



What has become of our cenosis¹? For a renewed cenology

Benoît Vincent

Paris, France

Corresponding author: Benoît Vincent (benoit.vincent@amboilati.org)

Subject editor: Daniela Gigante ♦ Received 3 January 2021 ♦ Accepted 7 December 2021 ♦ Published 31 December 2021

Abstract

An opinion paper that tries to show that the concept of cenosis has been withheld over time, seeks to understand the reason why, and aims to rehabilitate it. Different definitions of biological and ecological communities types are then proposed. Finally, the paper presents some possible paths for a renewed science of cenosis (or cenology, or biocenotics).

Keywords

biocenotics, biocoenotics, biotic community, cenosis, coenosis, epistemology, phytosociology

Overture

‘These ambiguities, redundancies and deficiencies remind us of those which doctor Franz Kuhn attributes to a certain Chinese encyclopaedia entitled Celestial Empire of benevolent Knowledge. In its remote pages it is written that the animals are divided into: (a) belonging to the emperor, (b) embalmed, (c) tame, (d) sucking pigs, (e) sirens, (f) fabulous, (g) stray dogs, (h) included in the present classification, (i) frenzied, (j) innumerable, (k) drawn with a very fine camelhair brush, (l) et cetera, (m) having just broken the water pitcher, (n) that from a long way off look like flies’ (Borges 1952).

Historical and epistemological background

In 1950, the French National Centre for Scientific Research (CNRS) organised a congress with 29 participants, including 16 French and 13 (mostly German-speaking) foreigners. This congress can be described as remarkable

(Acot 1994) for two reasons: it is one of the very first in history to be thoroughly dedicated to ecology, and not, as was the case until then, brought together as a set of interventions within an ecological section in zoology, botany or geography congresses (or even as an ecological society annual meeting). The other reason is more directly theoretical: the colloquium focused on ecology since this science was growing in Europe in the wake of historical natural sciences, for which phytogeography had become the essential conceptual reservoir that would gradually lead to talk of *biocenotics*.

Thus, the symposium presented a peculiar point of view beside the contemporary concept of ecosystem, which would soon become the main one on both sides of the ocean and fundamental in the history of the discipline. As we know, the term ‘ecosystem’ appeared in the pen of the British ecologist Arthur Tansley (1935), in a paper significantly entitled ‘Use and abuse of vegetational concepts’. The spread of ecology in the United States, where phytosociology had always been viewed with suspicion, would consolidate the dominant place of the ecosystem as a singular entity with circulation of matter and energy. Shortly after that congress, in 1953, the famous manual

¹ The specific writing *cenosis* is here used on purpose by the author, to avoid ‘unpronounceable and unwritable umlauts or ligatures’, as Klugh (1923) stated for ‘biocenosis’, a word introduced by Möbius (1877) written ‘biocoenosis’.

edited by the Odum brothers '*Fundamentals of Ecology*' (1953) was published to popularise the American vision of the young discipline among generations of students (it is sometimes spoken of as '*Odumian*' ecology).

Be it will or intuition, it was therefore for the organisers and participants of the Paris congress to move away themselves from the 'ecosystem approach' and to promote developments from their own point of view, i.e. that of *cenology*, at the time essentially dedicated to plants, and with the ambition to generalise it to the other great kingdoms of life, animals in particular.

It should be pointed out, as Jax (1998) remarkably shows, that a concept similar to the one of ecosystem existed in Europe, and could have completely supplanted it, if not fed by an organicism held in suspicion by the scientism of the beginning of the 20th century. It is that of 'holocenosis' or 'holocoen' coined by Karl Friederichs and clarified again and again until his death in the 1960s (e.g., Friederichs 1958). It was also very close to the concept of 'biogeocenosis' coined by Vladimir Sukachev (e.g., 1942) with the help of the concept of 'biosphere' from Vladimir Vernadsky's (e.g., 1930). Figure 1 shows a synthetic proposal from the 1970s by the malacologist Jürgen Jungbluth (1978).

As Pascal Acot suggests (1994), post-war continental ecology was at the crossroads between three different thoughts:

1. *Human ecology*, born from a development of Paul Vidal de la Blache's human geography; particularly dynamic in the US (with Chicago school), it gradually declined in sciences, and social sciences, as a subject of widespread suspicion (cf. Halbwachs 1932).
2. '*Odumian*' ecology, which tended to consider a closed zone of nature environment (typically the lake) as a perfect subject for exchanges of energy and matter studies (see e.g. Forbes 1887, Cowles 1899, Lindemann 1942, etc.); the term 'ecosystem' was soon considered as the 'minimal unit of ecology', and as a kind of productive machine. This view grew up, as to embody the whole ecology itself; it naturally led, by a troubling analogy, to an economic or 'resourcial' approach², also clearly consolidated with the contribution of statistics, which was soon to explode thanks to improvements in computer science.
3. *Phytosociology* (which could also be called *phytocenology*), finally, or description and classification of plant communities, whose roots are twisted in classical phytogeography (Alexander von Humboldt, August Grise-

bach, Auguste Pyrame de Candolle, and so on) and the old conception of the *formation*, as a link between a set of vegetation types and a landscape organisation.

Phytosociology took off and quickly became somehow independent of the ecosystem approach, particularly under the impetus of the Station Internationale de Géobotanique Méditerranéenne Alpine (SIGMA, hence the word 'sigmatist') where Josias Braun (soon Braun-Blanquet, originally from Zurich, hence the name of 'Zurich-Montpellier' school³) was starting to stabilize concepts and methods (Braun-Blanquet 1932, 1964).

If concepts and methods of phytosociology began to infiltrate zoology in the 1950s, questions about animal communities are obviously much older. Biocenotics (or synecology, as it is also called) was a topic in full swing from the first part of the century (e.g. Gams 1918, Du Rietz 1921, Phillips 1931, Taylor 1935), but especially from the 1950s until the 1970s. Several theoretical statements were published, as for instance, the ones of Mörzner Bruyns (1950), Tischler (1950), Rabeler (1951), Gisin (1951), Grassé (1951), Quézel & Verdier (1953), Rioux (1958), among many others. An important reference is certainly Whittaker (1962) who produced an impressive synthesis of the question of biological communities, with an massive bibliography. The proceedings of another historical congress, which was held in 1960, were published under the direction of Reinhold Tüxen: '*Biosozologie*' (Tüxen 1966). In 1971, a handbook written by Pierre Vignes and Roger Molinier was published, the only one of its kind: '*Ecologie et biocénologie*' (Molinier & Vignes 1971). Unfortunately we must observe that, except in the field of phytosociology, biocenology seems to be outdated. And the ecosystemic point of view will soon dominated all the fields of ecology.

Of cenosis

Ecosystems or biomes ?

Acot & Drouin (1997) expose the progressive ingression of American theories of ecology within the European institution. At that times, a conceptual dispute divided the scientific community between Frederic Clements' position (e.g., Clements 1916, 1936), and Henry Gleason's one (e.g., Gleason 1926, 1939). To summarize roughly, for the first, the plant formation can be seen as a whole body, a complex 'super-creature' made of each species working

2 I use this awful term in the sense of the 'ecosystem services' thought endorsed initially by the Millennium Ecosystems Assessment (MEA), which every naturalist must consider aberrant and irrelevant. Although the word is unfortunate, I shall henceforth use it to refer to 'that which is a resource (natural or other)'. See for example Nahrath & Gerber (2014), who translate it like that in their English abstract.

3 Among other schools like the important 'Uppsala school' (Robert Fries or Gustav Einar Du Rietz) in northern Europe: based on the same phytogeographical collection, but with a more physiognomic vision, independent of strict floristics, that was, therefore, more in line with the 'ecosystem' thought (and in which it will be more favourably received); of course its supporters curtly rejected Clements' vision.

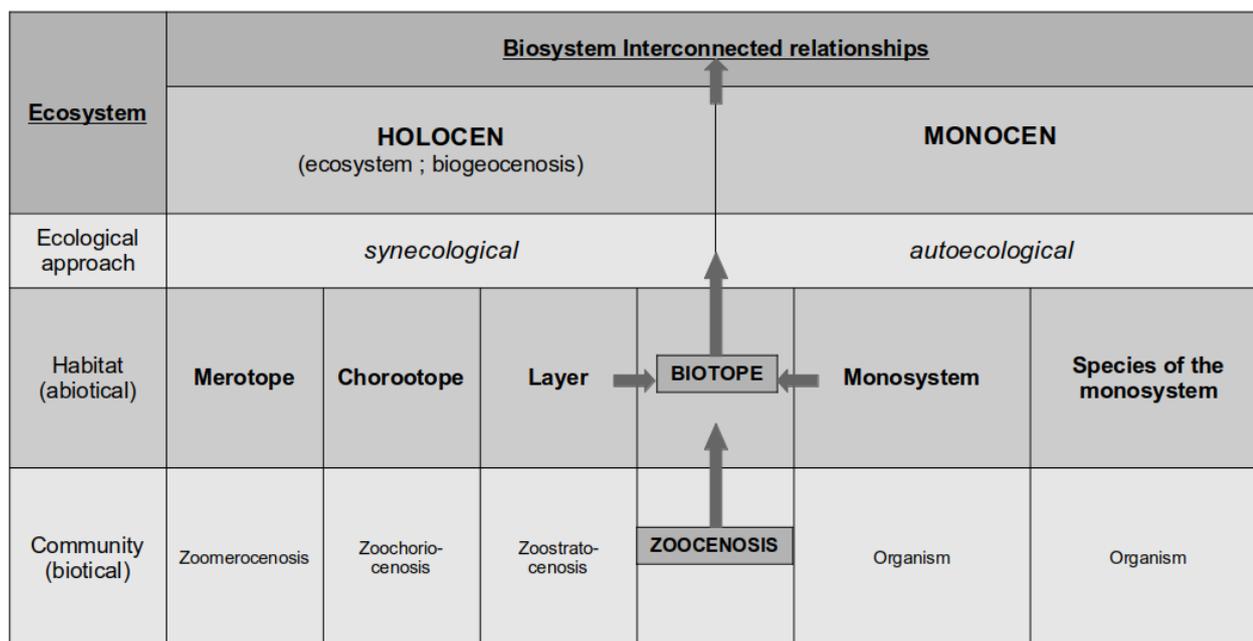


Figure 1. The ‘Ecosystem’ structure proposed by Jungbluth (modified from Jungbluth 1978).

with the other ones; for the second, plants are randomly distributed on the globe as individuals fighting for their own survival. Tansley (1935), who had cultivated a long friendship with Clements, thought, like him (and his fiery disciple Phillips), that some peculiar relationships exist between different species in the same place. Reluctant to consider the biome as an autonomous whole, which was far too transcendent to him, he sought and found a worthy exit out of the debate, and coined the word 'ecosystem'. This is not the place to review the whole debate, but in order to see how this opposition has been understood, and how its reception changed over years, let's recall e.g. Westhoff (1951), Poore (1955abc, 1956, 1962), Whittaker (1962, 1973, 1978), Westhoff & van der Maarel (1973), Werger (1974), Barkman (1978), Beard (1978), McIntosh (1985), Nicolson (1990), Hagen (1988, 1992), Journret (1991), Mirjin (1994), Palmer & White (1994), Golley (1996), Jax (1998), Nicolson & McIntosh (2002), Eliot (2007), Egerton (2009), van der Valk (2013), Guarino et al. (2018), Mucina (2019).

When Tansley (1935), proposed the new concept, in a way, and put an end to a long discussion, he sent Clements and Gleason back to back and, in doing so, he seemed to leave apart the concept of *biome* (created by Clements, like the one of *climax*), or more precisely, he sent it back to its origins: as a legacy, imagined by Clements, of the vague concept of formation, of ancient phytogeography (Grisebach 1838).

It seems that the ecosystem replaced the biome; it is defined by the association of a biotope and a biocenosis.

As we can see, the word cenosis is part of the concept, but it is relegated at the same level as the biotope – a term that appears to be very difficult to define today.

In fact, what I wish to emphasize when I argue that the ecosystem studies have taken over in ecological science, is that studies on the biotope, considered alone (often confused with ecosystem itself) largely dominate ecology: the observation, the description, the classification of cenosis appear today to be accessory, except for what concerns plants (phytosociology), and practically not considered at all for what concerns animals or other organisms (with few exceptions, like littoral bionomics or rivers cenosis).

It should be noted, moreover, that the biome, which may have become synonymous of formation, i.e. the great bioarchitectures (essentially vegetal, but not only) recurrent on the planetary scale, is no longer directly linked to the communities (vegetal or other) that compose it.

In fact, Braun-Blanquet and his successors would have full opportunity to imagine a classification of plant communities independently of it. The result, at the end of the 1950s, was a complex phytosociological system (which did not call itself phytocenological yet), separated from both ecosystem studies and biomes studies.

The first ambition of cenology should therefore be, on the one hand, to extend the achievements of phytosociology to other living organisms (to re-equilibrate the biotope with its whole biocenosis), and on the other hand, to try to define the articulation between synsystems (already existing with plants, still to come for other organisms)

and the classification of biomes: in other words, to articulate biocenology with biogeography⁴.

Between the two classifying systems, phytosociology synsystem and phytogeographical classification, thus, some kind of gap exists - which I described as 'quantum jump' (Vincent 2021a) - and we must keep this in mind in order to quietly consider the cenosis/cenology statement. It should be noted, however, that when Braun-Blanquet (1932, 1964) or Passarge (1966) were seeking for a maximum superior unit, they inexorably needed a 'physiognomic' (a phytogeographical) concept: the first one spoke of 'vegetation circle', the second, expressly, of 'formation'.

To achieve these objectives we mentioned above, it is first necessary to define the different concepts of groupings of living beings that are currently used.

Conceptual review and proposal of renewed definitions

There are many ways to classify species, and many groups can be proposed. They can be more or less precise, more or less imaginary, more or less arbitrary. We can separate for instance herbivorous from carnivorous animals, or perennials from annual plants, or black from white animals, or edible from non-edible mushrooms, and even animals that belong to the Emperor from those that broke the pitcher... Clades, communities, assemblages, populations, guilds, associations, synusia, etc.: all these terms exist, are frequently used and are more or less familiar to us, but they are also often mistaken for each other. Thus, many researchers regret the lack of harmony and precision. I shall consider a few examples to try to retrieve consensual definitions and measure why this confusion is still active: Wilson (1991, 1994), Keddy (1993), Fauth et al. (1996), Looijen & van Andel (1999), Lockwood (2011). All of them contain a huge bibliography on the topic.

One of these papers (Fauth et al. 1996), regretting the confusion observed between these different terms, where usage often associates certain terms to certain groups, denoting the conceptual 'weakness' of ecological science, attempted to synthesise 'once and for all' the different types of groupings. The authors argue that groups can emerge from different conceptual approaches, depending on the type of relationship or link the members of the group studied have with each other. They define three 'sets' of relationships, 'delineated by phylogeny, geography, and resources', which would be the three main types one can find in the literature: phylogenetic studies are concerned with the specific relationships between the members, geographical studies with the portion of space where mem-

bers are gathered, and resource studies with the grouping from the point of view of feeding, that is to say, for biological reasons, concerning metabolism - breathing is probably another side of the problem, however it is not mentioned (Fauth et al. 1996). They propose to represent those relationships in the form of a Venn diagram, which represents each of them individually, in a two-by-two overlap, and the central overlap of the three of them. I reproduce it in Figure 2.

The independent units, the first grade sets, are, respectively: taxon, community, guild. For the second grade sets: the taxon-community association (A+B) defines an 'assemblage', the community-guild one (B+C) a 'local guild', and the taxon-guild one (A+C) does not have a particular name, but can be characterised by the description of its components. Finally, the set composed of the three sets (A+B+C) is, for the authors, the 'ensemble'.

As a synthetic review, it is obvious that several questions need to be asked:

1. Is it true, or sufficient, that only three 'sets' are useful, and not less (or more) than three? In what follows, I shall consider that is the case (there is no place here to discuss to a higher detail).
2. In calling the synthesis of the three groups an 'ensemble', the authors use a term which, in addition to being vague, is nothing less than rare in ecology, not to say very original.
3. Finally, it seems to me disturbing, on the one hand to designate a set by a void (A+C), and on the other hand to designate another set (B+C) by a name already used elsewhere.
4. Moreover, no account is taken of *society*, *population*, *community* in the sense of 'settlement', even crowd, etc., other common terms in ecology, and of course *association*, *cenosis* or *synusia*. How can these problems be solved?

First of all, I propose to keep the term *community* (what stands for 'population' for the authors) for any biological group of organisms, as biological societies, in the Taylor's (1935) or Phillips' (1931) meaning, 'irrespective of its nature' (whether phylogenetic, geographical or resource), as stated by Mörzer Bruyns (1950). A synusia, an alliance, a life-form, or a clade should be considered as such (yet different) types of communities, and we'll see below how those communities can be articulated with each other. I should exclude this term from the diagram.

Let's review the other terms. The two-dimensions community defined by the overlapping of geographic and phylogenetic sets: as far as 'assemblage' is a random grouping of different species, and a vague term as showed by Looijen & van Andel (1999), I think it is not at its right

⁴ The topic here is the study of the biocenosis (within a biotope or not). For instance, phytosociology is willingly mobilised in current popular handbooks of description and classification of natural environments (French milieux), which also include typical animals - see e.g. Delarze et al. (2015), Terrisse (2012), Villaret et al. (2019): those are diverse from vegetation-only classifications (that I don't consider here), and present themselves as biocenosis guides (but sadly only from a botanic point of view: how to classify the milieux with no plants then?).

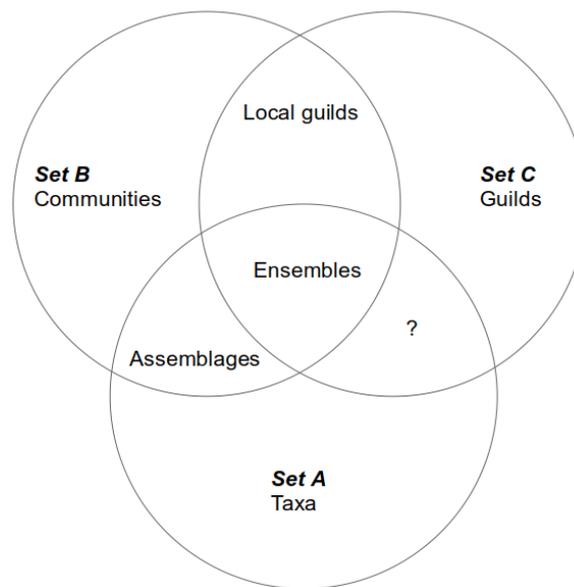


Figure 2. The three 'sets' of relationships defined by Fauth et al. (1996) in the form of a Venn diagram: 'Populations under study may be divided into three distinct sets'.

place: the species maybe part of the same clade (as in paleomalacological sense, like in 'quaternary tufa molluscs assemblage' studies) but it is not necessary (let's remind classic intertidal, or underground assemblages). The overlapping of geographic and phylogenetic community is clearly to me what is generally called a 'population' as in 'a population of hippopotamus', or 'of edelweiss'. Therefore, the term 'assemblage' should be reserved for the mere first grade geographical group: there is no phylogenetic and scarce trophic links (in sociology it may refer to *crowd* or *mass*, cf. Grassé 1951).

The second two-dimensions group, defined by both geographical and resourcial sets, is not easy to resume; but there is a French term that fits: 'peuplement', in the English sense of 'settlement' (as in an human sense it refers to a mix of various groups gathered together with an economic link). 'Peuplement' should be literally translated in 'community', which is not usable a second time. It is not very satisfying, but I keep the French term in the diagram.

Let's consider the third two-dimensions grouping, which is an empty space; this one is defined by both phylogenetic and resourcial sets, and is what I understand exactly as a 'guild'.

So here again, the replacement of terms calls for another word (for the resourcial set alone). But if we want to be very accurate, this metabolic, biologic function reminds of some kind of autoecological setting, as life-form. If acceptable, it would represent the best conceptual bridge between growth-form and life-form sciences (*sensu* Raunkiaer 1934) and applied ecology.

The new three sets should then be: resourcial > life-form; geographical > assemblage; and phylogenetic > taxon; even if the latter term is correct, I would prefer to use

'clade' (and keep 'taxon' in a linguistic sense: the name of a clade, whatever the rank be). Their crossing brings to population, peuplement, and guild.

The last step leads to qualify the set made up of all these elements. A community of organisms linked by phylogeny, sharing the same resources in a given space and time, isn't what we simply call... a *cenosis*?

To sum up, if we apply the arguments made so far to the Venn diagram of Figure 2, we obtain Figure 3.

One should mull things over, but it is hard to see how any community could be separated from one of the three dimensions: they are interconnected at the very root of both individual 'organism' and living 'creature'; it is the matter of their own being.

Communities can be studied at least from three different points of view: the phylogenetic one (cladistic > taxonomy), the spatio-temporal one (chorology and phenology: what we should call *territory*, considered in a dynamic sense, whose studies could be called 'choriology', on the model of Figure 1's 'choriotope': "science of territory", from gr. 'χῶρος', but distinguished from the prefix of 'choreology') and the resources one (metabolic > biological or autoecological; see in Figure 4 Barkman's three kinds of merocenosis).

But I retain that we must consider the cenosis as the real basic-unit of any community of living beings. In clear, there is little chance that any creature is not at least partly linked either to a family, a species, a space and time, or any kind of metabolic function as breathing and feeding. What I mean is that there is little chance that, in ecological studies, we easily escape a cenological implication, where ecological elements (synspecies) share the same 'household', and therefore the same clades, the same spatio-temporal dimensions and the same resources.

Science can obviously speak about one of the second-grade sets, and that is what exactly happens, and that is very useful for the plain knowledge of life beings. But it is also true that the constant difficulty of defining and naming these different communities may indicate certain problems of conceptual permeability. First, it is possible that 'groupings' overlap is due to organisms overlaps too or, to put it better, that individuals share different groups contemporary. This is the great problem of heterogeneity and boundaries pointed out by Looijen & van Anel (1999). That is: there is a distance between concrete group of individuals and abstract communities (and that is why these authors prefer to speak about 'community individuals', which is only part of the solution). Since groups, as any classification types, are a self-oriented, mind-constructed reality, confusion must be admitted as part of the problem: and the articulation between concrete and abstract realities is part of the question phytosociology fronts since its debuts.

Maybe the problem stands in the conceptual lack of rigour shown by scientists and researchers, as asked by the philosopher Lockwood (2011). It is possible, but it is still an incomplete reason, many researchers demonstrating a strong epistemological stature.

What is much less emphasised, however, and which is spectacularly obvious in the diagram (apart from the game of musical chairs between notions) is, above all, the total absence of one of them, the loser of the game: cenosis.

Why withholding cenosis?

Once we consider the cenosis as a logical minimal unit of ecology (rather than ecosystem), indeed, it's still quite surprising, and extremely revealing, to note that the field

of cenology has been gradually evacuated to the point where the term cenosis has become practically a rare and endangered one - whereas it seems to me to be the very foundation of ecology itself! Lockwood (2011) argues that it may be 'equivalent to 'community' but the ambiguity in use is such that the term is probably not a clear expression of a particular perspective', which is a clear statement of the actual situation (but not of the historical process). A simple research on any online library browser shows very significant results: on Google Scholar, the search of 'ecological guild' reaches 145,000 results, that of 'ecological assemblage' 475,000, 'ecological communities' peaks at 2,990,000, while biocenosis and cenosis respectively get 28,500 and... 4320.

Another noticeable clue is given by scientists' bibliographies: if specialists of the topic still refer to Clements, Gleason and Tansley battles, the whole school of the 1930s, the enormous continental European production of the 1950s is almost absent from the radar and nobody talks about great thinkers like Rioux, Rabeler or Mörzner Bruyns.

So, why have ecologists gradually abandoned the terms 'cenology', 'cenotics' and 'cenosis' (or have left them to botanists, which is the same thing)? Is it simply because of the confusion between roughly equivalent notions that they have gradually been marginalised? Probably not, since the others remain, on the contrary, prominently alive. It cannot neither be because the term itself is too complex. I therefore assume that one reason may be epistemological. What displeases or frightens the scientist is the part of subjectivity and interpretation in the observation, description and classification of life which formed the core of natural sciences in the past (until the 1970s) (Vincent & Catteau 2021; Cramer & van den Deale 1985). The development of statistics in ecology studies expresses the ever-growing positivism that nourishes science but

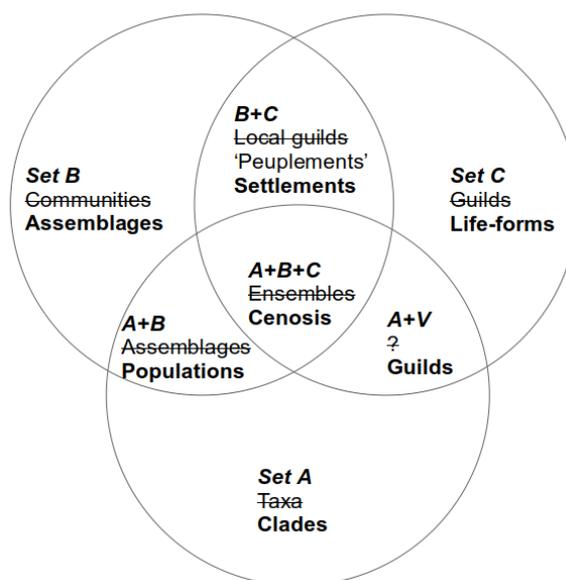


Figure 3. Modified version of the Venn diagram; A = household/species = clades; B = space-time = assemblages; C = resources = 'life-forms'; A+B = populations; B+C = settlements/'peuplements'; A+C = guilds; A+B+C = cenosis.

also society, obsessed by numbers and evaluation. By the way, the ever increasing use of statistics in phytosociology shows what could be called a notable epistemological bias, since phytosociology retrieves its own matter from statistical methods! To improve the synsystem viability and validity on the ground, as it's often the case with statistics tests, should not be the only task of phytosociology; it should be one of the methodological steps, but statistics must be considered as a tool, and never as a finality, as it seems to be nowadays. Statistical studies on various traits, but also gradients, patterns, and factors are much more about autoecology, and even biology, than synecology (another word for cenotics) and ecology.

Following again Lockwood (2011), the solution of such ecological and epistemological issues lies precisely in a perspectivist approach, balancing objectivity with subjectivity, calculation with interpretation (and I'd add: laboratory studies with ground studies). This predominance of numbers in ecological studies, the loss of inspired descriptions and theoretical interpretations are maybe the reasons why cenology increasingly declined. Factors, patterns gradients, traits, are all made of measurable quantitative information, but phytosociology, and biocenotics in general, as a morphophysics (de Foucault 1986) must point on qualitative information *first*. And this would resolve the other problems mentioned before, the ones of heterogeneity (the researcher decides which boundaries he states, in order to find a homogeneous milieu).

And the process is not over (as we see with old debates about phytosociology). In a recent issue of the journal *Naturae*, of the Paris Natural History Museum (MNHN), Yves Meinard and Gilles Thébaud even advised researchers, managers and naturalists, and I quote, 'avoid using taxonomic identifications' (Meinard & Thébaud 2019)! One cannot simply regret the lack of precision of the system or the difficulty of access to phytosociological resources (because this is not true). On the contrary, this strong stance tends to suggest a willingness to get rid of phytosociology's so-called stranglehold on current applied ecology.

Conceptual implications

If we agree that cenosis is the 'true' minimal unit of ecology, it remains to review the various conceptual problems of such an assertion. Indeed, very often, we do not measure the practical consequences of small theoretical arrangements, and we find ourselves either with tools that are unusable in the field, or with vague concepts that are all more or less synonymous.

I specify that these are reflections on the fly, and that I do not go into detail about these problems, each of which could be the subject of detailed and referenced notes. Especially, it is up to each specialist to define their own methods, the limits of their expertise field, and improve the rightful and useful tools directly on the ground - as I tried to do with malacocenosis problems in Vincent (2021b).

The problem of the clade

Cenosis is a grouping within a clade. It is up to the researcher decide the clade in which he operates; phytosociology operates within the *Viridiplantae* clade; generally it leaves apart algae, and sometimes also ferns. We sometimes find cenosis associating lichens and annual plants: as usual, this is not problematic since this choice is well defined beforehand but, technically, it seems as risky as associating frogs with fish or mammals (even if they are all tetrapods) (see Berg et al. 2020).

The problem of biological type and synusiae

This is no small problem because, even within the same clade, molluscs for example, further subdivisions can be found: Cephalopods can be easily distinguished from Gastropods; but in the latter, is it necessary to ask whether the *pulmonates* should be separated from the *operculates*? *A priori* no, but from another point of view, their way of life is totally different as concerns water resources! If we are interested in fishes, should we separate Chondrichthyes from Osteichthyes? *A priori* yes, but don't they form fairly a mixed group? And what about Cetaceans?

In fact, we can therefore ask ourselves whether we should not operate on the cenosis based on the notion of biological type (*sensu* Raunkier e.g. 1934)? This would mean, for example, that there would be groupings roughly comparable to strata or layers (for vegetation), but considered from an ecological point of view. This is where *synusia* comes into play, carried and defended by the alternating current of *synusial phytosociology* (Gillet et al. 1991; useful original definition in Gams 1918). The *synusia* proposed by 'sinusialists' are often (but not only) assimilated to biological types, being understood that the ecologies of annuals and perennials, for instance, cannot be similar, and therefore cannot be mixed together. It would then be a matter of determining the major biological types in animals, mushrooms, and else, which is no small task - especially as these probably differ more or less from one clade to another... (see Berg et al. 2020 again).

The problem of relations between systems

Many studies about zoocenosis try to link those zoocenosis to phytocenosis, but most of them conclude that it is not that easy, if not impossible, or even foolish. Indeed, 1) there are far fewer animal species in most clades (except arthropods) and it is probably impossible to get the same degree of precision such as in phytosociology; 2) many animal species are either extremely endemic or very common; and 3) big cenosis like certain vegetation types are at the same time inhabitants and habitats (for other cenosis): they are at the same time contents and containers - which is also the case for most organisms in relation to the world of bacteria.

There are two consequences of this: first, that all syn- systems should be built independently from the others, at least at the beginning of the research; second, that each system can be linked to each other to reach, at the end, but in another dimension, the biogeographical one.

For a renewed cenology

Philippe Julve has a habit of telling his interlocutors that phytosociology is like the music of Bach or Mozart: it is useless. This is a beautiful non-definition, because not only it insists on the arbitrary (i.e. linguistic, i.e. human) character of phytosociology as a classification, like any classification; but it also underlines the subjective part of the practice, the side that can be assimilated to a know-how or a talent (Gisin himself speaks of 'flair', cf. Guinochet 1973: 15, Chapter VIII & Conclusion), in any case to a personal creation, which may or may not be shared by peers.

Phytosociology is both an objective-subjective, theoretical-practical apparatus that is able to account for all the ecological dimensions of any living beings. If we want to speak of 'biocenotics', we will recall its main foundations and applications (Figure 4).

Definition

In order to reconnect with the original definition of plain ecology, we must define our topic. Molinier and Vignes (1971), for instance, after having stated that ecology (which they prefer to call 'ecobiocenotics') is the heir of environment ('milieu') studies and autoecological (biological) studies, claim that: 'ecobiocenotics results from the confluence of two great scientific currents [...]. It represents the culmination of the natural sciences known as 'field survey' [...] it could not be exceeded one day by a larger discipline. It constitutes a limitation towards which

tend asymptotically, voluntarily or not, all the efforts of the naturalists who devote themselves to the study of the environment' (Molinier & Vignes 1971: 7).

'Biocenotics' (also called 'biocenology' or 'synecology') seeks to observe and describe ecological communities called cenosis, based on their recurrent specific composition, on a given scale of a given clade; those cenosis can be structured within the clade in an integrative system ('synsystem'), with specific ranks, from microhabitat and synusia up to the higher ones.

Epistemology

Rioux (1958) rightly points out that 'biocenotics' it is the branch of ecology that is precisely interested in living beings and their relationships (he then speaks of 'ethological' ecology); it is opposed to what he calls 'mesological' ecology, which rather studies the flows of matter and energy (i.e. the 'ecosystem thought!').

'Ecobiocenotics' integrates the system of biology, according to Gams, Du Rietz, etc. Gams (1918) stresses that there are four fields in biology: the relationship between species and between species and the environment, classification, distribution, history; these fields are considered either from a static point of view or from a dynamic point of view.

It relies on biogeography, which describes the great formations, or biomes. There is a meeting point (which is a tipping point) between the two, and it usually concerns what many ecologists or botanists call 'formation' and what I call elsewhere (Vincent 2021a) a 'biocen', i.e. the sum of all the biocenosis, within a biome.

It is thus also a synthesis (Gams 1918: 298; Rioux 1958: 129; Mörzner Bruins 1950: 1-3); of the knowledge of cenosis according to their singular features, that is to say, in the fields of systematics, genetics (or phylogeny), choriochronology, ethology, physiology, morphology (Table 1).

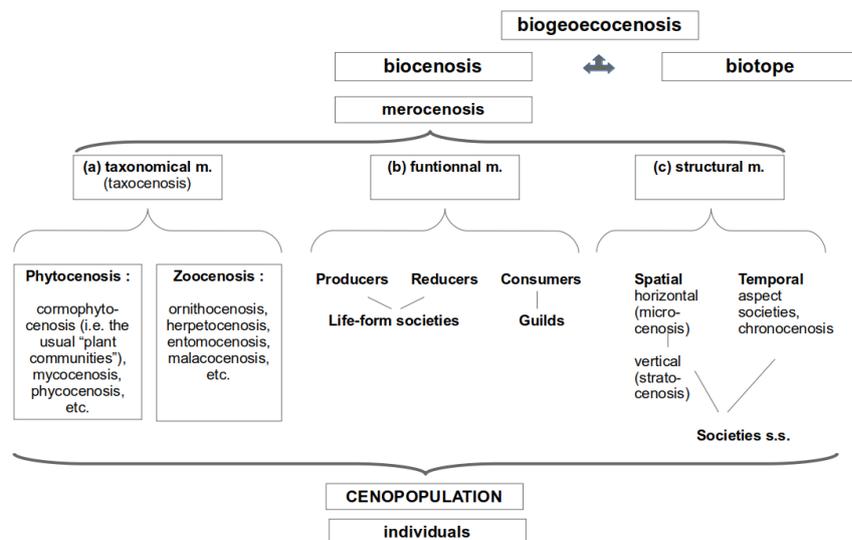


Figure 4. Barkman's cenosis system (modified from Barkman 1978).

Methods

I will conclude with a few words about the spirit of the methods, which each cenologist can adapt according to the considered clade. It is inspired by phytosociology, which duly and regularly improved it. It is a structuralist

method, that involves different stages: field and laboratory, analysis and synthesis, objective and subjective phases. This last point should not be surprising: the whole part of creativity, but also of imagination, but finally of interpretation requires this flexibility and sharpness that only the human eye and brain are able to provide (Figure 5).

Table 1. The system of biology (modified, from Gams 1918).

	I. Science of the single organism = Idiobiology		II. Science of organism communities	
	static	dynamic	static	dynamic
A. Relationship of elements to each others and to environment	morphology	1. physiology 2. autoecology	qualitative and quantitative analysis of the community	1. symphysiology (= science of correlations) 2. synecology s.str
B. Division of the multitude	morphological systematics	autoecological systematics	biocenological systematics (topographical systems)	synecological systematics (ecological systems)
C. Geographical distribution	science of species spatial distribution = autochorology	science of species movements = epiontology s.str.	synchorology	science of local successions
D. Temporal distribution	stratigraphics = autochronology	phylogenetics	synchronology	science of temporal successions

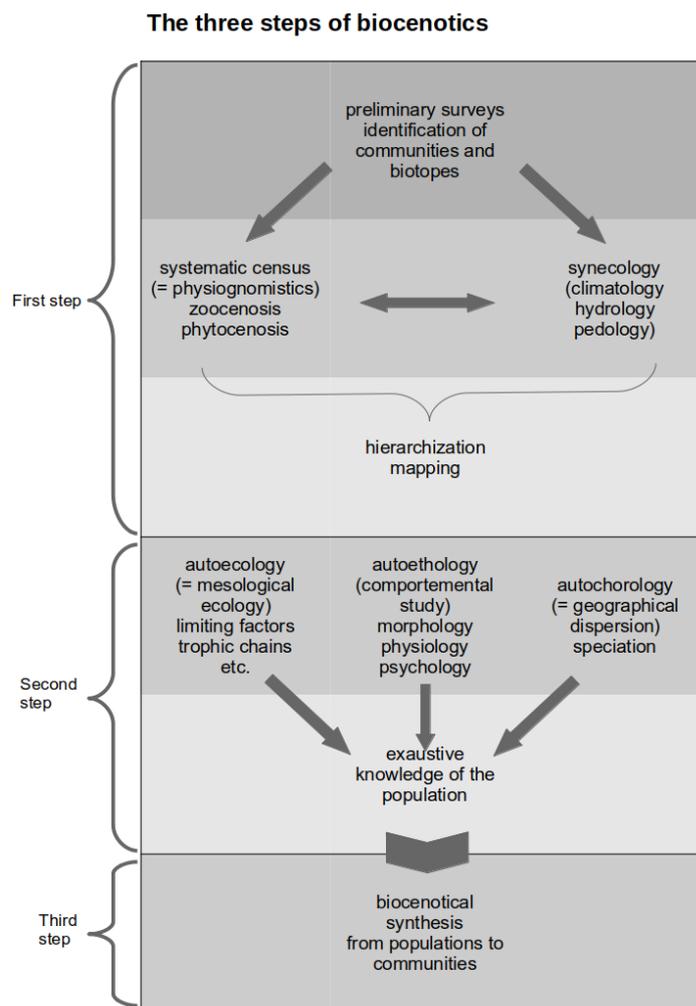


Figure 5. The three steps of biocenotics (modified, from Rioux 1958).

Thus, on one hand, observation, inventory, sorting and data analysis, lead on an interpretation, a sort of a novelization that allows to apprehend the biological dynamics in progress, the interactions between the different cenosis, or between species within the cenosis. On the scale of a natural site, the cenosis provides a robust insight into the issues at stake, as well as the effects of possible human interventions. Then, monitoring is able to enter.

Conclusion

It's been a practical problem that led me to consider that biocenotics mysteriously disappeared, and I assume it is a pity; I argue we should try to revivify it, and this text tried to elaborate a theoretical statement. Its cousin/cousin-partner, yet cited (2021b), on malacocenosis, to which I would like to refer, stated that, apart from epistemological effervescence, direct applications seem obvious, not only from a knowledge point of view, but also in a conservation approach. We hope the recourse of biocenology/biocenotics will feed ecological studies, both in functional, monitoring and evolutionary ecology.

Acknowledgements

I would like to thank all those who contributed to my reflection, particularly Frédéric Bouffard, Emmanuel Cateau and Philippe Julve.

I thank the editor and the three reviewers for their support and great helping.

Bibliography

- AAVV (1951) Actes du colloque sur l'écologie de 1950 à Paris. Colloques Internationaux du Centre National de la Recherche Scientifique XXXIII. Paris, C.N.R.S.
- Acot P (1994) Le Colloque international du CNRS sur l'écologie (Paris 20-25 février 1950) in Gayon J & Debru C (Ed.) Les Sciences biologiques et médicales en France 1920-1950. Paris, CNRS: 233-240.
- Acot P, Drouin JM (1997) L'introduction en France des idées de l'écologie scientifique américaine dans l'entre-deux-guerres. *Revue d'histoire des sciences* 50(4): 461-480. <https://doi.org/10.3406/rhs.1997.1304>
- Barkman JJ (1978) Synusial approaches to classification. In Whittaker RH (Ed.) *Classification of plant communities*: 435-491. https://doi.org/10.1007/978-94-009-9183-5_5
- Beard JS (1978) The Physiognomic Approach. In Whittaker RH (Ed.) *Classification of plant communities*: 33-64. https://doi.org/10.1007/978-94-009-9183-5_2
- Berg C, Ewald J, Hobohm C, Dengler J (2000) The whole and its parts: why and how to disentangle plant communities and synusia in vegetation classification. *App. Veg. Sci.* 23: 12-135. <https://doi.org/10.1111/avsc.12461>
- Borges JL (1952) The analytical language of John Wilkins. In Borges JL. *Other Inquisitions*. Translated by Simms RLC, Austin TX. University of Texas Press.
- Braun-Blanquet J (1932) *Plant Sociology*. New York & Londres, Conard & Fuller.
- Braun-Blanquet J (1964) *Pflanzensoziologie*. Berlin, Springer. <https://doi.org/10.1007/978-3-7091-8110-2>
- Clements FE (1916) *Plant succession: an analysis of the development of vegetation*. Carnegie Institute of Washington Publication 242: 1-512. <https://doi.org/10.5962/bhl.title.56234>
- Clements FE (1936) Nature and structure of the climax. *J. of Ecology* 24: 252-284. <https://doi.org/10.2307/2256278>
- Cowles HC (1899) The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan. *Botanical Gazette* 27/5: 95-117, 167-202, 281-308, 361-391. <https://doi.org/10.1086/327840>
- Cramer J, Van Den Daele W (1985) Is Ecology an 'Alternative' Natural Science? *Synthese* 65(3): 347-375. <https://doi.org/10.1007/BF00869275>
- Dansereau P (1945) Essai de corrélation sociologique entre les plantes supérieures et les poissons de la beine du Lac Saint Louis. *Revue Canadienne de Biologie* 4(3): 369-417.
- Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) *Guide des milieux naturels de Suisse*. Bussigny, Rossolis.
- Du Rietz GE (1921) Zur methodologischen Grundlage der modernen Pflanzengeographie. Vienne, Holzhausen.
- Egerton F (2009) Homage to Frederic E. Clements Historian of Plant Succession Studies. *Bulletin of The Ecological Society of America* 90: 43-79. <https://doi.org/10.1890/0012-9623-90.1.43>
- Eliot C (2007) Method and metaphysics in Clements's and Gleason's ecological explanations Studies. *Stud Hist Philos Biol Biomed Sci* 38(1): 85-109. <https://doi.org/10.1016/j.shpsc.2006.12.006>
- Fauth JE, Bernardo J, Camara M, Resetarits Jr. WJ, Van Buskirk J, McCollum JS (1996) Simplifying the Jargon of Community Ecology: A Conceptual Approach. *The American Naturalist* 147(2): 282-286. <https://doi.org/10.1086/285850>
- Forbes SA (1887) The Lake as a Microcosm. *Bulletin of the Peoria Scientific Association* 77-87 (reprinted in 1925 in *Illinois Natural History Survey Bulletin* 15: 537-550). <https://doi.org/10.21900/j.inhs.v15.303>
- Friederichs K (1958) A definition of ecology and some thoughts about basic concepts. *Ecology* 39: 154-159. <https://doi.org/10.2307/1929981>
- Froment P (1953) La Phytogéographie et la Phytosociologie en France du début du XIXe siècle à nos jours. *Bulletin de la Société Botanique de France* 100(7-9): 362-387. <https://doi.org/10.1080/00378941.1953.10833233>
- Gams H (1918) Prinzipienfragen der Vegetationsforschung. Ein Beitrag zur Begriffsklärung und Methodik der Biocoenologie. *Vierteljahrsschrift der Naturforschenden Gesellschaft* 63: 293-493.
- Gillet F, de Foucault B, Julve P (1991) La phytosociologie synusiale intégrée: objets et concepts. *Candollea* 46: 315-340.
- Gisin H (1951) La Biocénotique. *Ann. Biol* 27: 81-88. <https://doi.org/10.2307/410253>
- Gleason HA (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7-26. <https://doi.org/10.2307/2479933>
- Gleason HA (1939) The individualistic concept of the plant association. *American Midland Naturalist* 21: 92-110. <https://doi.org/10.2307/2420377>
- Golley FB (1996) *History of the ecosystem concept in ecology: More than the sum of the parts*. New Haven, Yale University Press.
- Grassé (1951). *Biocénotique et phénomène social*. *L'Année Biologique* 27(2): 73-80.

- Grisebach HRA (1838) Über den Einfluss des Klimas auf die Begränzung der natürlichen Floren. *Linnaea* 12: 159–200.
- Guarino R, Willner W, Pignatti S, Attorre F, Loidi J (2018) Spatio-temporal variations in the application of the Braun-Blanquet approach in Europe. *Phytocoenologia* 48: 239–250. <https://doi.org/10.1127/phyto/2017/0181>
- Guinochet M (1973) *Phytosociologie*. Paris, Masson.
- Hagen JB (1992) *An Entangled Bank: The Origins of Ecosystem Ecology*. New Brunswick, Rutgers University Press.
- Hagen JB (1988) Organism and Environment: Frederic Clements's Vision of a United Physiological Ecology. In Rainger R, Benson KR & Maienschein J (Eds.) *The American Development of Biology*. Philadelphia, University of Pennsylvania Press: 257–280. <https://doi.org/10.9783/9781512805789-011>
- Halbwachs M (1932) Chicago expérience ethnique. *Annales d'histoire économique et sociale* 13: 11–49. <https://doi.org/10.3406/ahess.1932.1486>
- Jax K (1998) Holocoen and Ecosystem: On the Origin and Historical Consequences of Two Concepts. *Journal of the History of Biology* 31(1): 113–142. <https://doi.org/10.1023/A:1004261607170>
- Jax K, Jones CG, Pickett STA (1998) The self-identity of ecological units. *Oikos* 82: 253–264. <https://doi.org/10.2307/3546965>
- Journet D (1991) Ecological theories as cultural narratives: F. E. Clements' and H. A. Gleason's 'stories' of community succession. *Written Communication* 8: 446–472. <https://doi.org/10.1177/0741088391008004002>
- Jungbluth JH (1978) *Der Tiergeographische Beitrag Zur Ökologischen Landschaft-sforschung. Malakozoologische Beispiele zur Naturräumlichen Gliederung*. La Hague, Junk. <https://doi.org/10.1007/978-94-009-9968-8>
- Keddy P (1993) Do ecological communities exist? A reply to Bastow Wilson. *Journal of Vegetation Science* 4: 135–136. <https://doi.org/10.2307/3235741>
- Klugh AB (1923) A Common System of Classification in Plant and Animal Ecology. *Ecology* 4: 366–377. <https://doi.org/10.2307/1929183>
- Lindeman RL (1942) The trophic-dynamic aspect of ecology. *Ecology* 23(4): 399–418. <https://doi.org/10.2307/1930126>
- Looijen RC, van Andel J (1999) Ecological communities: conceptual problems and definitions. *Perspectives in Plant Ecology, Evolution and Systematics* 2(2): 210–222. <https://doi.org/10.1078/1433-8319-00071>
- Lockwood JA (2011) The Ontology of Biological Groups: Do Grasshoppers Form Assemblages Communities Guilds Populations or Something Else? *Psyche: A Journal of Entomology*. Article ID 501983. <https://doi.org/10.1155/2011/501983/>
- McIntosh RP (1985) *The Background of Ecology: Concept and Theory*. Cambridge, Cambridge University Press. <https://doi.org/10.1017/CBO9780511608537>
- Meinard Y, Thébaud G (2019) L'identification syntaxonomique dans les démarches de gestion et/ou de restauration d'espaces naturels en France: pour ou contre? *Naturae* 6: 165–173. <http://revue-naturae.fr/2019/6>
- Mirkin BM (1994) Which plant communities do exist? *Journal of Vegetation Science* 5: 283–284. <https://doi.org/10.2307/3236163>
- Möbius K (1877) *Die Auster und die Austernwirtschaft*. Verlag von Wiegandt, Hempel & Parey: Berlin.
- Molinier R (1960) L'étude des biocénoses marines du Cap Corse. *Vegetatio* 9: 121–192, 217–312. <https://doi.org/10.1007/BF02917032>
- Molinier R, Vignes P (1971) *Ecologie et biocénétique*. Paris/Lausanne, Delachaux et Niestlé.
- Mörzer Bruyns MF (1950) On biotic communities [1947]. Montpellier, Station Internationale Géobotanique Méditerranéenne et Alpine.
- Mucina L (2019) Biome: evolution of a crucial ecological and biogeographical concept. *New Phytologist* 222: 97–114. <https://doi.org/10.1111/nph.15609>
- Nahrath S, Gerber JD (2014) Pour une approche ressourcielle du développement durable. *Développement durable et territoires* 5(2). <https://doi.org/10.4000/developpementdurable.10311>
- Nicolson M (1990) Henry Allan Gleason and the individualistic hypothesis: The structure of a botanist's career. *Botanical Review* 56: 91–161. <https://doi.org/10.1007/BF02858533>
- Nicolson M, McIntosh RP (2002) H. A. Gleason and the individualistic hypothesis revisited. *Bulletin of the Ecological Society of America* 83: 133–142.
- Odum EP, Odum HT (1953) *Fundamentals of ecology?* Philadelphia, WB Saunders Company.
- Palmer MW, White PS (1994) On the existence of ecological communities. *Journal of Vegetation Science* 5: 279–282. <https://doi.org/10.2307/3236162>
- Passarge H (1966) Die Formationen als höchste Einheiten der soziologischen. *Vegetationssystematik Feddes Repertorium* 73(3): 226–235. <https://doi.org/10.1002/fedr.19660730308>
- Phillips J (1931) The Biotic Community. *Journal of Ecology* 19(1): 1–24. <https://doi.org/10.2307/2255934>
- Poore MED (1955a) The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet system. *Journal of ecology* 43(1): 226–244. <https://doi.org/10.2307/2257132>
- Poore MED (1955b) The use of phytosociological methods in ecological investigations. II. Practical issues involved in an attempt to apply the Braun Blanquet system. *Journal of Ecology* 43(1): 245–269. <https://doi.org/10.2307/2257132>
- Poore MED (1955c) The use of phytosociological methods in ecological investigations: III. Practical application. *Journal of Ecology* 43(2): 606–651. <https://doi.org/10.2307/2257014>
- Poore MED (1956) The use of phytosociological methods in ecological investigations: IV. General discussion of phytosociological problems. *Journal of ecology* 44(1): 28–50. <https://doi.org/10.2307/2257153>
- Poore MED (1962) The method of successive approximation in descriptive ecology. *Advances in ecological research* 1: 35–68. [https://doi.org/10.1016/S0065-2504\(08\)60300-1](https://doi.org/10.1016/S0065-2504(08)60300-1)
- Quézel P, Verdier P (1953) Les méthodes de la phytosociologie sont-elles applicables à l'étude des groupements animaux? Quelques associations ripicoles de carabiques dans le Midi de la France et leurs rapports avec les groupements végétaux correspondants. *Vegetatio* 4: 165–181. <https://doi.org/10.1007/BF00297017>
- Rabeler W (1951) *Systematik der Vogelgemeinschaften im Hinblick auf Biozönologie und Pflanzensoziologie*. Ornith. Abhandl. 9: 3–10.
- Raunkiaer C (1934) *The Life Form of Plants and Statistical Plant Geography*. London, Clarendon Press.
- Rioux JA (1958) De quelques concepts en biocénétique. *Service de la Carte Phytogéographique bulletin série B*: 127–150.
- Sukachev VN (1942) Ideja razvitija fytknologii [Thoughts on plant community dynamics]. *Sovietskaja botanika* 12: 399–418.
- Tansley AG (1935) The use and abuse of vegetational concepts and terms. *Ecology* 16: 284–307. <https://doi.org/10.2307/1930070>

- Taylor WP (1935) Significance of the Biotic Community. *Ecological Studies* 10(3): 291–307.
- Terrisse J (2012) (Ed.) Guide des habitats naturels du Poitou-Charentes. Fontaine-le-Comte, Poitou-Charentes Nature.
- Tischler W (1950) Kritische Untersuchungen und Betrachtungen zur Biozonotik. *Biologisches Zentralblatt* 69(1-2): 33–43.
- Tüxen R (1966) (Ed.) *Biosoziologie*. La Hague Junk. <https://doi.org/10.1007/978-94-011-7597-5>
- Van der Maarel E (1976) On the establishment of plant community boundaries. *Berichte der Deutschen Botanischen Gesellschaft* 89: 415–443.
- van der Valk A (2013) From Formation to Ecosystem: Tansley's Response to Clements' Climax *Journal of the History of Biology* 7(2): 293–321. <https://doi.org/10.1007/s10739-013-9363-y>
- Vernadski V (1930) The Biosphere and the Noosphere. *American Scientist* 33(1): 1–12.
- Villaret JC, Van Es J, Sanz T, Pache G, Legland T, Mikolajczak A, Abdulkhak S, Garraud L & Lambey B (2019) Guide des habitats naturels et semi-naturels des Alpes. Turriers/Gap, Naturalia/Conservatoire Botanique National Alpin.
- Vincent B (2021a) Cap au seuil. Available at <http://www.amboilati.org/dehors/cap-au-seuil>
- Vincent B (2021b) Éléments pour la description des communautés animales de mollusques. Application aux malacocénoses suivi d'un Synopsis d'un prodrome des malacocénoses de France et d'Europe. *Folia Conchyliologica* 63: 3–71.
- Vincent B, Cateau E (2021) Sciences naturelles = sciences littéraires? *Carnets botaniques* 71. <https://doi.org/10.34971/8267-XC69> Available at <https://sbocc.fr/publication/sciences-naturelles-sciences-humaines-reequilibrer-les-sciences-naturelles/>
- Werger M (1974) The Place of the Zürich-Montpellier Method. *Vegetation Science Folia Geobotanica & Phytotaxonomica* 9(1): 99–109. <https://doi.org/10.1007/BF02851406>
- Westhoff V (1951) An analysis of some concepts and terms in vegetation study or phytosociology *Synthese* 8: 194–206. <https://doi.org/10.1007/BF00485904>
- Westhoff V & van der Maarel E (1973) The Braun-Blanquet approach. In Whittaker RH (1973) (Ed) *Ordination and Classification of Communities*: 617–726. https://doi.org/10.1007/978-94-010-2701-4_20
- Whittaker RH (1962) *Classification of Natural Communities*. *The Botanical Review* 28(1): 1–239. <https://doi.org/10.1007/BF02860872>
- Whittaker RH (1973) (Ed) *Ordination and Classification of Communities*. The Hague, Junk. <https://doi.org/10.1007/978-94-010-2701-4>
- Whittaker RH (1975) *Communities and Ecosystems* New York City, MacMillan.
- Whittaker RH (1978) (Ed) *Classification of plant communities*. The Hague, Junk. <https://doi.org/10.1007/978-94-009-9183-5>
- Wilson JB (1991) Does vegetation science exist? *J. Veg. Sci.* 2: 289–290. <https://doi.org/10.1111/j.1654-1103.1991.tb01131.x>
- Wilson JB (1994) Who makes the assembly rules? *Journal of Vegetation Science* 5: 275–278. <https://doi.org/10.2307/3236161>