will be. The highest degree of dispersion in insects is that of the adults, because this is the stage that best expresses the spatial needs of the species. A high degree of dispersion can result in a population getting below the detection threshold, thus a low abundance does not necessarily mean a minor role in the coenosis.

A gradation of *Aporia crataegi* larval population can reach unheard of densities, denuding all fruit trees over considerable areas. The resulting adult population will, inevitably, be smaller; not only because the adult population must be smaller than the original larval population, but also because the adults disperse, and they do this more readily if the trees have been denuded by the larval population. Birds and larger mammals are also rare within a biotope due to their large area needs; this must be independent of anthropogenic effects, because their hunting areas cannot support more individuals. Species with high spatial needs always tend towards their detection threshold during regressive phases of the population dynamics, while during gradations, they grossly exceed it (*Dociostaurus maroccanus, Loxostege sticticalis*).

Consequently, the constant presence of a species, given that this needs to be proven by our imperfect detection methods, stands on shaky logical grounds and, if our studies nonetheless indicate that certain plant stands always contain certain species combinations, even if this mirrors the fauna, this points to the suitability of our primitive methods to allow a view into the composition of animal communities. This view will only be complete if the constituent catenae, and the resulting catenaria, are uncovered; otherwise, the current practice of coenological surveys and analytical methods leads to the emphasis on the populations of common species, those that have wide ecological tolerance limits (valence). The "stable" species detected will project only a mirage of stability. We have to assume that the characteristic species combinations will be subject to smaller or bigger changes by the gradocoen; some species may go missing or sink below the detection threshold, but the zoocoenosis can also be enriched by a sudden gradation of otherwise rare species. Such species with narrow tolerance limits may, infrequently, get above the detection threshold; let us see an example from my own studies.

Neoglocianus maculaalba followed by *Dasynerua papaveris* and *Aylax papaveris* are usually members of the catenarium on poppies. *Stenocarus ruficornis* is not a member everywhere and in every year. We know of cases when *Ceutorrhynchitena maculae-albae* and *Dasyneuraetena papaveris* have occupied 95% of the poppy heads, but there have been cases when, through the 80% presence of *Ceutorrhynchitena maculae-albae,* hardly any *Dasyneuraetena papaveris* were observed. Finally, there was a case when the *Ceutorrhynchitena maculae-albae,* only occupied 7% of the available poppy heads, and only traces of the *Dasyneuraetena papaveris* were found. *Stenocarus ruficornis* was present at high densities last time in 1934 and, since then, has been sporadically present, including cases when it was under the detection threshold.

The above example proves two things: the proportions of constituent populations of zoocoenoses – in the given case a catenarium – can show large shifts, but a certain constant species combination can still be detected. If we only consider the most common species, we can, indeed, talk of species combination stability but, if we consider all the species that find their energy sources in the oecus, the species combinations will fluctuate in time. In our opinion, the latter is the correct approach, because the reality is that all populations are active members of the community (dominant or not) if they are present, irrespective of our views.

§ SUCCESSION IN ANIMAL COMMUNITIES

There is a question left to consider: is there succession in animal communities, or not?

Succession is the phenomenon that manifests itself, at the same location, in the formation of sequential communities.

Thus presented, the question will have an affirmative answer even on theoretical grounds. The changes in the composition of plant communities, progressing towards a climax, will obviously generate profound transformations, with the result in animal communities of a complete change in composition.

The zoocoenological succession is, therefore, the consequence of the changes in the energy sources. These, however, can be of two kinds: either they accompany plant succession, or the energy source changes, due to the activity of some animal community, so much so, that the original zoocoenosis becomes extinct, and its place is occupied by another one.

In plant succession, there is often a constructive element, while zoological succession is often triggered by destructive factors (Tischler, 1950: 184). During succession, a plant cover will become ever richer in energy sources, and the environmental conditions, due to the development of several levels, will allow an expansion of the zoocoenosis. Such a change is, naturally, very slow, and we can assume that, above a certain degree, it will trigger an opposite effect: a pine or beech forest of closed canopy, with its subdued undergrowth, is less favourable to support animal life than a thinner forest or a grassland-forest mosaic.

Succession due to the activity of animal communities can happen when the constituent populations exhaust their energy sources, destroying their own living conditions (Tischler, 1950: 184). Thus, in an agrilignosa, an *Aspidiotitena perniciosi* can be followed by an *Eccoptogastritena rugulosi,* not forgetting that the latter is not linked to a previous zoocoenosis, as it can also appear in an oecus of frost-damaged trees. Catenae on the excreta of herbivorous animals also follow each other in a succession-like manner (Madle, 1934; Kuehle, 1950 cit. Schmidt, 1935; Mohr, 1943 cit. Park see Allee et al., 1949), directed not only by the atmospheric effects on the excreta, but also by the activity of the intercalary elements that serially follow each other, causing transformations of the resource base. The succession often only impacts a part of the zoocoenosis, as we can see in the succession of intercalary elements feeding on debris (Pukowski, 1933; Fourman, 1938 cit. Kuehnelt, 1950) that, in the different phases of disorganisation, are represented by different populations. The decisive role of plant-based energy sources is indicated by the fact that, on excreta of the obstants, no catenae develop composed of intercalary elements (Kuehnelt, 1950:229). We do not know if a similar difference exists between cadavers of corrumpent vs. obstant mammals.

The changes mentioned undoubtedly belong to the phenomenon of succession, even if restricted to a small area and a single energy source (microsere, Mohr, 1943 cit. Park see Allee 1949). On the other hand, changes that accompany the gradual extension of zoocoenoses do not constitute succession (Kuehnelt, 1950:281). In cases where an uninhabited area is colonised, such as a rock (Falger, 1914, 1922–23, cit. Franz, 1950; Bachmann, 1910; Heinis, 1910; Rahm, 1910, cit. Kühnelt, 1950: 281; Oosting and Anderson, 1939, cit. Park, see Allee et al. 1949: 464.), species that once colonised remain to be detected, and the community will gradually become richer by the arrival of new populations. Here, we do not talk about succession but the "filling out" of a zoocoenosis. The first signs of succession appear when changes in the plant cover cause the disappearance of the first pioneer species, assuming that these are accompanied by similar disappearance of animal associations.

What we observe on cultivated areas mirrors these phenomena. The main difference between the arvideserta and agrilignosa and the less disturbed biotopes is that, in the former, human interference prevents succession; the soil is cultivated, and the producents are regularly changed in a rotation as if on a chessboard. Here, we cannot talk about succession, as succession cannot happen;the catenaria are facing a new situation every year, and they have to move to another area, while the presocium and supersocium can be sustained because the area in question remains arvideserta or agrilinosa for decades, and there is no possibility for successional changes. The cultivated biotopes (secondary sequences, Park see Allee et al., 1949, 578; culture-biocoenosis, Balogh, 1953: 39) therefore are the exact opposites of a natural succession.

VI. METHODS OF A ZOOCOENOLOGICAL ANALYSIS

From the previous arguments, we can see that a zoocoenosis can undergo constant changes, both of quality and quantity. The same association, according to the change of the seasons, will bring different populations to the surface.

Consequently, a full inventory of a zoocoenosis is only imaginable if our surveys are continuous, or at least are frequently repeated throughout the growing season. The more frequent our surveys are, the more complete picture we gain of the composition of the zoocoenosis while, if we have longer gaps, we run the risk of detecting only certain aspects, and miss dynamic events that may be crucial for the understanding of the zoocoenosis.

When studying zoocoenoses, two additional circumstances need to be considered. One is that some populations lead a secretive life (even if above ground), and their surveys must employ special methods. The other is that all populations are members of the zoocoenosis, be that eurichron or stenochron. We accept that, from the perspective of production biology, only constant and dominant populations are of interest but, from a zoocoenological point, all are equal subjects of study because they are members of the zoocoenosis. The aim of zoocoenology is to study this, and not nutrient cycling – a census should not lead to a one-sided, probably false impression about the real composition of the zooconosis by counting only the constant and dominant populations.

§ THE AIM OF THE ANALYSIS

That said, we can pose the question: what are the aims of coenological studies?

There are three answers to this question: 1) to establish the qualitative composition of zoocoenoses: the *species* spectrum; 2) to establish the quantitative composition of zoocoenoses: the *quantitative* spectrum, and; 3) to unearth the between-species relationships of the constituting populations: the *synphysiological* spectrum.

The two first are static, seeking the unchanging elements in the zoocoenoses, trying to grasp the constancy, while the third is dynamic, trying to show the changes, and uncover the shifting elements.

There is a lack of a synthesis of these foundations in zoocoenology, but if agrozoocoenology did not attempt this exercise, it undermines its reason for existence. Our opinion is that all three need to be utilised when we want to characterise a zoocoenosis; the three together provide the coenological characteristics, the first is the qualitative, the secondquantitative, and the third, structural.

Zoocoenology as it has been practiced so far, and in part continues to do, is largely synmorphology, restricting itself to the description of qualitative and quantitative characteristics. The available coenological measures are, in essence, limited to these factors, perhaps because, to a large degree, these were adopted from phytocoenology in the belief that they are also sufficient for uncovering the structure and composition of zoocoenoses.

However, these characteristics are not sufficient for a full representation of animal communities and, due to the substantial differences between plant and animal communities, this is not even possible. There are signs in the literature of the desire to also consider the synphysiological spectrum during the analysis of zoocoenoses, mainly in the attempt to group the populations of zoocoenoses into trophic or life form groups (Elton, 1927; Balogh, 1946; Balogh and Loksa, 1948; Tischler, 1949, 1951; Franz, 1950; Dudich, Balogh and Loksa, 1952).

The above-mentioned trio of characteristics involve certain sequential stages. The first step is, obviously, the description of the species spectrum, the identification of the species identity of the constituting populations, followed – and often accompanied by the measurement of the quantitative relationships; while the synphysiological spectrum clarifies the roles filled by the individual populations, considering the trophic relationships and other interactions. Certain authors assume that, in a zoocoenosis, the dominant populations play the decisive role and believe that the study of interactions must start with these populations (Schwenke, 1953). We cannot be so sure about this without clarifying the relationships and, thus, we claim that all research must be performed without prejudice, and by looking at the whole zoocoenosis. It is self-evident that the dominant populations occupy the focus of our attention, given that dominance itself is a characteristic that can be explained by synphysiological factors.

The aim of a zoocoenological analysis is the study of the zoocoenosis, that is, of the associative categories, and not the spatial relationships of the individual populations. A given community is not a community because of its relationship to a habitat area or volume, but because its constituent populations are connected through trophic links. Due to the spatial constraints of energy resources that are also linked, indirectly, to an area, any spatially-limited coenological study is constrained; it represents a "window", through which we try to examine a zoocoenological category, but not the zoocoenosis itself. We can only compare populations that belong to the same associative category; therefore, the coenological categories are associative, and not faunistic, characteristics.

This view gives the coenological characteristics a different content than can be seen in even the current literature. However, in order to minimise changes to the existing terminology, we used them unchanged, but used them also for associational categories.

The quantitative characteristics do not reflect the structure of the zoocoenosis, but the quantitative characteristics of the communities of otherwise similar structure. This is clear from the fact that, in the same zoocoenosis, the dominant populations can be different, yet the category itself remains. The overall structure must remain unchanged during these fluxes of populations; thus, we cannot consider as structural elements anything else than the life form groups already discussed, namely the coeti of zoocoenoses. A zoocoenosis is not held together by the dominant populations but by the coeti that coexist. In these coeti, certain populations are dominant at certain times, which can be a time- and space-bound feature of the coenosis, but this is not a matter of structure.

This view is not distant from other Hungarian authors, as two of the triad of Dudich, Balogh and Loksa (1952) are identical with the intercalary and obstant coetus. They also write that "within the groups, species can substitute each other. This ecological vicariance creates a very variable ecological structure." These words clearly refer to this sustained structure that can be filled by different species combinations, different zoocoenoses, whose structure is, nonetheless, identical. In his latest work, Balogh (1953) retains this view and, in a tabular list, the species are grouped into trophic groups. This indicates that a coenological anlaysis cannot end with the establishment of density and mass relationships, but is inseparable from methods that shed light on the roles of individual populations.

§ THE WORKFLOW OF THE ZOOCOENOLOGICAL STUDIES

When a phytocoenologist works in the field, all that is evident is a stand of coexisting plants. They have no other task than to identify the associative categories in the plant stand, to analyse them using established, and well-known characteristics, and to draw the appropriate conclusions based upon them. An experienced phytocoenologist does not have much difficulty in identifying the species in the plant community.

When the zoocoenologist works in the field, they are confronted by a few animals, a small fraction of those that are really present. Their first task is to capture them, and then to find most of those that must be present but are not immediately visible. This assemblage cannot be usefully analysed by the phytosociological toolkit, because this will not reveal a community – it remains the assemblage of that area. The full identification of species constituting the assemblage in the field is not possible by anyone, if only due to the small size of most animals that prevents a precise identification.

There are two consequences: a zoocoenologist must collect most of the animals from the field, and the material identified in the laboratory must be analysed by methods that allow delimitation of the individual associative categories. These are also warnings that, in the place of phytocoenological characteristics, or in addition to their use, we need other characteristics that will help to achieve our goals.

Therefore, all zoocoenological research has two methodological stages: censusing the association, and analysing it.

The aim of the census is to collect information about the totality of the animal assemblages of a given area, the entirety of its constituent population. This definition indicates that this phase is nearly identical with the task of faunistical research. Indeed, the difference is only that the aim of faunistics is only to identify all species living in the study area, while the coenologist also wants to know about their roles. In practice, a zoocoenological collection phase is different from the faunistical one, because it has to be performed so that the collected material is suitable for a subsequent coenological analysis. The first criterion is that the overall picture would not only reflect the constituent species, but also of their density and relative abundance. It is impossible to use the same survey method for all groups, yet it is a necessary condition that the methods used for a given group be identical in all cases. Thus, for example, on a wheat field we should take the same number of soil samples (this would be an error – as the size of the field needs to be taken into account, otherwise the sampling intensity will be different); on the soil surface, we ought to examine the same number of quadrats; from the plants (in order to study endophytes) we should take the same number of samples, and; from the plants, we collect animals by sweep netting, using the same number of sweeps taken at the same time of the day. An exhaustive sampling, due to the complicated life patterns of animals, needs a set of different methods, thus the sampling methods can be grouped into three:

a) collecting methods can be used when full compilation of the studied assemblage can be attained by methods used in faunistical studies

b) incubating methods need to be used when a population cannot be properly sampled by any methods, because of its hidden way of life, or because it is "hidden" within another population, thus its presence is impossible to detect using traditional collecting methods. Such methods need to be employed when censusing animals living in stems, seeds of galls. Also, incubation is necessary to assess the degree of infestation by endoparasites, i.e. to what degree a given parasite population is present in the zoocoenosis.

c) observational methods are to be used when neither collecting nor incubation methods are usable, either because of the high vagility of animals, or the strong dispersion of semaphoronts. In such cases, only observations can enlighten us as to how these animals live in the community, how they spend their time, and what role they fulfil. Thus, observation – be that under field conditions if possible, or in the laboratory, if necessary – firmly belongs to the analysis of the zoocoenosis, but can also be employed for census (for example, birds, grasshoppers, bees; see Palmgren, 1930; Nagy, 1951; Móczár, 1954).

The methods listed above cannot be described in detail. Not only because these have already been detailed in two recent publications (Dudich, 1951; Balogh, 1953) that describe a rich treasure trove of sampling methods, but also because we could only provide a very incomplete description of what is available in the literature. The sampling, and incubation as well as observation methods are not only variable because of the different features of the different target groups, but also because none of them are precise; most collectors and researchers trying to keep developing species under laboratory conditions have always strived to perfect the methods used by making individual modifications. We can be certain that every collecting method will be criticised, and thus we avoid repeating these. Justified criticism is regularly voiced even in connection to soil faunal sampling (see Kuehnelt, 1950; Franz, 1950; Jahn, 1951; Dudich, Balogh and Loksa, 1951, etc.), and even more critical analysis can be expected towards above-ground survey methods where the conditions are much more complicated. The important thing is to have at our disposal an ample range of different methods, whereby we can find a suitable one for every group. Imperfections cannot be unsurmountable obstacles in the way of shedding light on the species spectrum of a given zoocoenosis. We need to add an assessment and hope for clarity. The censusing of the assemblage is an essential part of zoocoenological studies but it is not carried out for its own sake, as is also the case for faunistical studies. The aim of zoocoenology cannot be to capture all the animals living in an area, but to establish their presence and give reliable information about their relative abundances, because these data are necessary preconditions to describe the associative boundaries, and the mutual relationships of the constituent populations. Therefore, any survey needs to maintain only one rigid condition; to consistently use the same methods, although the methods can be freely chosen if they are appropriate for the above goal.

The zoocoenological census, in most cases, means collections. Therefore, we need to add a few comments about incubation and observation methods. The former, by necessity, is combined with the collecting methods, the latter might have to be combined with another collecting method.

The perfection of incubation methods is a matter of experience and feeling. Any one of the multitude of methods can be chosen if that seems suitable to allow the selected taxonomic group to reach adulthood. The big advantage of this method is that, in an optimal case, we obtain the whole population, and we may be able to get a glimpse into the life of the zoocoenosis. A precondition for this is that we do not only keep the collected parts (galls, stems), but we subject them to special studies, that may necessitate the dissection of the studied plants. The only disadvantage of the incubation method is that we have to move the material from its original site, and thus distance it from the direct effects of the biotope. Hence, we can underestimate the species spectrum, because had we left the developing animal in its place, the degree of parasitism might have increased, with additional, new parasites appearing. This disadvantage can be eliminated by taking repeated samples from the same material.

The observations are suitable to detect animals that appear very rarely in the zoocoenosis, or to gain data about the activity of the populations present. An important disadvantage is that the identification of the observed semaphoront is often limited. Consequently, we usually cannot avoid capturing the species, if its identification is not possible while running or flying.

All these methods will provide us with smaller or greater amounts of material. All censuses will provide data only about the animals present in a given space, without clarifying the zoocoenosis itself. In the material, collected by repeated and quantitative sampling, one or another species will be numerous, while the presence of others will only be signalled by one or two individuals. The material, once gathered, must now be analysed.

The aim of the analysis is to establish the relationship of the constituent populations to each other, as well as to the habitat.

The first thing to declare is that we cannot fit all semaphoronts into associative categories, and, in many cases, we cannot say much about their relationships to the biotope, either.

We saw that the structural elements of zoocoenoses are represented by trophic life forms called coeti. To recognise the associative category of a semaphoront, we need to know its life history, because only this will reveal its coetus as well as that of the semaphoront group. If we have no information about this, the coenological evaluation of the taxonomically (or otherwise) identified semaphoront will be impossible. In this case, we cannot say more about the relationship of the semaphoront or the biotope or oecus, than that it is present there. This occurrence, this existence, is not necessarily existential; its co-occurrence with the other semaphoronts can be just co-occurrence and not really living together: not a coexistence at all (Szelényi, 1955).

Thus, in our opinion, coenology is in error when a spatial co-occurrence gets classified as coexistence. This perception necessarily results in dealing with the species of striking dominance (not being able to interpret the semaphoront groups of lower abundances), and the zoocoenosis of a given plant community will be described by a list of these species. In doing this, nothing more has been achieved than characterising the animal assemblage of a plant community by its most common species. This is more than faunistics, because not only was the species identified, but their abundance relationships as well; this step is not zoocoenology, only "faunal statistics", a kind of faunistics that uses new parameters. By performing a continuous, quantitative census, we get a better characterisation of the fauna of the studied plant community, but not yet the zoocoenoses: the quantitative census is but the first step towards this. It merely reinforces the known conclusion that faunistics has established long ago, namely, that in certain plant communities, particular animal species are conspicuously common. These species indeed form consistent combinations and create an impression of stability that may be present at a faunistic level, but not at all in the zoocoenosis. We know that the fauna of the forest differs from that of a meadow or a reedbed, or a field of poppies, and the task of zoocoenology cannot be to prove this again by using new methods of faunal analysis. The aim of ecofaunistics is to deepen the knowledge about the fauna by unearthing these details.

This perception leads to drawing the border of a zoocoenosis where the ascendency of the dominant species stops (see Shelford and Towler, 1925; Balogh, 1953) and, in this case, the border of the zoocoenosis will, more or less, coincide with that of a homogeneous plant community. A high abundance, though, provides only one certainty: the population in question, as a semaphoront group, is bound by something to that given point in space – but this is no proof for a similar bind for the whole zoocoenosis, with all its aspects.

The zoocoenological school that, in copying phytocoenology, identifies animal communities by their constancy and dominance relationships, commits the logical error of categorising zoocoenoses by their quantitative characteristics, and pushes structural characteristics to the side-lines; yet the co-dependency between certain populations can only be clarified by these latter factors. These structural characteristics cannot change, while the quantitative ones can, from hour to hour. A further mistake of this school, is to hold that only the spatial relationships are of importance (thus straying toward faunistics), and forces populations that occupy the same space, but have nothing to do with each other, into one zoocoenosis (e.g. moles and soil mites, bark-boring beetles and roe deer, wheat stem fly and the poppy fly, etc.).

All populations have spatial relationships, but how these populations relate to space, and chiefly, to each other, is by no means a question of quantitative, but of structural characteristics. Zoocoenology studies associative categories, not spatial distributions. Spatial distributions are only considered within a given zoocoenosis. Space as an environment is important for a zoocoenosis but is not identical with it, so, whilst all zoocoenoses are also studied in space, this is not sufficient. A given space, if it is a biotope, can have a zoocoenosis, and a zoocoenosis will certainly have a spatial component, but neither can a biotope be delimited by a zoocoenosis (as it remains a biotope even without a coenosis, at most an unused one), and the limits of a biotope are not those of a zoocoenosis, because a zoocoenosis is composed of populations, and only these can have spatial borders. This is not changed by the fact that a border of some zoocoenoses does not extend beyond that of a biotope or oecus.

With these caveats, let us attempt a zoocoenological analysis of a given part of an animal assemblage.

VII. ZOOCOENOLOGICAL CHARACTERISTICS

When the zoocoenological characteristics are organised into their main groups, the individual characteristics are placed within them as follows:

	Synphysiological characteristics	**Qualitative characteristics**	**Quantitative characteristics**	
Structure	Relationship		Quantitative relationships	Mass relationships
1. Life form	3. Community relations	4. Species identity of semaphoront groups	7. Abundance	10. Gravitas
2. Coetus value		5. Association with biotope: constancy	8. Dominance	11. Production
		6. Fidelity		9. Spatial distribution

§ SYNPHYSIOLOGICAL CHARACTERISTICS

These express the essence of zoocoenoses, and include the factors that are most important in identifying them. They are of prime importance over other characteristics, even that of species spectra, because any of the further characteristics can only be used if the synphysiological links of the studied populations have been proven, that is, if the studied assemblage fits the criteria of a zoocoenosis. There is no doubt that we can have synphysiological information about a zoocoenosis, even if we know nothing about the species identity of the constituent populations (in other words: a zoocoenosis exists even if all its species are, as yet, undescribed); the situation is the same when studying species. In the latter case, we, firstly, encounter a semaphoront, and similarly, during the study of a zoocoenosis, we initially discover a semaphoront group, and its taxonomic identification is a necessary task after the first encounter, just as in faunistics or taxonomy. During the study of a zoocoenosis, the first step is to identify the life forms.

Concerning the life form categorisation, we agree with Remane (1943) who distinguished two groups. “Lebensformtyp” includes species that, due to adaptation to similar conditions and life history, have similar morphologies, and helps us deduce their life history; “Lebensweisetyp” includes species that display similar life history (i.e. sapro-, copro-, or necrophages) but this cannot be deduced from their morphology. We call the first a structural life form, and the second trophic life forms. The latter only approximates with Remane’s Lebensweisetyp, which stands between our concept of coetus and Balogh’s (1946) syntrophium, but is more like the latter. From a zoocoenological point of view, of course, only the trophic life form can serve as a structural characteristic.

The studied semaphoront groups will be classified into appropriate coeti by their life forms, but only if the populations have real community relationships. From the first two structural characteristics, therefore, the trophic relationship is indispensable, because only this association will prove the true coherence of the structure. The semaphoront groups and coeti are only building blocks; the (trophic) relationship is the force keeping them together.

1. Life form

We can distinguish two categories based on trophic relationships. One is the coetus, a necessary part of the framework for the zoocoenosis. We know four of these: corrumpent, sustinent, intercalary and obstant coeti. Within each, because of the endless variety of specialised life forms, we find populations with the most diverse life histories, autecology and behaviour. Therefore, it is necessary to establish a second category, that of the elementary life form, syntrophium.

The populations that damage the producents of the biocoenosis belong in the individual coeti (corrumpent coetus), playing a role in its continued existence (sustinent coetus), removing the non-living debris and excreta (intercalary coetus), or living off the previous three categories (obstant coetus).

Within the same coetus, the populations that have adapted to the common energy source in similar ways, belong to the same syntrophium.

According to Thienemann’s first biocoenetic principle (1941), the richer the fauna of an area, the broader the syntrophium spectrum of the coeti of the resident zoocoenosis, while the less variable the life conditions in a biotope, the narrower the syntrophium spectrum, as argued by Thienemann’s 2nd and Franz’s (1951b) 3rd biocoenotic principles.

The life form groups are remarkable for two reasons: zoocoenoses can be grouped by: 1) their structural elements, and; 2) the coetus rank of the dominant population.

Based on the identity of the structural elements, we can distinguish zoocoenoses with 2, 3 or 4 coeti, meaning initial, precedent or plenary zoocoenoses.

The initial zoocoenosis contains only a corrumpent, syrmatophagous-intercalary, or sustinent coetus, and the connected obstant coetus. Most catenae are of such types.

We can consider precedent zoocoenoses as the ones to which a zoophagous-intercalary coetus is attached as a third element. Some catenae can be included here (for example, the catenarium of a beehive), and catenaria that can be traced back to a host plant without an intermediary insect species (for example, Oscinellaenarium frit).

In a full (plenary) zoocoenosis, all four coeti play a role. The presocia and supersocia belong here, and catenaria that have base host plants that need insect pollinators for their reproduction (for example, Cydiaenarium pomonellae).

This three-way classification mirrors the development and growth of the zoocoenosis, but also poses a question. This emerges as we trace the development of the zoocoenosis from its origin; we end up at the first coetus, that includes corrumpents, sustinents or intercalary elements. There can be an oecus with several co-existing corrumpent or intercalary populations without attached obstant elements. The question emerges: can we consider these assemblages as a form of zoocoenosis? There is no doubt that this assemblage displays important criteria of a zoocoenosis: it relies on the same energy source and, thus, its elements can mutually influence each other. Can such a coetus, relying on a plant as energy source, be considered a zoocoenosis?

The answer can only be affirmative, given that the concept of the coetus includes a criterion of association. Given that all coeti include populations that share the same energy source, and the three above named coeti are directly attached to the plant cover, they need to be considered as a special category, as they can come to existence and can survive. The initial, precedent (intermediary) and complete (plenary) zoocoenoses are composite ones, the corrumpent and intercalary (syrmatophagous) coeti, and in a few cases even sustinent coeti, can be considered simple zoocoenoses, a kind of communitas incompleta, in which a food chain could possibly have developed but does not, breaking down after the first link that is directly connected to the plant-based energy source. Such is the case when, in a corrumpent or intercalary coetus, we cannot find any parasite or predator (although not disproving their presence) and, consequently, we have to assign the catenarium or presocium category of this assemblage, because the food chain may be continued through the obstant elements of the supersocion. The associative character of these links can be rather intimate, either in reciprocal or non-reciprocal form (see Jermy 1955), via commensalism or symbiosis (for example, the association of the poppy seed head fly and the poppy seed weevil within the poppy head); therefore, we cannot exclude these associations from being a zoocoenosis, even if they were simple coeti utilising the same plant base.

The other classification can be designated using the coetus rank of the constituent populations. We can only include catenae into this grouping, considering their structural base, and they can be corrumpents, sustinents, or intercalary catenae. An example of the first is *Ceutorrhynchitena maculae-albae,* of the second, *Apiditena mellificae,* and the third one *Eccoptogastritens rugulosi.*

The number and kind of constituent coeti is a characteristic of a zoocoenosis. If, among the constituent populations, there is only one linked to the plant energy source, such a zoocoenosis can only be a catena. According to the coetus association of this population, it can be a corrumpent, sustinent or intercalary catena; by the number of coeti, it can be an initial, or a precedent, zoocoenosis. If, at the base level, there are more populations linked to the same plant as an energy source, the zoocoenosis is a precedent one, and it is ranked as a catenarium. If the plant base is composed of multiple species, the zoocoenosis can be considered a plenary one, with a rank of presocium or supersocion. A community that, apparently, has only a single coetus, should, in theory, be considered a catenarium or presocion. The supersocion occupies a special position because, *sensu stricto,* it does not have a sustinent coetus. A supersocion is not linked to a specific plant community, nor to initial links or pre-existing catenaria, but assumes the pre-existence of plenary presocia, with the plant community serving as its energy source. The sustinent elements, therefore, as an indispensable part of presocia, belong to the supersocion, as its first trophic level is the presocium itself, or its totality.

2. Coetus value

The coetus value must appear among the characteristics of zoocoenosis, because the populations with multiple coetus values can increase the linkages between the members of the zoocoenosis, and can have a profound influence on its formation. The greater the coetus value a semaphoront group represents, the more independent it is from the needs of other semaphoront groups; thus, the lower the need for association, and it can fit easily into various zoocoenoses. Certain species of Formicidae, due to their coetus values of 2 or 3, can occur practically everywhere, provided that the abiotic conditions are suitable. Birds that live on insects in the summer, and seeds during the winter, can be constant in a biotope, while swallows, having a single coetus value, must move once insects become scarce.

The coetus value is an important zoocoenological characteristic because the populations with higher coetus values are members of more widespread zoocoenoses, and they can have a profound influence on the changes and sustainability of various zoocoenoses, even if they are, themselves, uncommon populations.

3. Community relationships

Given that populations co-existing in the same area are not necessarily connected by coenological links, but mere co-occurrence, an indispensable characteristic of a zoocoenosis is a community relationship. We have already presented the essence of direct and indirect, unilateral or mutual coenological links (p. 127). These links create the coenological relationships that force certain populations into a coenosis, or create important links between given associations.

Populations belonging to the same association must, at least, be linked by a unilateral, coenological association (catenarium, presocium, supersocion) and, whilst these can be held together by mutual coenotic links, catenae can only be held together by direct coenotic links. Only the existence of these links enables us to declare that certain groups of populations belong to one coenosis.

The special quality of the coenotic relationships is justified by a further factor. The symmetric, indirect coenological association refers to cases when there is one, or more, obstant populations of the same species in two or more zoocoenoses. Such links reveal a "kinship" between zoocoenoses that develop independently of each other, which we can call *species overlap* (after Balogh, 1953, although with a slightly different interpretation). The *species overlap means that populations of the same species appear in two, or more, different zoocoenoses.*

The importance of species overlap is considerable, because the dominance relationships of a community can be influenced by the fate of another one, and can even change its species spectrum. The effect of this kinship due to species overlap can be manifested between individuals of the same zoocoenosis, as well as between different zoocoenoses; in the former case, by the identity of the foundation member of the zoocoenosis while, in the latter, due to the identity of a structural element.

This is all because a population should be considered as a structural element of a species (Gilyrov, 1954). All species are divided into populations, and their relationship with other species materialises through these populations. In respect of the survival and fate of a spatially isolated *Aporiaetena crataegi* catenarium, these are no different to the fate of the *Aporiaetena* catenae on the other islands of *Aporiaetena crataegi.* Between such catenae there can be a direct kinship; a direct kinship exists among zoocoenoses that rely on taxonomically identical herbivorous elements.

There can also be species overlap via an obstant element: the *indirect kinship*. In this case, we are faced with different zoocoenoses, that have kinship because they are identical energy sources for one or more obstant populations. Consequently, *zoocoenoses that share one, or more, obstant elements (populations) that belong to the same species are in indirect kinship.*

Direct kinship is intuitive, and this is also expressed in the zoocoenological terminology. A species overlap relating to indirect kinship is a characteristic that commands special attention during the investigations of a zoocoenosis. If we neglected this, we would follow a path that artificially isolated the studied zoocoenosis. A zoocoenosis is connected to its environment through multiple links, and one of the most important is through indirect kinship that, through shared populations, connects "our" zoocoenosis to others.

There is no doubt that these links establish a certain reciprocity between the communities that have kinship, and whose effects should always be considered because they can be more important than the reliance on the same energy source. Therefore, one could question whether it would be better to categorise the zoocoenoses by these kinships, rather than based on energy sources.

This, however, would hardly be acceptable, because the communities in kinship may be distant from each other and, apart from one or two populations that form the kinship, they have no other links. Most of the constituent populations have nothing to do with each other. Such a categorisation would lead us to the point we reached with the connex schemes, and we end up in a maze of complicated arrows, indicating the ever more tentative and accidental connections that link a community through kin that are also kin with another community, etc. Ultimately, these mapped connections would lead to communities so far removed in space and impac that the term "coenosis" becomes meaningless. The bilateral, indirect coenological link does not create a coenosis; it shows the direction whereby one zoocoenosis *can* impact another one. Such an impact can, occasionally, be substantial, and it can be necessary to assess its effects to explain the processes and changes in abundance within the coenosis, but the coenosis itself remains, despite the outside impact. A coenosis that is formed around a common energy source, that can be described and identified by its stable elements, and that is not fragmented by its kinships into one or more other coenoses, only goes to prove the importance of environmental factors; a coenosis can only be properly studied through taking account of its environment. Zoocoenology must view zoocoenoses through populations and not species, because the latter approach leads to an undecipherable maze, making the recognition of the coenotic categories impossible.

§ QUALITATIVE CHARACTERISTICS

4. The species identity of semaphoront groups

In theory, there is no obstacle that prevents forming an overall impression about the coenotic relationships of a semaphoront group before identifying its species. The latter, however, is still necessary, and not only because science strives for full knowledge, horizontally as well as vertically. It is also a cognitive necessity to establish this first qualitative characteristic. The knowledge of the species is not merely a name – a useful shorthand in further work but the basis of morphological, onto- and tokogenetic information that is essential to delineate, unequivocally, the semaphoront groups. Species identification is not ranked below the synphysiological characteristics, but represents the next level in our increasing knowledge about the zoocoenosis, because the life forms do not fit together because we know the constituent species; to identify the semaphoront groups with confidence, we need to determine species identity.

This identification serves only to connect our conclusions to a taxonomic entity and, this way, they can become a manageable aspect of the data, as well as part of the general zoological knowledge. From this perspective, the use of species names is an essential condition of a proper coenological analysis. However, the species in zoocoenoses are represented by populations, and the coenological analysis has to deal with these populations, not abstract species. The population is the structural unit of a species (Gilyrov, 1954). The species is abstract, while the population is a reality, that connects to other populations, according to its coetus value. We must consider it an error if authors, again and again, lapse into an idiobiological view, and coenological characteristics get attributed to species, and not populations. Coenological characteristics can only be ascribed to populations and not to species, whose presence can fit into various associative frames within the area of distribution (for example, the larval population of a generalist ichneumonid parasitoid can be present, simultaneously, in several catenaria). Such relationships of a species are important for the overall knowledge about the species, but this is idiobiology; there are synbiological aspects, but these manifest themselves, in different ways, through the associated populations. Zoocoenology can only evaluate these populations, and not the species, because at a given place and time, we only encounter a population.

A zoocoenosis can only be considered to really exist if such semaphoront groups permanently coexist, if this coexistence can be classified a community and, if this form of community can be repeatedly found. Consequently, there must be some sort of regularity in the zoocoenoses, that – above the structural identity – makes them distinguishable. These regularly-occurring characteristics can only be qualitative, and of two origins. One is the relationship of the semaphoront groups to the biotope and, the other, the links to the other semaphoront groups, i.e. to the coenological framework. Thus, are born the characteristics of constancy and fidelity.

5. Constancy

Constancy in phytocoenology serves to assess how a plant species is distributed among the various stands of the same association and, considering its perceptual presence, establishes five degrees (Felföldy, 1943; Soó 1945, 1953). Constancy in phytocoenology is a fully justified structural category, given the totally different structural framework compared to zoocoenology. Essentially, it is not difficult to realise that this definition of constancy is a relationship to the biotope, and expresses an immutable constraint.

Zoocoenology adopted this concept without substantial changes and, also, evaluated itbased on sampling units. Furthermore, a clear indication of this is that constancy in zoocoenology expresses the relationship to the biotope, and its measurement, based on spatial units. It is, though, by no means a structural characteristic because, here, the structure depends on the coeti present, and not on their species identity (more precisely, semaphoront groups), because these are only qualitative features, expressions of qualitative differences among structurally identical coenotic frameworks.

One cannot dispute that, for the formation of a zoocoenosis, the quality of the biotope is of fundamental importance; therefore, all zoocoenoses, including their constituent semaphoront groups, relate to the biotope in some manner. Hence, the associations in, for example, poppy vs. oilseed rape, or beech vs. pine forest are substantially different; constancy can only be an expression of these relationships.

The expression of constancy by units of sampling (quadrat, sweeps, volume, etc.) is an error, because these units contain fragments of the coexisting zoocoenosis. The constancy, expressed in this way, refers more to the dispersion, the spatial distribution of populations than their connection to a given biotope. If, for example, from 25 quadrats sampled in a plant community, we find semaphoront group representations of a certain species in only 12 quadrats, with abundance in two, this says no more than that the given population is very unevenly distributed; this has nothing to do with either its link to the biotope, or zoocoenosis, and gives no information about the homogeneity of the zoocoenosis, either. The constancy of the given population in the studied biotope is not proven or disproven by its spatial distribution, but is related to its continuous or discontinuous, aspect-linked presence.

The concept of constancy, as used in phytocoenology, cannot be appropriated by zoocoenology. Its current use amounts to *contradictio in adjectio*, because "constancy" measured this way is not constant at all, but changes from hour to hour.

It is obvious that we obtain a perception of constancy from our samplings, but constancy cannot have degrees (euconstant, constant, accessory, accidental; Tischler 1950) as a population is either constant or it is not. A given population is constant not because of its occurrence in all the sampled units (although it occurs consistently in all sampling units), but because its relationship to the studied biotope (oecus) holds constant for the duration of an aspect, thus it can repeatedly be found there. The constancy of a population cannot depend on its density. Constancy does not depend on abundance, or regular or irregular distribution, but merely on the occurrence itself. This presence assumes the existence of life conditions that the given population will find all the time, or during a certain period, in a biotope (oecus). If, for example, during a study of zoocoenology of apple trees, we find that out of 1000 leaves, 364 support gynopedia of *Aphis pomi*, but the larvae of *Coccinella septempunctata* occur on only 187 of them, would this mean that the former has higher constancy than the ladybird? Not at all, both populations should be considered constant, without any difference in rank, because constancy is not decided based on abundance but on whether the given populations regularly occur in the biotope or not.

Therefore, what can we correctly call zoocoenological constancy?

Constancy expresses the existential connectedness of a population to a biotope. This can have three degrees: stenoconstant populations are continuously present in one biotope; heteroconstant populations are present only during a given time, and, euryconstant populations are present in more than one biotope at any given time. Thus, equivalent semaphoront groups are present in more than one biotope at the same time.

Stenoconstant populations live in only one lake, forest or orchard, within one zoocoenosis. Stenoconstant populations are represented by highly specialised trophic semaphoront groups and, if these are corrumpents, they can anchor whole catenaria to a biotope (oecus), where they are monophagous. Such a stenoconstant element is the larval or adult population of *Neoglocianus maculaalba* or of *Anthonomus pomorum.* All populations of stenotopic species are stenoconstant, although an onto-population of a species can be stenoconstant, while the next one is euryconstant (e.g. frogs).

It is characteristic of euryconstant populations that identical semaphoront groups exist in different biotopes at the same time, often in different catenaria, such as the larval populations of *Baryscapus diaphantus* that may be present in a cultivated field, a mesophilous meadow and a forest, in different catenaria.

For heteroconstant populations, it is vital that they can leave a biotope after a certain time, and fit into another one (damselflies, host-changing parasitic worms, etc.).

Being tied to a biotope is a qualitative characteristic because, from the point of view of zoocoenoses, it is not indifferent as to whether a biotope has oeci that allow the insertion of stenoconstant populations, or the biotope has the conditions that a stenoconstant population needs in addition to its trophic requirements.

Without doubt, constancy has a certain idiobiological nuance, but its operation with semaphoront groups, not species, does not debase its value as a coenological characteristic.

6. Fidelity

The source of the static nature of the qualitative characteristics is the relationship to the zoocoenosis as a framework. This relationship, to differentiate from the previous constancy, *sensu stricto,* is termed fidelity.

Fidelity expresses how strictly a population is linked to a certain biocoenosis. Fidelity also has three levels: *stenofidel* populations can be detected only in one community; the *heterofidel* populations are present only at certain times in a community, and, *euryfidel* populations are active, concurrently, in several communities.

An example of stenofidelity is the larval population of *Norbanus scabriusculus* in a *Cephitena pygmeai* catenarium. Heterofidelity is represented by *Theronia atalantae* in the *Cephitaetena cuneae* catenarium, whilst euryfidelity *Trichogramma semblidis* in the *Pandemiditena heparanae* catenarium, because it is also present at the same time in *Cydiaetena pomonellae*.

The corrumpents, and all the populations relying on plants as their primary energy resource (around which initial zoocoenoses or catenae are formed), occupy a specific position in relation to fidelity. Given that the formation of such catenae is not possible without populations of the first level, and that opens the energy source to further exploitation, these populations could be considered stenofidel eo ipso, if it was not for the frequent situation that the same corrumpent is associated with other species in different biotopes. From this, we can only conclude that fidelity can be related only to the element that first exploits the plant-bound energy, and not vice versa. It is not the corrumpents that are faithful to the connected obstant and intercalary populations, but their degree of fidelity is demonstrated by the corrumpent population.

Within a catena, we cannot speak of the fidelity of the population that is the base of the catenarium, but of those elements at higher levels. A case of fidelity is obvious in the symbiosis between two corrumpent elements. The *Papaver somniferous* oecus hosts the *Ceutorrhynchinarium maculae-albae* catenarium and, to this, the *Dasyneura papaveris* population will be stenofidel, because it is able to lay its eggs only in poppy heads that have been pierced by the poppy seed head weevil; furthermore, its adult semaphoront cannot even emerge if a corrumpent or obstant semaphoront of the *C. maculae-albae* catenarium does not chew a hole in the poppy head.

It is obvious that antagonistic relationships act in the opposite direction to fidelity, while a mutually enhancing effect between two populations relying on the same energy source – in the absence of symbiosis – can only be a case of fidelity. The fidelity of a population to a certain zoocoenosis can be a feature of the landscape as well. Among catenae composed largely of the same populations, there can be one, or more, that does not occur elsewhere. These populations can be called character species. This concept, however, needs to undergo close zoocoenological scrutiny.

If we insist on our original standpoint, that co-occurrence does not necessarily mean association, we see that the concept of character species seems ambiguous. When we study populations according to their relationship to a biotope or a zoocoenological unit, then it becomes obvious that both the biotope and the zoocoenological unit (e.g. a catena) can have populations that are only present there. A character species of a biotope is, however, a zoogeographical and faunistic – but not a zoocoenological – concept, and can only have an associative connection. In this case, however, the concept of species can only be used exceptionally, and not generally. In zoocoenology, we can only speak of character species when all ontostadia of a species stay within the same associative category, and only if this framework, precisely due to the constant presence of this species, is uniquely characteristic. Given that such populations are always of stenoecus and stenotopic species, the concept of character species has an unmistakeable idiobiological flavour and, for this reason (even though its importance in phytocoenology is not doubted at all), we cannot encourage its adoption in zoocoenology, at least not in this form. An equivalent term, though, that in phytocoenology is the character species, is also needed in zoocoenology. However, as the variability of idiobiological factors is incomparably larger among animal than plant species, we are only correct in using the term character species in zoocoenology if we restrict it to populations that are strictly linked to a certain catena, or presocium.

The term remains ambiguous even after this restriction, because we can use it to 1.) name a population that is known from only one catena (for example, *Norbanus [Picroscytus] globulariae* is a character species in the *Stagmatophoraetena albiapicellatae* catenarium), or, 2.) denote a population that is characteristic of a zoocoenosis in a specific landscape.

There is no doubt that the first case is identical to the definition of the stenofidel population. From this, it follows that every stenofidel population is, *eo ipso*, a character species. The second case could be a zoogeographical term, had we not modified it so that the criterion is not the association with a landscape or biotope, but of its close link to a zoocoenotic category, even if in a specific landscape.

Thus, it is unavoidable to define, precisely, the meaning of character species, otherwise we have to deal with a murky concept, and the potential confusion in its interpretation.

We define stenofidel character species as "populations that will appear exclusively in one given zoocoenosis", without considering any landscape limitation of the coenological affinity.

For landscape character species, we understand populations that give a landscape-limited special character to a zoocoenosis. Such populations are not necessarily stenofidel; their main feature is that they are members of the zoocoenosis in question only in the given landscape.

Naturally, we can only talk about character species if we study, or compare, several individuals of the same zoocoenosis. For example, the species spectrum of the *Hyphantria cunea* in the various landscapes of the Carpathian Basin, or the changes in this catenarium on the Hungarian Plain, the Czech-Moravian Basin and Steierland. Likewise, we can only talk about fidelity in connection to such a comparative analysis.

The question of fidelity has another side to it. It can occur that a certain zoocoenosis contains, albeit at a restricted space and for a limited time, populations that are not normally part of that coenosis. These transitional variants, always limited in space and time, show different facets of the same zoocoenosis; the species creating these components are the differential species.

Differential species include populations that characterise various facets of the same zoocoenosis that are limited in space and time. The differential species are distinguished from character species in that the former are not constant, but exceptional, members of the coenosis, limited to a small area and for a short time interval. Such a differential species in a *Hyphantriaetena cuneae* catenarium are the obstant populations of *Tetramopria aurocincta* and *Diapria nigricornis* that were only found in 1948 at Pákozd (Jermy, 1952), or the *Theronia atalantae* obstant population in the same catenarium, detected in 1954 in the Nyirség (Szalay-Marzsó, 1957).

§ QUANTITATIVE CHARACTERISTICS

7. Abundance

Abundance (density) indicates the number of individuals of a population in each zoocoenosis.

Abundance is an absolute characteristic, using an unequivocal number to indicate actual size of the studied population in a zoocoenosis. Given that, here, we should express relations between numbers, even if this is tangential, we have to relate these numbers to a unit of area. Even if not ideal, we cannot dispute the analytical methods when using area or volume. However, we ought not to lose sight of the fact that a unit of area, or volume, does not represent a zoocoenosis but only a small fragment, that happens to be present in the space being studied. The extrapolation of data obtained in this way is always risky (see Kuehnelt, 1950), and we have to keep in mind that, even if we see absolute numbers, their value is only relative.

Abundance itself is of relative constancy. Even in a locality-bound populace (scale insects, leaf miners), the numbers always change; some animals perish, fall prey to obstant elements, or are subject to the incursion of endoparasitoids, and that, then, they do not really represent their own population, but that of the given obstant element. In the case of a population of high vagility, abundance is even more relative because, here, not only space, but time should also be considered (for example, when counting bees, see Móczár, 1954).

However, animals do not associate with a unit of space or volume but with the energy sources present in the given space. Consequently, the causes of abundance is not the unit of space, or volume, but the plants occurring, or the animals living, there. If this is so, then the abundance cannot always be related to a unit of area or space, because only the plants that occur there can be attributed to this space. As we have seen, from the point of view of a zoocoenosis, the biotope means both a space suitable for its activity, and the plants growing in that space; therefore, for the animals, the plants also constitute space. Space interpreted in this way allows that we measure the abundance by area or volume of space, but only for elements that are directly linked to plant-based energy sources.

This view places the evaluation of abundance into a totally different light, liberating it from all artificiality. Studying the abundance of sustinent elements using, for example, a quadrat, strip or other artificially separated spatial method, will say nothing if we forget that, for the zoocoenosis, plants are not only "space" but also a source of energy. The abundance of *Adrena hattorfiana*, that visits only *Knautia, Cichorium* or *Scabiosa*, or that of *Melitta nigricans*, visiting exclusively *Lythrum salicaria* (Olberg, 1951), can reach a certain (positive) value only where these plants are present. Likewise, the abundance of *Aporia crataegi* cannot be measured in regularly placed quadrats, only on trees where it can survive. Certain oeci can attract disproportionate numbers of flower-visiting Apoidea: Móczár (1954) found that in a *Festucion sulcatae* stand, 31.3% of apoid species, and 45.9% of their adult semaphoronts, visited one plant species, *Eryngium campestre*. The quality of litter will probably exert a significant influence on the abundance of litter-consuming intercalary elements. It may be that our knowledge in this area is not vast but, again, this indicates that zoocoenological studies are not possible without deep idiobiological knowledge.

The abundance of corrumpent, sustinent and intercalary syrmatophagous elements is studied through projection onto the plant cover, and the abundance of other elements will be related to this factor. Naturally, this will happen in space, not because the zoocoenosis is identical to some spatial extent but, since parts of the coenosis are linked to the plants occupying this space, and others are related to these first elements of a census. Space, in this situation, fills a secondary role, but this is still an important role because – in addition to providing energy sources – it also contains macro- and microclimatic conditions that, although secondary, still have a profound influence on the formation of the zoocoenosis.

The measurement of abundance currently uses heterogeneous, and – consequently – incomparable, methods: units of surface or volume, both in the canopy, counting on leaves, etc. These methods lead to a confusing mass of data, leading, inevitably, to false conclusions. The abundance of the larval population of *Operophthera brumata* can, justifiably, be related to the number (either surface area or mass) of leaves, but the ants hunting for them cannot be censused in the same way because they do not search the canopy for the leaves but for the larvae that are there, and ant abundance will be greatest where the presence of larvae is high. The abundance of ants can, therefore, only be related to the number of *Operophthera* larvae. For example, out of 14600 cherry leaves, 8760 had a single *Operophthera* larva; on these larvae, 64 *Formica rufa* were found, and 147 larvae also contained larvae (a total of 1598) of *Eulophus abdominalis*.

The abundance values obtained as a result look totally different to those that were realised using the same spatial reference that we used for one population (for a corrumpent, let us say). From these numbers, that shed light on the relative abundance relations of a zoocoenosis (or a catena), we can draw important conclusions. If, for example, at a subsequent census, we find that the number of larvae on 100 leaves decreased from 600 to 546, while the number of ants increased from 4.6 to 29.8, solely based on these numbers, we can assume that the ants forage in the canopy not just for the looper caterpillars because, if that were the case, their numbers should have decreased. There can be two possibilities: that the ants are related to other populations as well, or their presence in the canopy is aimless meandering (see Elton 1927, 56: "All cold-blooded animals and a large number of warm-blooded ones spend an unexpectedly large proportion of their time doing nothing at all, or at any rate, nothing in particular"). In the former case, ant numbers should also be related to these populations (that is, the combined populations of *Operophthera* + *Archips* + *Pandemis* spp.), meaning that *F. rufa* cannot be constrained in one catena, but associates at the level of a catenarium and, in considering this, we should not overestimate the obstant role of ants in the regulations of the *Operophthera* population (see p. 111 – degree of obstancy). Thus, the numbers representing abundance are full of detail, providing additional information about the borders of the zoocoenosis its internal trophic relationships, and are not merely "dead" columns of numbers, that we are unable to explore and analyse.

The value of abundance should express the number of individuals in the zoocoenosis. However, we have to register the number of individuals in a unit of space and, perhaps, even combined with a unit of time; the result obtained can only tell us that, in the examined part of space, the size of certain populations had certain values. Anything further relies on assumptions, and the more studies we do, the closer we get to the truth, without being able to reach it with our current methods.

Abundance can have two meanings, depending on whether it refers to the number of individuals in a population or the number of populations (see Tischler's (1950) "Individuenabundanz vs. Artenabundanz"). Both are informative because the population density can refer to the role of the given population group in the zoocoenosis, whilst the species density can refer to the completeness of the zoocoenosis. The high abundance of some population can be a cause of low species abundance in others, because those other populations are squeezed out. We can see this in the case of *Diaspidiotus perniciosus*, whose high abundance can cause the absence of *Sphaerolecanium prunastri, D. ostreaeformis,* and *Epidiaspis leperii.*

8. Dominance

Dominance (relative abundance) expresses the percentage of the abundance of a given population in relation to the total abundance of all related populations in the zoocoenosis.

In the definition, the emphasis is on the term “related”. Given that dominance is a relative characteristic, it is inconceivable that we compare elements that have got nothing in common (Tischler, 1950; Kuehnelt, 1951; Balogh, 1953); therefore, the preconditions for the correct interpretation of dominance is that we employ it within an identified zoocoenosis and, even within that, we compare only population groups whose trophic position allows this comparison. It is peculiar that, in zoocoenological practice, the literature is full of dominance values that were obtained by comparing all species collected. The explanation is, clearly, that the fauna of the given area was analysed, but not the zoocoenosis present and, not knowing the real role of the populations found, no attempt is made to establish the species combinations of the given zoocoenosis. Behind this procedure lurks the thought that dominant species have the biggest role in a zoocoenosis, which is not the correct starting point (Smith, 1928), because this projects something that is still to be proven onto the zoocoenosis. In a zoocoenosis, there can be small, rare but sharply delimited catenaria, where all constituent populations have low abundance. If we determine dominance by projecting it onto a given area, it can lead to us not even notice these catenaria, as their dominance values will be far inferior than those of others that may play a minimal role (for example, because they are in diapause), yet have high abundance.

By calculating dominance, one or more populations will be elevated above others, therefore we must ask: how can we establish dominance within a given zoocoenosis, and the dominance of which population should be considered the outstanding characteristic of the studied category?

Without doubt, populations belonging to plant-dependent coeti must show some surplus to serve as energy sources for obstant and intercalary elements, and the same holds for higher trophic levels, too. Such a surplus can be of three kinds: if semaphoronts of two populations, that are in a trophic relationship, have largely similar mass and numbers, the surplus in the host populations is indicated by higher numbers, and its dominance is clear and unequivocal. If the semaphoront of the host population is significantly bigger (in mass and size), it can support several, or many, individuals of a smaller (by mass or size) obstant. In this case, the obstant element can be dominant (by abundance) over the host population, while the latter is dominant by mass. If the members of the obstant semaphoront are much bigger than the host individuals, the prey population must be highly dominant, numerically, so that only one-two semaphoront of the obstant will stand against an overwhelmingly bigger population of the host, or (which seems to be more common) the obstant has to relate to several, occasionally many, hosts.

From this it follows that numerical dominance does not necessarily mean a greater, or more important; this cannot always be expressed by numerical ratios. The use of dominance as a quantitative characteristic is general, and it would not be practical to try to change this; confusing the alternative circumstances detailed above can only be avoided if the conceptual ambiguity is removed. To this end, we introduce two new concepts, those of degree of obstancy and degree of corrumpency. Zoocoenoses depend entirely on the energy available to them, and their existence requires, automatically, that a certain amount of the available energy is used. The condition of permanence of a zoocoenosis is that its rate of energy use is slower than the rate of the concurrent recharge. In the case of a population relying on a plant energy base, it means that the available plant biomass cannot be used up until it is replaced. Populations relying on animal biomass can also only survive in the long term if they do not use up all the available animal biomass. The zoocoenosis, for this very reason has a destructive character that was correctly recognised by Tischler. This destructive nature necessitates that the evaluation of dominance is extended by these two additional concepts. As all zoocoenoses (directly or indirectly) have to use plant-based energy, or gain the necessary energy from plants, the destructive activity of the corrumpent elements towards the energy source is a factor that has to be considered during the assessment of dominance.

For example, the corrumpent coetus of an apple tree catenarium includes several syntrophia (leaf-chewing caterpillars, flower-living populations, aphids on leaves, etc.). Which one should be considered dominant (the listed corrumpent populations are, after all, very heterogeneous) for the whole category (the catenarium), and are we allowed to place one of them above the others, based on the statistical analysis of mere density data? Which dominance is more important, that of the scale insects, the bud weevil, or some obstant element?

Let us consider the corrumpents first. The corrumpent activity impacts in two ways: in one direction, it influences the producent organisms, and this is named *transformative effect.*

The transformative effect is [characterised by] the amount of plant biomass that is destroyed by the feeding activity of the corrumpent semaphoront groups. If this is on cultivated crops, we call it “damage”, while the same impact on weeds can be considered “useful”. The concept of damage is, consequently, rather subjective and, in an objective manner, it is restricted to those cases of transformative effects that cause noticeable yield loss in cultivated crops.

The impact of corrumpent activity in the other direction is realised in the zoocoenosis. This is the *degree of corrumpency.*

The degree of corrumpency is the influence on the composition of the zoocoenosis by a corrumpent population. This can be measured by the transformative effect on the producents. If, for example, there are 1000 *Operophthera* caterpillars on 1000 leaves, obviously, no leaf is left undamaged, and if 1000 *Athonomus* are present in 1000 flower buds, there will be no pollinated flowers. In both cases, a series of populations will be excluded from the coenosis. This is manifested in the degree of corrumpency of the winter moth caterpillar population. If, because of an *Eurygaster maura* attack, the shoot withers, there will be no support for an *Oscinella frit* or *Oulema melanopus* semaphoront group. The actual amount of biomass, or plant resource, taken by the plant bug is a tiny quantity compared to the effects of this feeding activity on the physiological consequences for the plant. This is the transformative effect.

We can see the degree of corrumpency, based on the transformative effect, for two reasons. One is that the effect can be measured, in biomass, surface area or percentage loss. The second reason is that, according to all indications, in terrestrial habitats, a given amount of plant biomass does not necessarily assume the presence of a given amount of animal biomass; the plant biomass remains in considerable surplus (Heikertinger, 1951). The existence of a plant-based energy source allows, potentially, the colonisation by certain populations, or the formation of zoocoenoses, but to what degree this is realised, is not related to a fixed proportion of the plant biomass. Consequently, at least with our present knowledge, we cannot predict that on a quantity of *x* of apples, a number of *y* codling moth larvae will develop as, for various reasons, this number can be *y+n* as well as *y-n*. Therefore, the degree of corrumpency can only be measured by the transformative effect, and if this is 100% (i.e. all the energy source is used up), the degree of corrumpency must also be 100%, as all other populations are excluded from the community. The degree of corrumpency can change in an "island-like" manner, 100% in a smaller part of the plant cover, while decreasing, gradually or precipitously, in farther parts. The higher the abundance of a corrumpent, the greater the degree of its corrumpency on groups of populations (species present, species density), or effects on their abundance.

From this, the degree of corrumpency will be manifested within precedent or plenary zoocoenoses. In initial zoocoenoses – organised around corrumpents – we will only see cases where the catena in question is a relative of other catenae in the catenarium. In such cases, it is possible that certain obstant elements will be restricted. However, due to our scarce knowledge, we cannot present an example of this expected phenomenon.

Based on the possible degree of corrumpency, the corrumpents of a catenarium can be ranked. Given that the catenarium is composed of populations dependent on a common energy source, the population that has the biggest impact on the oecus will have the highest potential degree of corrumpency. A precondition is that this population be present over extended period, and attack vital parts of the plant. The population of decisive importance in the given space exemplifies this, and the name of the catenarium can, logically, only relate to one of these populations. If several such populations are present, the catenarium is named after the one with the highest degree of corrumpency.

On apple trees, such a population is that of *Diaspidiotus perniciosus, Eriosoma lanigerum,* or a tortricid with two-three generations per year. In a wheat field, these include *Agriotes* spp., *Agrotis segetum,* or species of wheat flies, etc.

The population with the highest degree of corrumpency is not necessarily also the dominant one. In a square metre of wheat field, a few larvae of *Agrotis* can have a higher degree of corrumpency than a dozen of *Oscinella frit.* To what degree numerical dominance is unsuitable as a characteristic of the real role of a population can be seen especially well when the corrumpent activity is by the larval semaphoronts, and not the adults. In such cases, the degree of corrumpency of the adult population is zero, and the degree of corrumpency of the given species can only be assessed via the activity of the larval population that follows the adult generation. This clearly indicates what sort of errors we can make during the study of zoocoenoses, if the importance of a species is evaluated based only on the collected adults.

In many cases, we cannot yet measure the transformative effect. To assess, for example, the impact of a caterpillar population, we ought to know the per capita foliage consumption. Once we know this, we can calculate the expected transformative effect by a simple multiplication (as in Rudnev 1951), that, from the point of view of the community, expresses the share of the available plant energy source that was used by the studied population. This is also an indirect measure of the degree of corrumpency, because the larger the transformative effect, the lower the chance for new populations to fit into the coenosis, meaning the greater the degree of corrumpency of the population responsible for the transformative effect.

Under our current knowledge, however, we cannot calculate, precisely, the degree of corrumpency, because we do not yet know the constancy of the species composition of the various zoocoenoses. The flourishing of producent elements in a zoocoenosis is a potential condition for the full development of a (partially- or nearly-developed) zoocoenosis. Any corrumpent exhausting the producent energy source will impair this possibility, forming a mechanism that acts against the expansion of the biocoenosis. This factor is the degree of corrumpency whose magnitude is inversely proportional to the degree of threat to the vitality of the producents. The manifestation of the degree of corrumpency results in the interaction between populations that utilise the same energy source. This interaction, through degree of corrumpency, is the proof that the catenarium, presocium and supersocion are indeed zoocoenological categories.

Currently, we can distinguish three levels of corrumpency. If most of the energy source remains in a condition that it is available to the corrumpent populations that become apparent later, the degree of corrumpency is *regressive*. This degree is regressive when the transformative effect is <50% of the energy source. The degree of corrumpency becomes *progressive* when this energy use becomes >50% and, as it exceeds the 50% level, greater food limitation is experienced by the remaining populations of the coenosis. The full (or near 100%) utilisation of the energy source is classified as a *destructive* degree of corrumpency, as it leads, inevitably, to an impoverishment of the zoocoenosis (a forest without leaves, an orchard destroyed by scale insects, a crop field devastated by caterpillars, etc.).

When declaring a destructive degree of corrumpency, we ought not forget that this is realised within a given catenarium, and results in disturbance of the species spectrum that could otherwise have developed there without hindrance. This, however, does not mean that there is no possibility for the appearance of another catenarium, with a different species spectrum. Devastation by scale insects, for example, could trigger an increase in xylophagous populations; dead trees will provide an opportunity for colonisation by a different group of populations. There is no doubt, however, that the original status has changed, that something happened to instigate change; the factor that triggered this change is identified in the concept of degree of corrumpency.

Thinking about the plant-dependent structural elements of the zoocoenosis, we realise that, so far, we have only discussed the role of the corrumpent coetus. How can we judge the role of the syrmatophagous, intercalary and sustinent elements?

The discussion about sustinents will be very short; given that they are sustinents, we cannot speak about degree of corrumpency. If a sustinent element steals honey, its status has changed to a corrumpent semaphoront, and this activity should be characterised by the degree of corrumpency. The assessment of the dominance relationships of the intercalary elements should also be measured by their role in the processing of plant debris. This is the degree of recuperation. This reminds us that, in the litter, the most important role is not necessarily played by the numerically dominant population, but the one that processes most of the available plant debris.

The obstant elements of the zoocoenosis have a totally different kind of activity, and they impact certain populations of the zoocoenosis directly, not indirectly. This impact certainly results in a decrease in density, and the *degree of obstancy* is the effect of the obstant elements that causes a density decrease in the host population.

The degree of obstancy can be interpreted in two ways: whether we consider the numerical output of the density decrease, or whether we also take account of the further consequences. Following this reasoning, we can distinguish empirical and gradological degrees of obstancy.

The *empirical degree of obstancy* is the influence that an obstant population has on the density of the host population. This degree is expressed as percentage, and indicates the proportion of the host semaphoront group that was prevented in its development by the obstant population. This percentage can be by density, but also of mass, as in Nagy (1956), when measuring the food consumption of *Arma custos.*

This degree of obstancy refers, exclusively, to the relationship between two semaphoront groups; for example, the % infestation by tachinid larvae of the pupae a certain butterfly species. As this interpretation of the degree of obstancy does not indicate the real role of an obstant element in the mortality of a given generation of a *species*, this empirical degree of obstancy should be distinguished from the gradological degree of obstancy (e.g. apparent vs. real mortality, Thompson, 1929; Chapman, 1931:206).

The *gradological degree of obstancy* is the influence of an obstant population on the host species population size through decimating a given host population. There is no doubt that the empirical degree of obstancy is also a numerical expression of the decrease in density of the host resulting from the activity of a parasite or predator. This role, however, is restricted to one semaphoront group, and the number obtained does not express the importance of this factor among other mortality factors that also contribute to the overall mortality of the generation. If we compare the empirical degree of obstancy to this, it may turn out that the overall effect of this factor among the others is surprisingly small. The real role is expressed by the gradological degree of obstancy. Using an example, we can demonstrate the gradual diminishing of a generation and the gradological degree of obstancy of these factors. The example is the yellow scale insect of the pear, *Diaspidiotus pyri* (Szelényi, 1936).

Mortality factor	**Empirical obstancy, %**	**Remaining population, %**	**Gradological obstancy, %**
Unhatched eggs	80	20	80
Larval mortality, predation	65	7	13
Mortality of established larvae	25	5.25	1.75
Mortality of L2	5	4.99	0.26
Parasitism, L2	5	4.74	0.25

It is evident that the precise quantification of the gradological degree of obstancy requires profound and idiobiological studies that can, realistically, only be madein small catenaria. Given that different populations of the same species may belong to different zoocoenoses, the assessment of the gradological degree of obstancy will, in most cases, go beyond the boundaries of the studied zoocoenosis. For this reason, when studying the relationships among populations of a coenosis, we can only establish the empirical degree of obstancy. The reason for discussing it here is that we can underline the relative value of the numbers expressing the empirical degree of obstancy, and that we appreciate that these are valid only within the studied coenosis, and not related to the species, but its one semaphoront group. The line of argument, through the gradological degree of obstancy, leads from the studied zoocoenosis to other ones.

The degree of obstancy can be of minimal importance and, indeed, it frequently is; gradology expresses this by saying that the studied animals have no effective natural enemies. We have a substantial body of evidence proving that the population dynamics of insects, in most cases, are largely determined by abiotic factors, dwarfing the influences from the direction of the zoocoenosis. Opposite cases are also known (Szelényi, 1954), and we ought not forget that, in the absence of systematic zoocoenological analyses, we know very little about the processes operating within zoocoenoses. Especially little is known about the degree of obstancy of temporal elements, yet their study can lead to surprising results, as shown in studies on grain-infesting Heteroptera by Treml and Batkina (1951).

Several studies indicate that the degree of obstancy is influenced by the abundance of the host population. Smith (1935), among the mortality factors acting on populations, distinguished both density-dependent and density-independent ones. Solomon (1949) modified these terms by referring to processes not factors (density-dependent or density-independent processes or actions), correctly arguing that these factors do not act in isolation but within the framework of the ecosystem dynamics. The biotic factors usually act in a density-dependent manner, while the physical factors act independent of density. If this is so, then the degree of obstancy will clearly be greater with an increase of density. This does not hold for all obstants. Parasitoids are most effective when the density of the host population triggers a noticeable transformative effect, while at lower densities, the degree of obstancy by predators is at the forefront (MacPhee and Sanford, 1954). The degree of obstancy of a phytophagous predator, thrips (*Haplothrips kurdjumovi),* on phytophagous mites, depends on density, but the effect of the same obstant on the codling moth and the apple tortricid is independent of density (MacPhee, 1953). The obstants on the scale insect *Lepidosaphes ulmi* are exposed to the effect of low winter temperatures, and this will determine whether the parasitoids, or the predators, have a higher degree of obstancy (Lord, 1947). The density-independent factors are often combined with density-dependent ones, and the intensity of a given factor is also variable in time, but this is not influenced by the density of the population that is affected (Solomon, 1949).

The degree of obstancy can reach high levels and, the earlier in the life cycle it is manifested, the bigger the impact. The importance of obstants usually declines along the egg-larva-pupa-adult continuum. A long diapause of an ontostadium can increase the degree of obstancy of relevant obstant elements, as in the case of the pine sawfly (Ruevkin, 1953).

Therefore, we must distinguish between obstant elements, not only from a gradological but, also a zoocoenological viewpoint. This also involves dominance, because it seems appropriate if, besides the statistically based evaluation, we also consider the zoocoenological role of the population in question. This does not mean that, when evaluating dominance, we would detour from the path of quantitative analyses, which is the only correct route; we need to acknowledge the fact that the dominance of obstant populations can only be assessed correctly in the context of the whole (meaning whole-year) life of the studied zoocoenosis, otherwise we risk overemphasising the importance of the role of populations that dominate in certain parts of the season. If we register, for example, that on tortricid eggs, there is hardly any obstant activity, but the larvae are exposed to *Colpoclypeus florus,* and the pupae to some *Brachymeria* sp., even if both have similar densities, due to the higher degree of obstancy, the formerqualifies as the dominant population of the coenosis, because its role in host mortality is greater. For the same reason, the larval population of *Trichogramma evanescens* will be classified as the dominant one of the *Cacoeciatena*, if its degree of obstancy is high, even if it is only linked to the catenarium for a short period. Its dominance effects on the fate of the population was more decisive than any of the obstants that appear later in the season and, due to a density-dependent effect, also influenced their abundance.

Therefore, we did not deviate from the quantitative route when assessing dominance but, by introducing the term "degree of obstancy", and using it to rank the obstant elements, we created an additional, new platform for assessment. This allowed us to evaluate co-dominance correctly, and we could also put the dominance limited to a single aspect into perspective.

However, we also found an additional complication, caused by obstant "A" living with 25-30 of its conspecifics in a single caterpillar host, while "B" and "C" are solitary. In the *Hyphantriatena cuneae* catenarium, an example of the former is *Psychophagus omnivorus* and, of the latter *Theronia atalantae* and *Pimpla rufipes*, both as larval populations. This is a typical matter of degree of obstancy because, by abundance, the *Psychophagous* is clearly dominant, but its semaphoront represents a smaller degree of obstancy than a *Theronia* or a *Pimpla*. The *Psychophagous* degree of obstancy can be calculated by dividing the number of pupae parasitised with the number of emerging adults. The number obtained by these means is only an approximation, because the number of parasitoid larvae per host is very variable.

In this case, the *Psychophagus* is host to *Pedobius pyrgo,* and the *Pimpla* to *Dibrachys microgastri,* that are obstant hyperparasites; these cannot be considered together when calculating degrees of obstancy, because *Psychophagus* and *Pimpla* are obstants on corrumpent elements, but the hyperparasites act on the primary parasitoids. The dominance values calculated for the populations of the catena must, therefore, be supplemented by the degrees of obstancy: to the abundance of the primary obstants, the individuals hosting the secondary hyperparasites will have to be added. The degree of obstancy of the primary parasitoid must be calculated this way. This is fully justified, because the decrease in abundance in the host population can be linked to the primary parasites, and its absolute value is not changed by the fact that part of the primary parasitoid population fell victim to the secondary (hyper)parasite. The degree of obstancy of the latter will have to be related to the primary parasite, because its impact is on this, rather than the corrumpent host of the primary parasitoid.

To obtain the degree of obstancy of episitic populations is much more difficult, because their activity does not leave recognisable traces on which we can assess their impact on their prey. Their role is a good illustration of the dynamism of the zoocoenosis, and that this dynamism is played out in time, rather than space. The degree of obstancy of episitic populations can be established by observation, because only laboratory studies will provide information of theoretical value, and these are difficult to use when we want to assess another zoocoenosis. Prey consumption depends on many factors, and the precise degree of obstancy realised by an episitic population in a community can only be registered through observations over a longer period. Based on these arguments, the relationship between dominance and zoocoenological role is as follows.

Given that, in every catena, the corrumpents have to be the majority, this population can only be the dominant element because, if the combined dominance of the obstants threaten the existence of the catena, then the whole zoocoenosis formed around it would, inevitably, fall apart.

In both the catenarium and the presocium, there are several corrumpent elements, of which one is dominant, or more than one are co-dominants. The decisive role in a zoocoenosis will be reflected not through dominance by numbers, nor by body mass, but by the degree of corrumpency. In the case of co-dominance, this is to be judged by the transformative effect exerted on the energy source of the studied population, without considering its aspect position.

The same applies when judging obstant elements: their importance is assessed based on thedegree of obstancy, and not by dominance. This allows the proper assessment of the role of an episitic syntrophium, which has a high degree of obstancy but its dominance lags behind the others – yet it can have the biggest influence on the coenosis. Due to the presence of endoparasitoids, we face a peculiar situation, namely that, at a certain stage of the coenosis, the number of individuals surveyed does not match reality. This becomes understandable if we realise that, in such cases, two populations occupy the same space because, within one semaphoront group, another one is hidden. The host is still alive, and the parasite developing inside it is also alive. The 400 caterpillars are 560 semaphoronts, because in 160 caterpillars, there is a larva of a tachinid parasitoid. At the end, we will see 240 butterflies and 160 tachinid flies, which equals the starting number; but, it is also possible that the final number will be considerably higher because, out of 160 flies, 55 hosted gregarious secondary parasites, so, when they hatch, the number of individuals is even higher.

In the evaluation of a supersocion, dominance is also diminished in importance. The relationships of this category to itself, and its environment, is much “wider” than we can express by numerical dominance values. We must, instead, consider biomass relations, degree of corrumpency and degree of obstancy. The relationship between presocium and insectivorous vertebrates, for example, is so complicated that this can be best expressed by the mass of food consumed, rather than by abundance values. The degree of obstancy, on the other hand, can be established – at least in individual cases – by the decrease in abundance of the target populations. The corrumpents will be related neither to individual plants nor oeci, but to whole plant stands, even if they only consume certain parts of it (e.g. granivores). The degree of corrumpency manifests itself in the direction of presocia, and the food consumed can be measured by mass.

9. Dispersion

Examining the spatial distribution of any zoocoenosis based on abundance, we find very uneven numbers, indicating that the spatial distribution of populations is extremely patchy.

Dispersion expresses the spatial distribution of a population. This is the only characteristic that exclusively expresses spatial distribution, and can only be studied in space, without considering the inter-population relationships.

Our perception of dispersion is formed through censuses of abundance. The abundance values obtained by the censuses will indicate that populations may be of heterogeneous distribution, even under similar conditions, although we can find the opposite, too. In larval populations of *Operophthera*, there may be no obstants in some parts of the canopy, causing different abundances of *Operophthera* at certain canopy levels, as the obstants are more abundant in the upper or lower canopy. It is also possible that the cynipid *Eulophus abdominalis* is more active on the sunny southern side of the canopy than in the shady northern one. Dispersion is, therefore, a strictly space-dependent feature, because the spatial distribution of species can be influenced by factors over and above the energy source, hinting at microclimatic influence. Hence, parts of an oecus can be suitable for the development of a different zoocoenosis.

Therefore, dispersion points to the “clumped” nature of the zoocoenosis, also indicating its varied nature, and hints at additional factors influencing their association. Even where the energy source is otherwise available, dispersion constitutes an important characteristic, allowing insight of the inner life and development of the zoocoenosis.

Dispersion is not a phenomenon that ceases to exist through increasing the number of samples (Balogh, 1953), but something that requires our close attention. An uneven dispersion does not become even if we perform various calculations, and this warns us about the reliability of quantitative calculations. Of course, this does not mean that such calculations are impossible in principle, only that sample size might not be great enough, and the quantitative data obtained are of uncertain precision.

The question of dispersion also raises the concept of homogeneity in zoocoenoses. What can we call a "homogeneous" zoocoenosis?

In phytocoenology, an association is considered homogeneous where the characteristics of the individual constituent species are approximately similar in the different quadrats. Can we transfer this criterion to zoocoenoses as well? In our opinion, this cannot be done because, in a phytocoenosis, the quantitative relations remain unchanged for a long period, but not so in zoocoenoses which are in constant flux. Quantitative relationships in a phytocoenosis indicate structure, but not so in zoocoenoses, where coeti are the structural elements, which can be filled by the most varied populations. It is impossible to talk about homogeneity in zoocoenoses based on the similarity of structural elements and, probably, no zoocoenosis can be declared homogeneous on the basis of its quantitative structure. Thus, we are left with a group of qualitative parameters that we must examine. From a qualitative point of view, we can consider a zoocoenosis homogeneous where it *has the same species representations in its whole area of distribution.* We can assume that such a zoocoenosis exists, even if it still has to be found. We can imagine a *Ceutorrhyachitena maculae-albae* composed of the same populations in a whole oak forest. We can, however, imagine the opposite, too: *a zoocoenosis is heterogeneous when certain groups of populations appear only at certain points of its area of distribution, in an island-like manner;* the species representation is richer at some points than in others, constituting different phases of the same zoocoenosis over a continuous area.

In defining homogeneity this way, we deviate from Balogh's (1953) viewpoint, who claims that "homogeneity in zoocoenoses is largely a matter of area" (Balogh 1953: 55). This contradiction arises because Balogh uses quantitative characteristics as criteria, while we consider a zoocoenosis homo-, or heterogeneous, based only on qualitative characteristics. This is in strict contradiction to Balogh, because we think that homogeneity is the more probable when the area is smaller and, with an increasing area, the formation of heterogeneity is more and more likely. Linking heterogeneity and dispersion is not useful, because the uneven distribution of populations remains, even across large areas.

There remains the question of how to evaluate different degrees of dispersion? This is not an easy question, because dispersion also depends on special features of population groups, thus its origins are idiobiological, and can only be considered a coenological characteristic, because the type of dispersion can influence the formation of a zoocoenosis.

Thalenhorst (1951) identified three types of horizontal dispersion for a species, which can be accepted and extended to the whole zoocoenosis. Dispersion can be:

1) continuous, when the constituent populations of the zoocoenosis are represented by semaphoronts over the whole area (in every sample unit) where the zoocoenosis is present;

2) semi-continuous, when, in some sampling units (partial areas), some populations are not represented by any semaphoront;

3) discontinuous, when certain areas are not inhabited by the zoocoenosis in question, i.e. the zoocoenosis is island-like and clumped in a few parts of the whole area.

This coenological dispersion must be distinguished from the dispersion of populations. The latter is often an idiobiological phenomenon and can, likewise, be continuous, semi-continuous or discontinuous; or, depending on the social predisposition of the species, can even be congregated in large numbers (Aphidae). Onto the combination of these differentpopulation-level dispersion characteristics, into which each species brings its own species-specific dispersion, our picture of the coenological-level dispersion can be projected.

For example, the fact that the *Zabrus tenebrioides* beetle has a clumped distribution on a 100 ha wheat field, does not indicate the dispersion type of the *Zabritena tenebrioidis* catenarium, only that of the species, whose distribution should then be categorised as discontinuous. The discontinuity of this corrumpent population, though, will certainly have an impact on the dispersion of the whole zoocoenosis, given that, on some locations of the occupied area, the semaphoronts linked to the corrumpent element will be missing. Thus, the idiobiological factors manifest themselves in synbiology, that is in the zoocoenosis; the latter must not be viewed through a single population, but always in its totality.

The dispersion of individual semaphoront groups can be quantified through censuses of abundance, if these can be related, through a corrumpent population, to a unit of space or volume.

10. Transformatum and gravitas

Characteristics related to mass relations are noteworthy mainly in relation to production biology; their zoocoenological importance, at least in terrestrial coenoses, is far from clarified. Today, when our knowledge is so imperfect concerning the mutual relations of zoocoenosis-forming structural elements, of their influence on each other and, not to mention their composition and its stability, it is difficult to imagine that we could assess the mass-related characteristics without grave imprecision.

The *transformatum (production of animal organic material) expresses the mean total mass by area or volume of a population of the studied zoocoenosis.*

Gravitas (mass dominance) expresses what percentage of the total zoocoenosis is contained in the given population.

These two terms are defined according to Balogh (1953); changing only the word "species" into population, and instead of production, we used the term "transformatum" (see p. 42).

The two definitions clearly mirror the difficulties, currently unresolvable, that stand in the way of clarifying these characteristics. To measure the transformatum of a given unit of area or volume, not even considering the measurement error, is open to serious inaccuracies when we try to assess larger areas. Given the large and uneven dispersion of populations, and their irregular distribution, several authors (such as Kuehnelt, 1950) justly warn against measurement on an exaggerated scale. This difficulty becomes even more acute when we attempt to calculate gravitas, because this is a relative characteristic, and has to be related to data that, themselves, stand on unreliable foundations.

We would like to point out a few additional considerations. A bigger body mass does not necessarily mean higher food consumption because, to truly assess this, we need to know the assimilation efficiency as well. A great many animals hibernate, for shorter or longer periods. Such a population can hardly be compared to others, whose members remain fully active during the period of study. Once we extend our attention to such aspects, the question of transformatum becomes devilishly complicated. The correct answer, especially for populations with two or more coetus values gets lost in the labyrinth of pre- and supersocia, and the transformatum of populations undergoing a change of coetus, or biotope that may originate from a totally different biotope and/or zoocoenosis.

Based on the above, we have to conclude that both the transformatum and the gravitas are characteristics that merit our attention, and that can prove very useful to unearth surprising relationships – at a more advanced level of zoocoenological study, after removing the methodological difficulties. Currently, however, they do not belong to the group of essential coenological characteristics. Ultimately, studies of biomass consider living material, and the attention of production biology is directed towards species representations that contain the largest mass of living material, as these are the principal nodes of manifestations of life. Zoocoenology is concerned, chiefly, with the forms of living material, and how these life forms are grouped along the massive flow of energy. The quantitative nature of this question is undeniable, yet it is even more certain that it is, firstly, a qualitative one. These are such fine nuances of animal associations that they cannot be approached by the major, not to say crude, methods of mass relations. Parasitology, for example, provides ample examples to indicate that a "small" mass can substantially disturb a much greater mass, and at the physiological level (Kotlan 1953). This would hardly be evaluated appropriately as a matter of mass relations, as the essence of the problem cannot be approached by this route. For this reason, the zoocoenological importance of characteristics of mass relations need to be re-evaluated and, therefore, we expanded the quantitative characteristics with the qualitative concepts of degrees of corrumpency, or of obstancy.

§ THE APPLICATION OF THE CHARACTERISTICS

To demonstrate the zoocoenological census methods and the use of characteristics, we use the following example.

The census location is a 7 ha field of sweet poppies belonging to the "Béke" Agricultural Cooperative at Nagykovácsi, and the zoocoenological category is a catenarium formed in the arvideserta biotope, on the energy source transformed from the oecus *Papaver somniferum.* To simplify the example, we omit the other semaphoront groups also caught there (that are obviously associated through the presocium).

The field census was performed weekly, starting after the first weeding of the poppies. During the census period, we distinguished four aspects of the catenarium: that of *Stenocarus ruficornis* (sprouting plants), *Apis mellifera* (flowering), *Neoglocianus (Ceutorrhynchus) maculaalba* larvae (development of the poppy heads), and *Aphis fabase* (after ripening). Only the last three appear on Plate II. The reason for this is the extraordinarily low abundance of *Stenocarus ruficornis* population (2 adults per 100 plants), and whose further development during the presence of the larval semaphoronts was not followed.

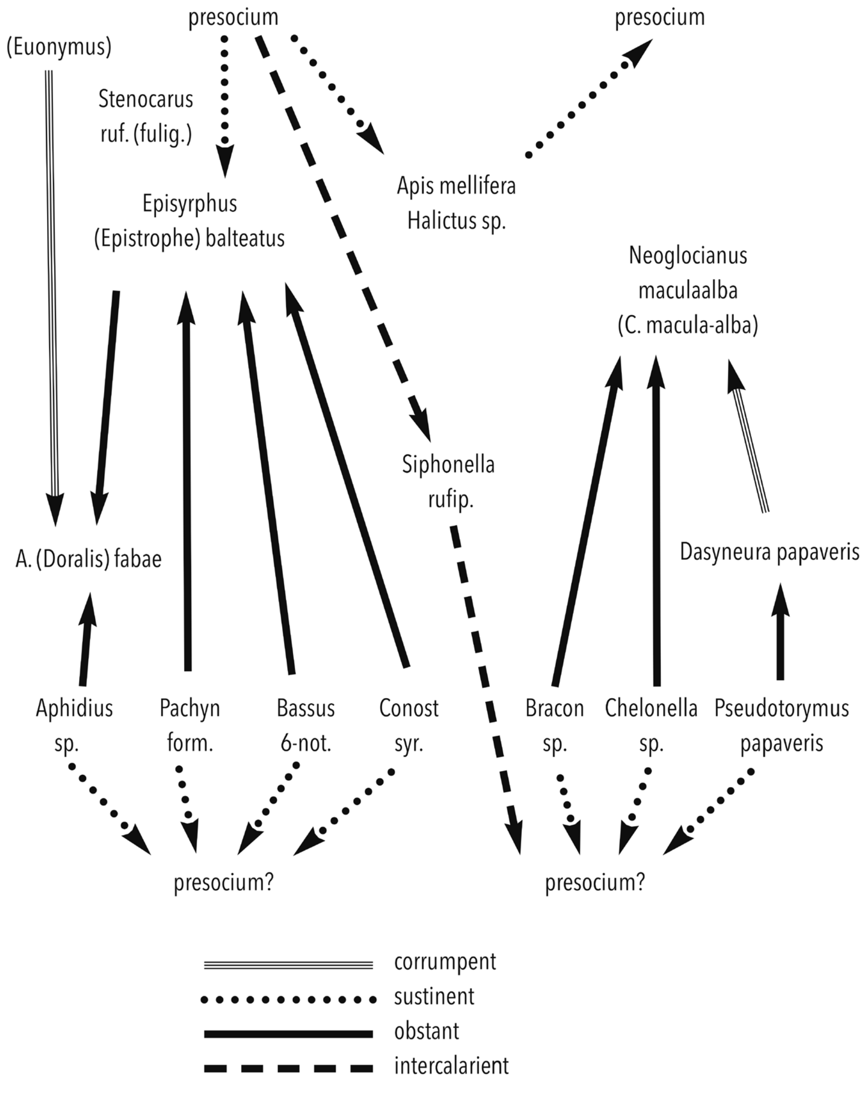
It follows from the appearance of the aspects, that a zoocoenosis is a process, composed of a series of events; a dynamic phenomenon during which both its quantitative and qualitative characteristics must change. The table aims to present this movement of the catenarium. To this end – deviating from the general practice – the data presented are not those obtained during the individual censuses, but those that convey the changes in the quantitative and qualitative characteristics within the individual aspects.

Plate II. The structure of the *Ceutorrhyachitena maculae-albae* catenarium at Nagykovácsi, 1954.

Species	Semaphoront group	Coetus	Abundance in aspectus*			Dominance in aspectus			Corrumpent degree	Obstancy degree
			I.	*II*	*III*	*I*	*II*	*III*		
A. mellifera	Adult	Sustinent	54			0.54				
***Halictus* sp.**	Adult	Sustinent	36			0.36				
E. balteatus	Adult	Sustinent	72		972	0.73		9.73		
	Larva	Obstant		1414			14.15			
N. maculaalba	Adult	Corrumpent	54		1232	0.54		12.36	reced	
	Larva	Corrumpent		1309			13.17		reced	
Dasyneura papaveris	Adult	Corrumpent	?		469			4.7	reced	
A. fabae	Adult+ larva	?	?	?	?	?	?	?	reced	
Siphon rufipes	Adult	?	?	-	34	-	-	0.35	-	-
	Larva	Intercalarient	-	34	-	-	0.35	-	-	-
***Bracon* sp.**	Adult	Obstant	-	?	19	-	-	0.19	-	-
	Larva	Obstant	-	(19)	-	-	0.09	-	-	1.45
***Chelon* sp.**	Adult	Obstant	-	?	56	-	-	0.56	-	-
	Larva	Obstant	-	(56)	-	-	0.56	-	-	4.27
Pseudotorymus papaveris	Adult	Obstant	-	?	2	-	-	0.02	-	-
	Larva	Obstant	-	(2)	-	-	0.02	-	-	0.15
Bassus 6-notatus	Adult	Obstant	-	?	344	-	-	3.45	-	-
	Larva	Obstant	-	(344)	-	-	3.45	-	-	24.32
Pachyneuron formosum	Adult	Obstant	-	?	1213	-	-	12.17	-	-
	Larva	Obstant	-	(1213)	-	-	12.17	-	-	12.23
***Aphidius* sp.**	Adult	Obstant	-	?	125	-	-	1.25	-	-
	Larva	Obstant	-	(125)	-	-	1.25	-	-	?
Conost. syrphi	Adult	Obstant	-	?	150	-	-	1.51	-	-
	Larva	Obstant	-	(150)	-	-	0.51?	-	-	1.76
Total	27	4	216	5135	4616	2.17	51.52	46.31	-	-

* Aspectus I: *Apis mellifera* (flowering); Aspectus II: *Neoglocianus maculaalba* (poppy head maturation); Aspectus III: *Aphis fabae* (after head maturation)

Plate III. The structure of the catenarium *Ceutorrhynchiarium maculae-albae* (Nagykovacsi, 1954).



The values in Plate II refer to 1811 plant individuals. Some extrapolation was unavoidable, and our distrust towards such manipulations have been expressed earlier. We have to emphasise that the numbers presented are only of theoretical value, and the actual census numbers were modified, only to improve understanding. Our standpoint is unchanged: the size of the censused area must be identical for every population. There remain differences, following from the methodology that cannot be eliminated. The flower-visiting sustinents, for example, are impossible to census using the same method as we used for the poppy-head-living poppy seed weevil larvae. The abundance of the imagoes was established by examining 35,000 poppy heads, while those of larvae was based only on 300 of them. We censused the sustinents by walking along a line, and counted the insects momentarily residing on the flowers of 500 plants. The hoverfly larvae were counted by a detailed examination of 200 plants, and their obstant elements based on the pupae that were collected and kept in the laboratory. All of these figures were then converted to values for 1811 plants, to demonstrate a way to present the life forms and relationships of a zoocoenosis in a detectable way. The numbers appearing on the table, while true for weevil abundance, cannot be claimed for the other, less intensively studied populations.

Both abundance and dominance data are presented in three columns, according to the three aspects. The abundance values represent the number of individuals counted, but dominance was calculated based on the observed, or reared, numbers of individuals. Thus, a column shows, during the aspectus in question, what species representations were present, and in what numbers, on 1811 plants; the relevant dominance column indicates the % share of individuals during that aspectus (where 100% is the total no. of individuals found during the whole year). Individual columns, therefore, contain the number of co-occurring individuals.

The characteristic features of the *Apis mellifera* aspectus were the sustinent elements, but, now, the semaphoront group of *Neoglocianus maculaalba* also appeared on the scene. This is also the time of the first appearance of the *Aphis fabae* gynopedia on the leaves; these were not censused, thus the question mark instead of a number. *Dasyneura papaveris* also appears, although it must have been present, because its adult semaphoront can only lay eggs in poppy heads opened by the poppy seed-head weevil. This must happen at the same time as the weevil lays its eggs, because the wound on the poppy head closes quickly. The presence of the poppy seed fly is proven by the data from the subsequent aspectus when many fly larvae were found. This case also shows that adult-based censuses, in many cases, may paint a false picture of the real composition of a zoocoenosis. The square brackets around the numbers referring to the three sustinents in the first column, indicate that these are only temporary elements of the catenarium, as it follows from their way of life that the three semaphoront groups are associated via a presocium. Therefore, the presociumclashes with the studied catenarium, yet it plays a necessary role in its formation. The relevant dominance values – even though their census was made using different methods than for the endophytobionts – reflect the role that these populations play in the quantitative composition of the coenosis.

The main characteristic of the *N. maculaalba* aspectus is that the sustinents disappear, and most populations living in the oecus occupy the internal parts of the poppy plant. The presocium, therefore, leaves the catenarium that continues its development regardless. On the poppy plants, only the *A. fabae* populations are visibly active, while the other populations of the catenarium are endophytobionts, or even endozoobionts, and for their census, the methods used so far, are insufficient. It is striking, although an entirely logical phenomenon, that the abundance of the semaphoront groups *Episyrphus* and *N. maculaalba* greatly increases. This is natural, because each female lays many eggs, thus the number of larvae are, necessarily, higher than those of adults, which is a characteristic of every intra-cyclical dynamic. The initial abundance of adults is always lower than that of their larval progeny, but the latter will also gradually decrease (see "Artgleichgewicht", Schwenke, 1953). Could we gain such an insight, even into the quantitative structure of this catenarium, not to mention other features, had we only censused the adult semaphoronts? This is obviously impossible, as a collection using sweep nets, or sampling quadrats, would have lead, unavoidably, to the result that the poppy seed-head weevil disappeared without a trace after flowering, leaving only the aphids with a noticeable population. From this, it also follows that a full census of a zoocoenosis is only possible by applying a multitude of census methods, even if their comparison, due to the methodological differences, can only be imperfect. In our case, it became clear that the seed weevil's disappearance was not real, and its larval semaphoront is really active at a higher abundance; we also detected semaphoront groups that we had not registered during the previous aspectus – even though they were present, but below the detection threshold.

The obstant elements connected to the larvae of *N. maculaalba* are, obviously, already active in the aspectus, as well as the endozoobionts of the *A. fabae* population. We only censused them during the subsequent aspectus, but also indicated their presence here. The parenthesis indicates that these are not data obtained by direct studies, but retrospectively from the values found during the *A. fabae* aspectus. We have to assume that they were also active during the preceding period, and it is likely that their number washigher, as these obstants are not exempt from various mortality factors.

Accordingly, the dominance values of the larval aspectus of the *N. maculaalba* increased. While the dominance value of the first aspectus was 2.17, this jumped to 51.52 during the second aspectus, indicating that this is the most dynamic stage in the life of the catenarium. Had we not considered the endophytobiont populations, most species would have to be deleted from the list, which is not permitted from an ecofaunistic point of view and, in zoocoenology, it does not make sense. Merely, a semaphoront has disappeared, but not the species itself that continues to be present, only represented by a different semaphoront. The obstants whose data are in parentheses, were already there, thus we cannot omit them. The futility of a viewpoint from production biology is exemplified in Woynarovich's (1954) opinion, who states that the ecto- and endoparasites are on the same level as their host. From the perspective of energetics, this cannot be faulted, yet it is unacceptable to a zoocoenologist, because what occurred here is very important form a synphysiological viewpoint: from a corrumpent, we gained an obstant and, during the flow of energy and material, both the life form and species representation have changed. The material, and the enclosed energy, now serves the aims of a corrumpent, and would have served a totally different purpose if it remained within a corrumpent element, because it would have contributed to the opening of a plant-based food source. The same energy now helps to complete the development of a completely different life form, which is no longer linked to the plant cover but, sooner or later, will link with a corrumpent. In the first case, it would have ended up in the soil, as a poppy seed weevil, where it would have rested inactive for many months; now, instead, it is incorporated into an obstant, which, during its adult semaphoront may have played a sustinent role, only to later establish a relationship with a totally different corrumpent. As a poppy seed weevil, it may have served as an energy source for an obstant population, but now it enters a completely different oecus, and plays a different role there; thus, the accumulated energy flows through different channels.

The *A. fabae* aspectus is the declining phase of the catenarium: the plant is maturing, then gradually dries; a part of the population enters a latent phase, other parts, as adult semaphoronts, change into presocium, occasionally reaching other catenae or catenaria. The dominance of *N. maculaalba* and *Episyrphus* decreases, as part of them became obstant elements. Data on the latter are again in square brackets because, as adult semaphoront groups, they cross into a presocium. The abundance and dominance values of *N. maculaalba* are also in parentheses, because they became latent. The *Aphis* also leave the drying poppy stand, where the obstants emerge and disperse, leaving the coenosis collapsed. The catenarium that will form during the next season continues by a thin thread: the population of the *N. maculaalba* and the larval semaphoront group of the *D. papaveris.* Their fate is unknown until spring, so we cannot say anything about the potential spring aspect that may form around them. It is likely that their diapause will not pass undisturbed, and they may possibly get into contact with obstants of some presocium and these, in turn, will temporarily link to the remaining, small core of the former catenarium.

Let us consider, briefly, the degrees of dominance and obstancy of the identified obstant elements. The difference between these two will express, reliably, the synphysiological roles of these populations. In general, the degree of obstancy will show higher values than those of dominance, except when there are several parasitoids in one host. We cannot say anything about the degree of obstancy of either *Aphidius,* or *Episyrphus,* because we did not census the host aphids.

It sounds odd that we talk about the formation and expiration of a zoocoenosis. We believe, though, that the above example throws light on the reality of this phenomenon. The associative needs that change with semaphoront groups causethe zoocoenoses to change, at least at the level of presocia and below; the dynamics – starting small – underpin a wave-like process of the species representation. Therefore, all zoocoenoseshave a stage (an aspect) that is richer than it was before, and will be later. In the life of poikilothermic animals, the cold season switches off any associative need. At the start of the cold season, the populations being in *de facto* association just "freeze" like a single film frame, keeping the status in which the paralysing impact found them. In this condition the zoocoenosis is indeed "stable", in which there is no change for months, unless a supersocion appears. Any change is triggered only by the weather. It is also known that several animals prepare for the winter, physiologically and behaviourally. This preparation often entails the suspension of any associations and, seeking out a place best fitting its ecological plasticity, the animals "retire" to overwinter.

All this means that zoocoenoses temporarily disappear, and then form anew.

VIII. AGROBIOCOENOSES AND THEIR ZOOCOENOSES

Can we speak of agrobiocoenoses at all, and can we call the cultivated areas biotopes, and their animal associations biocoenoses?

Several authors reply with a definite "no", which follows from making "balance" the criterion of a biocoenosis, and separating humans from the elements of the biocoenosis. We have already articulated our opinion about the concept of balance, now we must examine the role of humans.

As a preamble, we declare that we consider biocoenosis as any animal association that fulfils the criteria detailed in the chapter on biocoenosis, thus, also associations of cultivated areas. The only concession is that the biocoenoses influenced by humans will be called culture-biocoenoses (Balogh, 1953).

When culture-biocoenoses are defined as biocoenoses under continuous human influence, it becomes obvious that there are various degrees of influence, and the anthropogenic factors operating in culture-biocoenoses are active not only in cultivated fields and orchards, but, also – even if in milder form –, in meadows, forests, wetlands and watercourses, causing divergent changes there. We cannot draw a sharp line; humans have an impact wherever they settle. This is a most visible characteristic in forests, where all degrees occur from a minimal maintenance of a natural forest, to establishing a new plantation, including planting non-native species. As we leave a human settlement, where forest disturbance is highest, the impact diminishes with increasing distance. Can we draw a sharp line here and, if we cannot, are we justified in making the definition of a biocoenosis as dependent on human influence, or not?

The essence of the biocoenosis is not whether it is under human influence or not, but that it is an association of living things. This association can live, develop and undergo succession in the absence of human influence, and can do so without, or because of, human impact. The only difference is that, in the first case, we do not have to consider anthropogenic factors, while we must in the latter instance.

Rammner (1953) has, most recently, considered the question of a biocoenosis on areas under agricultural cultivation, and he concluded that these cannot be considered biocoenoses. We agree with the author that a biocoenosis is not a random collection of various animals and plants, but an association in which the organisms are connected by numerous links, most importantly trophic ones. We are not convinced, though, as to why a biocoenosis present in arvideserta should be excluded? The animal associations formed on cultivated areas cannot be called a random collection by any means, as even the plant stand is a very regulated result of the activity of a population of *Homo sapiens*, and the presence of the essence of a biocoenosis – the trophic chain – can be demonstrated.

Rammner set an impossible criterion at the centre of his concept of biotope and biocoenosis: “Eine Lebenstätte kann nur dann als Biotop bezeichnet werden, wenn für sie […] euzöne Arten bezeichnend sind und eine Organismengemeinschaft kann nur dann als Biozönose bezeichnet werden, wenn der von den Organismen besiedelte Raum einen Biotop mit Ökoklima darstellt, wenn in der Organismengemeinschaft für den zugehörigen Biotop ezuöne Arten (also Zönobionten oder Präferenten) vorhanden sind und wenn die vorgefundene Arten kombination durch Selbstregulation über längere Zeit erhalten bleibt.” (Rammner, 1953, 453)”. The concept of the “eucoen species”, as we have already pointed out, is an ecofaunistical one, and says nothing more than that there are areas whose fauna contains one or more species that are exclusive to that area. No one can doubt, though, that we could talk about the fauna of the same area, even if these were not forming a coenosis. In the zoocoenoses of such areas there will be stenoconstant populations that are exclusive to that area, but it is inaccurate to claim that there are no zoocoenoses amidst the animals living there, because it lacks stenoconstant elements.

If the essence of a biotope is that it is a space for life, this condition must be fulfilled also by an arvideserta, which obviously has life and, more so, this type of area is a necessary energy source for all human societies – which are dependent on it, and have close interactions with it. This biotope also has an ecoclimate and, even if Rammner states that the microclimate is dependent on the cultivated plant stand (with which we completely agree), this says no more than that the arvideserta does not have a uniform microclimate; more precisely an ecoclimate that shows the same values in all its parts. The same, however, also holds for less disturbed biotopes; the microclimate at the top of a forest is certainly different from that of the litter layer. And what can we say about the ecoclimate of a forest steppe?

Rammner is right to point out that the plants growing within agricultural areas do not grow there by themselves. Nonetheless, these remain producents, even if in a cultivated form and, as such, can and do serve as the basis of a biocoenosis. Their presence is only a mark of strong human influence, and we cannot declare this outcome to be “outside nature”.

Nothing justifies he lifting of *Homo sapiens* out of other natural phenomena (Glen, 1954). Humans are members of the biocoenosis, and cannot survive without it. Their activity extends to vast areas and, in this, is unparalleled among extant animals. Without human activities, domesticated animals would not exist, nor cultivated plants, and there would be no salt grasslands, nor fishponds, on the former flood beds. Under human influence, biotopes change but remain biotopes, and the biocoenosis can respond naturally, but it also remains a biocoenosis, with producents and along with all the other elements that are able to find their favourable life conditions. People keeping animals also grow plants, not only for themselves but also for their animals, and they use areas (biotopes) that are formed spontaneously. A zoocoenosis is formed around humans – a supersocion that includes, apart from humans, all populations that, whether corrumpents, obstants or intercalary elements, in their current life forms, depend on humans. This supersocion has a profound influence on all culture-biotopes. Rammner does not define these assemblages of organisms that populate the cultivated areas. Our attempt is that the only natural explanation is that the *Hominicion sapientis* has a property, and it includes everything that displays a human influence, whether exerted directly, or via domesticated animals. We cannot agree with Thienemann (1950) either ("man as an overarching organisational factor", p. 734), because, despite enormous mental powers, humans are still subject to the basic laws of nature and, so far, have been unable to change this. The *Hominicion sapientis* is not independent of the other elements of the biocoenosis; it is dependent, conclusively, on its sustinents and intercalary elements and, in the arvideserta, conflicts with *Arvicolaecion arvalis* – a struggle that must be won, to avoid an irreparable damage to its food base.

The view that places humans outside nature also led Schwerdtfeger (1956) to use the terms "biocoenoid" and "technocoenosis" to denote landscapes under human influence, denying their biocoenosis rank. We cannot see any structural difference between the two, and consider an ant hill, or termite mound, as much a phenomenon of nature as the cities of populations of *Homo sapiens*, which are their "habitat".

This step of declaring humans an organic component of biocoenoses may seem daring, or foolhardy, but it follows, unavoidably, from Linneaus's view that classified *Homo sapiens* as a species of primate.

This does not touch upon the mental superiority of humans, their social laws, their relationship to religion, science and art; yet their organismal needs link them to the totality of the biocoenosis, which they can modify according to their needs but cannot change its structure without endangering their own existence. Without a biocoenosis, cities equipped with all the achievements of civilisation could not be established, nor survive, and this biocoenosis puts its stamp on several aspects of the culture itself.

From this perspective, in culture-biocoenoses, it is impossible to see anything that differs, substantially, from biocoenoses where human influence is minimal. Production, the essence of biocoenoses, is undisturbed in agrobiocoenoses, which is confirmed, aptly, by the existence of a stable food base, that serves as an existential condition for humankind. Certain animal communities have unhindered access to these plant stands, which is reflected in the activity of corrumpents that, in turn, gives rise to plant protection. Therefore, we see no biological reason that the organisms living in culturally-influenced biocoenoses – more specifically, agrobiocoenoses – should not be considered as essentially similar biocoenoses to those living elsewhere. There is only one difference: the impossibility of succession, which provides the conditions necessary for crop plants to flourish.

In attempting to classify cultural biocoenoses, one should recognise that, because of human activities, the place of ancient, primer biotopes is occupied by secondary, culturally-influenced biotopes. Their biocoenosis is a cultural one, in which the producents are mostly cultivated plants, frequently of species that were introduced from distant lands. The corrumpents and obstants are, mostly, members of the autochthonous fauna, but also include domesticated and introduced species. If these biotopes are arranged according to the degree of human influence, it is obvious that the agrobiotopes are the ones that are most heavily influenced.

Among agrobiotopes, we count arvideserta, agrilignosa and, also – following Balogh (1953) – fish ponds, even if this may seem strange. Human influence can cease to operate, temporarily or definitively, in all three, in which case ruderal biotopes or biocoenoses are formed in the first two, that are not new formations, but ones that gradually return to the original biocoenosis determined by the biotope, unless they again become cultivated. According to Balogh, the essence of ruderal biocoenoses is that their production is not used, but remains *in situ*. This, however, does not always happen, so we would not make this a criterion of the ruderal biocoenosis, because their species composition can vary. In our definition, ruderal biocoenoses are associations where human influence has ceased, and succession restarted. Here we are faced with a conscious, directional human influence.

Hay meadows and grazing lands, as agrobiotopes *sensu lato*, deserve special attention because a unique feature is that their soil is not disturbed, unlike in other agrobiotopes. This difference is very important because, once human influence stops, instead of forming a ruderal biocoenosis, the community is enriched by the reappearance of species that are intolerant of regular grazing or cutting. The stand remains, only it becomes more species-rich. One can assume that the original ancient conditions will never return, unless the extinct plant species can recolonise from nearby refugia.

The third group of culturally-influenced biotopes are represented by areas where human influence is merely the introduction of species foreign to the biotope (for example, spruce in the Matra Mountains, or Scots pine plantations of the Buda Hills). These differ from agrobiotopes in that their soil is only disturbed – slightly – during the planting of the saplings, otherwise remaining undisturbed for a long period.

A few more words about the agrobiocoenosis *sensu stricto*. It be incorrect to consider the areas under dominant crop plants as separate biotopes, given that the whole arvideserta or agrilignosa is, essentially, under the same impacts; in the former, the crop rotation extends to the whole cultivated area. The individual fields are essentially groups of oeci, i.e. sub-biotopes, with characteristically different plant stands, and microclimate. The field edges and the grassy-bushy borders of orchards often do not belong to the arvideserta, and are not ruderal habitats either, but constitute undisturbed refugia of the original plant cover.

We hardly know the zoocoenoses of the agrobiotopes; perhaps their fauna is known but imperfectly; mostly those that specialise on various crop plants, plus parasitoids and predators that play a role in their limitation to various degrees. Therefore, a systematic analysis of agrozoocoenoses is premature; thus, the following are no more than rudimentary and, hence, somewhat daring sketches.

Although the populations of supersocion are dispersed among various biotopes, there is a difference between arvideserta and agrilignosa, because the former provides favourable conditions to species of mostly grassland origin. Therefore, *Arvicolaecion arvalis* is common in areas under agricultural cultivation, while *Talpaecion europeae* occurs in both arvideserta and agrilignosa. The bird populations of the supersocion are, incomparably, more species-rich from March to September than during winter when, in the agrilignosa, one encounters a supersocion with flocks of tits, mixed with woodpeckers, treecreepers and nuthatches, while flocks of crows walk the bare fields of the arvideserta. In the place of breeding birds that depart in the autumn, winter visitors fit into the supersocion. This supersocion also contains obstants of small populations, such as the sparrowhawk, goshawk, owls, fox, weasel, ferret, etc. Their zoocoenological relationships are scarcely known. The members of the supersocion are very mobile, roaming over a large area; fragments of their populations only reside in one place for no longer than a period of an aspect.

The presocia of arvideserta and those of agrilignosa differ more sharply, because the former is mostly herbaceous, while the latter contains mainly woody elements. The most constant presocia of arvideserta are the soil-living populations, from which *Agrioticium* or *Anisoplisecium* is formed, with species representations of *Agriotes, Anisoplia, Melolontha, Rhizotrogus, Dorcadion* spp. etc. The larval semaphoront group of *Agriotes* is often of clumped distribution, forming a characteristic *Agriotidicium segetis*. The *Dociostauricium maroccani*, forming on grazing lands, often extends to arvideserta, and, above them, the starling and the white stork are members of the supersocion.

In relation to the presocia on grazing land, studies by Nagy (1944, 1947, 1950) provide remarkable guidance, even if these are restricted to ecofaunistical studies of Saltatoria. Similarstudies were made by Marchand (1953) on the Saltatoria and Hemiptera fauna of various types of meadows. Both authors examined only a part of the zoon, and indicated an important effect of the microclimate ("even in the food specialists… the effect of food or availability of egg-laying sites is overshadowed by the dependence on microclimate"

Marchand, 1953, p. 142). Translating this to the language of zoocoenology, it means that there is no obligatory (proportional) relationship between a plant community and its zoocoenosis, at least quantitatively. The former, as a qualitative energy source, supports the development of the latter, but whether these really appear (and in what quantitative/or qualitative composition), depends on other factors, additional to the host plant impact. Based on the work cited above, we can assume that the identity of the plant association does not bring with it the proportional presence of food specialists, or zoocoenoses, because the energy sourceis not sufficient for this. The microclimate, influenced by the macroclimate (and possibly other, currently unknown, factors) will determine whether the expected zoocoenosis will appear, and to what extent. The warm-blooded members of the supersocion are probably less dependent on this than the poikilothermic populations, and with them, the other zoocoenoses, from the presocium down. The most important task of zoocoenology, and especially of agrozoocoenology, is to make the appearance of the expected zoocoenosis the central question. In practice, this means that the zoocoenoses must be followed for years, in the same plant community and the same place, because this is the only possible way to find out whether the assumed changes happen, and to what degree. This knowledge will make it possible to take the next step, to unearth the causes of the changes.

Concerning catenaria, through lacking the necessary quantitative surveys, we have no general picture. We attempted one such survey, using *Ceutorrhynchinarium maculae-albae.*

The pioneering ecofaunistical studies in alfalfa by Balogh and Loksa (1956) threw light on the composition of the catenaria, even though (because of their views) they included elements that belong to the presocia, primarily considering adults and totally excluded the endophytobionts. Even in this form, their carefully designed studies constitute an essential step towards the knowledge of catenaria that form in alfalfa. Móczár (1954) also studied alfalfa, restricting his investigation to the flower visitors, and making the fortunate step of studying the quantitative and qualitative composition of the sustinent coetus of the catenarium, making his studies very valuable for zoocoenology. He is also the first to provide data on the four coeti of the alfalfa catenarium. Studies of rye by Rabeler (1951) are more modest, at the level of fragments of ecofaunistical data.

We have rudimentary knowledge about numerous catenaria, but these are mostly restricted to the parasitoid fauna of singular corrumpents. In this respect, Sáringer's (1951) studies in *Oscinellaetena frit* are remarkable in that they show that in two, closely located plant stands, only one harboured a rich obstant coetus, which underlines the phenomena referred to above.

We are not in a much better position considering agrilignosa. We know that in our orchards, the *Aspidiotinarium persiciosi*, and on plum trees, the *Lecaniinarium prunastri* are, respectively, the most common catenaria and, that in mixed orchards, the former reaches the rank of presocium. We have the results of unpublished studies on Tortricidae, a few *Pyllonorycter* populations, and catenaria around *Cydia pomonella* and *Anthonomus pomorum*. To a large degree, however, our knowledge is restricted to selected obstant elements, but without clarification of their relationships to one, or more, zoocoenoses.

We also have studies that measure the consequences of human influence. These studies, though, are in their initial state; to a degree due to the recent impact on plant protection of fresh perspectives that lift this special field out of its current subordinate, and mosaic-like role. Plant protection, as a biocoenological science, has risen from an isolation to allow wider horizons. Even though we do not completely agree with Schwerdtfeger's (1956) somewhat cautious viewpoint (and completely rejecting his concepts of biocoenoid and technocoenosis), we acknowledge that his warning is justified. The mission of plant protection entomology is to assist in achieving higher yields; human actions directed towards this end, however, have biocoenotic consequences, and agriculture cannot reject their acceptance. The sustained existence of the agrobiocoenosis is vital for humankind, but the problems related to this aim are full of biocoenotic questions; in the first place related to plant protection, as indicated by the name. This being so, we can only get to the core of these problems if we interpret them in the framework of biocoenology; plant protection entomology is a biocoenological science.

CLOSING COMMENTS

All the above arguments are perhaps new and, in many respects, may seem daring. From the very beginning, our view of biocoenosis – the aim and methods of biocoenology – has been different from the dominant views of today. This brought with it the inevitable consequence of building a totally different set of biocoenological concepts. All the achievements of biocoenology, the immeasurable amount of work by biocoenologists to quantitatively and ecologically analyse faunas, can only attract the highest degree of appreciation from the author. This works and its results contributed to the formation of the author's views presented herein and, even if these views end up being contradictory, they do not amount to an underappreciation of the value of ecofaunistical studies, nordoubting their necessity. To pursue the aims of biocoenology, however, – and all authors agree on this – we need to press on, dig deeper, and start the useful and exquisite work of uncovering the linkages within biocoenoses. We are convinced that the emerging multitude of questions will be answered more reliably if we follow the path sketched here, rather than following the traditional route of faunal analyses. To this field of research, we invite those whose soul has been touched by the wonderful, great web of life; with this work, we would like to guide them along this path, where there is plenty to harvest but there are few harvesters.

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Note: items marked with a + sign indicate works which were not seen in the original.

Translator's note: we adhered to the reference style of the original. The changes with respect to the original include that Hungarian and Russian titles were translated, and Hungarian publication names were not abbreviated.

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X. GLOSSARY OF TERMS

Abiocoen – the non-living components of an environment, such as water, soil, air, etc.

Aciculilignosa – from Rübel's (1930) formation types. Lignosa = woody formation; aciculilignosa comprises aciculilisilvae (needle-leaved or coniferous forest) & aciculifruticeta (needle-leaved scrub)

Acoen – sub-categorisation (of eucoen) of animal association sharing the same space (Tischler 1947, 1950)

Aestifruiticeta – from Rübel's (1930) formation types; aestifruticeta (summergreen scrub), a plant association within the aestilignosa woody formations

Aestilignosa – from Rübel's formation types; comprises aestifruticeta (summergreen scrub) and aestisilvae (summergreen deciduous forest)

Agrilignosa – an agricultural woody formation (e.g. fruit orchard)

Agrobiocoenosis – a community of organisms that live on agricultural land

Agrobiotope – an agricultural habitat

Agrozoocoenology – study of the zoocoenoses of agricultural settings

Alieni – (= "foreigners") from Tischler's (1947, 1950) classification; a subgroup of peregrinant (wandering, dispersing) organisms in a spatially delimited zoocoenosis arriving from distant locations (see vicini)

Allogeneic – plant succession under external factors

Altherbosa – from Rübel's (1930) formation types. Tall herbage or forbland – from herbosa (herbaceous formations), also including duriherbosa (hardgrass prairie & steppe) and sempervirentiherbosa (evergreen grassland or meadow)

Arvideserta – lit. 'homogeneous cultivated field'. Soó (1945); vegetation of cultivated areas where all forbs and herbs are of a singles species

Aspect – season-dependent community, returning periodically

Associatio – term (Deegener 1918) for a social animal association where individuals do not have ethological links with other semaphoront groups

Association – plant sociological term (Balogh 1953) that mirrors a zoocoenological category; vegetation unit that may be defined by more than one dominant species in a layer

Associon – plant sociological term (Balogh 1953) that mirrors a zoocoenological category

Autecology – ecology of an individual species as opposed to communities (see synecology)

Autochthonous – describing an organism that is native to the place in which it is found.

Autogenous – a process, or plant succession, produced independently of external influence or aid

Biochor – used by Tischler (1947, 1950) for a microhabitat but also for a unit greater in size than a biotope by Hesse (1924)

Biochorion – a microhabitat

Biocoen – the living components of an ecosystem and/or biocoenosis

Biocoenoid – relating to landscapes under human influence

Biocoenosis (plural biocoenoses) – all the living organisms that form a community (plants, animals, etc.) living in a specific place at a certain time. It represents more than just the list of animals in a certain plant association, rather the interrelationships that bind the assemblage together

Biogeocoenosis – a concept above the biocoenosis that also includes all the effective abiotic factors that influence it, and are responsible for its appearance

Biogenetics – from biogenesis, the theory that all living organisms arise from pre-existing life forms

Biome – biogeographical term for a major regional ecological complex of communities (plant and animal) over large natural vegetation and climatic areas

Bionomics – the study of the mode of life of organisms in their natural habitat and their adaptations to their surroundings; syn. life history

Biontodynamics – an individual that provides material for functional studies

Biontogeography – the spatial distribution of the semaphoront in a biological system

Bio-ontology – comprises the combination of individual- and community-level organismal studies

Biontostatics – comprising the promorphology, eidonomy and anatomy of an organism

Bioregion – alternative descriptor for a zoon (Tischler 1947, 1950); a higher unit of biotope characterised by its faunal assemblage

Bioroph – a vertical division of the biotope (Thalenhorst 1950, 1951), equivalent of a stratum (Tischler 1947, 1950)

Biotope – a location (of undefined extent) that has a necessary set of environmental conditions that provides a place to live for a certain species or higher category of living organism

Catena (plural catenae) – a trophic chain, the basic unit of a zoocoenosis defined by trophic association. It can comprise monophagous corrumpent, sustinent or intercalary population(s), dependent obstants, waste-consuming intercalary populations

Catenarium (plural catenaria) – a group of catenae that are linked; the link is usually a non-monophagous consumer, but can also be a generalist predator

Choriocoenosis – a grouping of animals living on plant parts (Tischler 1947, 1950)

Coenology – the study of a collection of life forms that are found together, interacting as a community within an ecosystem.

Coenosis (plural coenoses) – collection of life forms that are found together, interacting as a community within an ecosystem. Beyond co-occurrence, a coenosis must include a functional connection between elements

Coetus (plural coeti) – structural elements of a zoocoenosis, represented by corrumpent, sustinent, obstant and intercalary semaphoronts

Connex – an equivalent term for catena (Friederichs 1930)

Consociation – plant sociological term (Balogh 1953) that mirrors a zoocoenological category. A plant climax community of natural vegetation dominated by one species; consociations can be grouped together to form an association. More often used in species-rich areas and sometimes where only the upper layer is dominated by a single species

Consocion – plant sociological term (Balogh 1953) that mirrors a zoocoenological category. A layer community with one constant dominant species or two co-dominant species – may be combined with any dominant species in other layers

Constancy – permanency; the continued presence of a species in an association

Corrumpent – primary consumer, a structural element of a biocoenosis. A plant or animal that utilises other living plants.

Culture-biocoenosis – a biocoeonosis influenced by humans (Balogh 1953). Syn. agrobiocoenosis: an association of species living in cultivated areas

Duriherbosa – from Rübel's (1930) formation types; terriherbosa herbaceous formation of hardgrass pairie and steppe

Ecofaunistics – the qualitative and quantitative study of a zoon. Ecological faunistics: a taxonomic list of the fauna of a habitat; a qualitative one only that includes a list of species present and may include quantitative measures e.g. abundances. The mutual relationships of the organisms present is not considered

Ecotop – a term for part of the biotope (Vite 1951) referring to the area used, daily, by a semaphoront

Eidonomy – considers the shape, size and colour of entire organisms as well as their substructures, such as body attachments. The characteristics relate to the way of life of the organism, helping to establish its ecology

Emersiherbosa – from Rübel’s (1930) formation types; aquiherbosa herbaceous formation of marshland

Endophytobiont – an organism that feeds internally on a plant

Endozoobiont – an organism that feeds internally on an animal

Episite (Episitic) - secondary consumer able to complete its life cycle by devouring a succession of victims.

Eucoen – animal associations sharing the same space as opposed to forming a trophic association (Tischler 1947, 1950)

Euconstant – a division of constancy denoting ‘real’/’strong’ constancy (Tischler 1947, 1950)

Eurichron – relating to season-dependent change (aspect) in an animal community where a sub-permanent population remains active during the whole period

Euriherbosa – a broad range of herbaceous plant communities replaced by agricultural activity

Euryconstant – animal population(s) able to tolerate conditions in more than one biotope; may be present constantly in many habitats

Euryfidel – related to how strongly linked an animal population is to a specific biocoenosis; euryfidel populations may have equal fidelity to a wide range of habitats/conditions

Faunistics – a study of fauna

Faunula – (diminutive of fauna) a subset of the fauna

Fruiticeta – an intermediate stage of succession between grassland and woodland, featuring shrubs and bushes

Gradocoen – a coenosis that develops in response to, or around, a gradation

Gradology (Gradological) – the study of gradations, i.e. mass increases in density

Gynopaedia – aggregation of larvae around mother organism (usually an aphid)

Heteroconstant – connectedness of an animal population to a biotope; only present at a given time (see euryconstant)

Heterofidel – related to how strongly linked an animal population is to a specific biocoenosis; heterofidel populations are only present at certain times in a community (see euryfidel)

Heterosynphagium – term for animals of different species that congregate on the same food source (Deegener 1918)

Hilophagous – wood-eating organism

Hospitant – a structural element of an animal assemblage; an occasional visitor

Hyemalis – during winter, a seasonal change in an animal assemblage related to winter-flowering plants

Hypotagology – the study of the environmental relationships of an individual and species, including autecological and ethological considerations

Idiobiology – the biological study of individuals

Indiginae – a classification (Tischler 1947, 1950) of structural elements of a spatially defined zoocoenosis, comprising corrumpents, obstants and intercalary elements

Intercalary – structural element of a biocoenosis; plants or animals that use non-living organic materials

Konnexus – the fauna of a small single environment, Balogh's category for synusium and faunula

Lignosa – from Rübel's (1930) formation types; a 'woody' habitat with trees

Merocoenosis – a grouping of animals living on plant parts (Schwenke 1953

Merotope – a structural part of the biotope (Schwenke 1953)

Mezochron – relating to season-dependent change (aspect) in an animal community where a sub-permanent population remains active during a long part of the vegetation period, although not the complete duration (Balogh 1953)

Microbiocoenosis – a division of a biotope containing a special association of species that is part of the overall biocoenosis

Mobilideserta – from Rübel's (1930) desert formation types; 'moving deserts', refers to vegetation of dunes and unstable soils

Obstant – zoophagous populations that are structural elements of the zoocoenosis, may be directly predatory or parasitic on herbivores and/or their episites and hyperparasites

Oecotope – a term for part of the biotope (Vite 1951) referring to the area used, daily, by a semaphoront, syn. oecus

Oecus (plural oecuses) – from Greek 'oikos'; the location where an organism lives

Ontogenetic – the entire course of an individual's development and life history

Ontopopulation – an aspect-related phase of a population that can endure conditions in different biotopes at different times

Ontostadium – period of activity of a life stage of an organism related to a temporal aspect

Peregrinant – lit. 'wanderer', a 'tourist' in current ecology; transient structural elements of the animal assemblage in a zoocoenosis, having no relationship with other association members

Physiognomic – the overall size and shape of an organism. Descriptions such as 'trees', 'shrubs', and 'herbs' are frequently used for plants

Physiography – relating to the physical geography that affects a zoocoenosis

Phytocoenology – the study of plant associations

Phytocoenosis (pl. phytocoenoses) the whole body of plants occupying a specific habitat; a plant association/community

Plant sociology – the study of plant associations

Presocium – higher level category of spatial association comprising animal populations that use energy sources from more than one catenarium

Producent – the basic structural element of a biocoenosis; the primary producers, either by photo- or chemosynthesis

Promorphology – a component of morphological research, part of bionostatics that relates to the study of the organization of the egg, especially regarding localization of subsequently developed embryonic structures

Pro tempore– (lit) 'for the time being'. Structural element of the animal assemblage of a biocoenosis that do not form part of the food chain, whilst living in extended – yet temporary – contact with a member of the zoocoenosis

Pterophytes –ferns

Recuperant – a group of intercalary elements (Woynarovich 1954) that live on carcasses or resources shed by other animals

Reducent – structural element of a biocoenosis; organisms that decompose organic matter

Rupideserta – from Rübel's (1930) formation types; desert formation comprising the vegetation of screes, talus, etc. Slopes formed by the accumulation of rock debris.

Saxideserta – from Rübel's (1930) formation types; desert formation of vegetation on rocks, tree trunks

Segetal – plants ('weeds') growing amongst crops

Semaphoront – a life stage of a species. The smallest zoocoenological element of a biological system, narrower than an individuum, a semaphoront represents the stages or changes of the individuum

Sempervirentiherbosa – from Rübel's (1930) formation types; herbaceous vegetation of evergreen grassland or meadow

Sociation – an association, categorical plant sociology equivalent (Balogh 1953) to zoocoenological term for an ecological association that is usually rather stable and of essentially uniform composition

Societas – an association or society; term (Deegener 1918) for a social animal association where individuals have ethological links with other semaphoront groups

Spermophage – specialised monophagous corrumpent feeding on developing seeds

Statio – a sub-division of the biotope; the spatial area of interest needed by an animal species to satisfy all life stage requirements

Stenochron – term for animal sub-permanent populations that are only active in certain times of the year in each (narrow, or well-specified) vegetation period

Stenoconstant – animal populations tied to a specific biotope but always present (i.e. constant)

Stenofidel – animal population strictly linked to one community in a biocoenosis and displays high fidelity to that community

Stenotopic – animal population that is zoocoenologically linked to a single biotope

Stratocoenosis – a coenosis of animals that only occur at a certain level (stratum) of a plant association (e.g. only living on roots) (Tischler)

Stratum – “layer”; a vertical division of the biotope (Tischler 1947, 1950), equivalent of a bioroph (Thalenhorst 1950, 1951)

Supersocion – an animal associational category above the presocium, and the presumed limit of animal communities that unites food chains with energy sources of a whole biotope

Sustinent – (sustaining) structural element of a biocoenosis; plants or animals that underpin the survival of others as symbionts or reproductive agents (e.g. pollinators)

Synbiology – study of biology at the level above populations

Synchorology – the study of distribution of plant communities, phytosociological zones, vegetation and geographical complexes

Synchronology – the study of changes in associations through time

Synecology – the study of ecology at the level of the associations/community, i.e. above populations

Syngenetics – field of research in plant sociology and zoocoenology that examines developmental history of associations

Synmorphology – field of research in plant sociology and zoocoenology that examines structure, composition and organisation of associations

Synphysiology – study of metabolic processes of plant species and communities in competition

Syntaxonomy – system of associated categories of vegetation units of a given area as understood by phytosociologists

Syntrophium – equivalent of a guild. Organisms with similar feeding habits in a specific habitat.

Synusium – a structural unit of a major plant ecological community characterized by relative uniformity of life-form or of height. Used by Balogh for animal associations of a bioroph

Syrmatophagous – feeding on dry plant material

Technocoenosis – an association created by humans

Terriherbosa – sub-division of Rübel’s (1930) plant formation types; herbosa (herbaceous formations)

Tocogenetic – of or concerning the relationships between individuals in a species to describe the ancestor-descendant relationship, as from mother to daughter across generations (Hennig 1950)

Transformatum – biomass produced from inorganic components (i.e. transformed from those) Also termed ‘assimilatum’

Tychcoen – sub-categorisation (of eucoen) of animal associations sharing the same space (Tischler 1947, 1950))

Valence – valency; tolerance limits

Vicini – (= neighbours) from Tischler’s (1947, 1950) classification; a sub-group of peregrinant organisms in a spatially delimited zoocoenosis arriving from neighbouring locations (see alieni)

Xenocoen – species that are foreign to the discussed community; they are adapted to other biotopes, they cannot live continuously and reproduce in the said biotope

Zoocoenology – study of animal associations

Zoocoenosis (plural zoocoenoses) – animal associations

Zoon – animal assemblage component of a biome (Tischler 1947, 1950)

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