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## Holism and reductionism in biology and ecology

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## CHAPTER 9

### ECOLOGICAL COMMUNITIES: CONCEPTUAL PROBLEMS AND DEFINITION

#### 9.1 Introduction

In the preceding chapter I have noted that there are no examples of reduction of laws and theories about communities and ecosystems for the simple reason that there are no general laws and theories about communities and ecosystems. I have also noted that one particular cause of this might be that the concepts of community and ecosystem have not been defined adequately and unambiguously. The terms 'community' and 'ecosystem' are being used for a wide variety of objects at different levels of organization. Considering that one of ecology's central aims is to describe and explain the structure of communities and ecosystems, as given by such properties as species number and composition, this situation is deplorable.

My aim in the present chapter is to try and improve upon that situation as far as communities are concerned. I will provide a conceptual analysis and clarification of the concept 'community' and I will attempt to define it unambiguously. Though occasionally the concept 'ecosystem' will also be mentioned, it will not be analyzed and falls outside the scope of this chapter.

In fact, there appear to be three major problems with respect to communities, all of which have to do with the fact that the concept is not adequately defined. The first problem has already been mentioned: the term 'community' is being used for various different objects at different levels of organization. I call this the *problem of ambiguity*. Apart from the confusion it creates, this problem alone seems to be sufficient to impede the discovery or development of 'general' laws and theories about communities. I will discuss this problem, and attempt to resolve it, in section 9.2. In doing so, I will hit upon the second and third problem, which will be discussed in section 9.3.

The second problem is formed by the fact that what are mostly called communities (groups of species populations which occur together in space and time) rarely if ever form discrete units in a landscape, but gradually blend into one another. It is often very difficult or even impossible, therefore, to draw objective, non-arbitrary boundaries between different communities. This problem is known as the *boundary problem*. It is probably the most notorious problem in community ecology and is generally considered irresolvable. As a result, most, if not all, ecologists today believe that communities are more or less arbitrary units of investigation (see, among many others, Cohen 1989; Krebs 1994; Begon et al. 1996).

The third problem is the *problem of heterogeneity*. It consists of the fact that communities, as presently defined, are often extremely heterogeneous qua species' composition. This is a problem because the occurrence of general laws appears to be linked to homogeneous entities.<sup>51</sup>

For one reason or other, ecologists have never been able to solve these latter problems and, as mentioned, even consider them to be irresolvable. This is a bit odd, because in my view there is a relatively simple solution. I will show that both problems result from a common cause and, therefore, can be resolved at the same stroke. Both problems result from the view that communities are certain groups of *populations* of different species. The solution is to view them as particular groups of *individuals* of different species.

Because these problems have received most attention in plant ecology, in particular

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<sup>51</sup>This point was brought to my attention by Theo Kuipers.

vegetation science, my emphasis in the relevant sections will be on plant communities. However, the issues addressed relate to communities in general, and my aim is to arrive at a definition of the concept of a community that is generally applicable.

In section 9.4 I will deal with a number of possible objections to the definition I will suggest. In section 9.5, finally, I will show its empirical adequacy by applying it to plant communities at the Oosterkwelder salt-marsh on the island of Schiermonnikoog in the Netherlands, where I have done some research myself (Looijen 1983; Looijen et al. 1984; Looijen & Bakker 1987).

## **9.2 The problem of ambiguity**

### **9.2.1 Different concepts of community**

Most ecologists, when thinking of a community, have in mind a group of species populations which occur together in space and time (for example Begon et al. 1996). Beyond that, however, opinions diverge. This formulation is so general that it allows any group of populations, no matter its size or structure, to be called a community. For the same reason, it is inadequate as a definition of the concept 'community'. For in a certain sense all contemporary populations can be said to occur together in space and time, and hence to belong to one single community. As this is, apart from Gaiasophical theories, obviously not what is intended, the question is what extra conditions must be met in order for organisms or populations to belong to a community. What criteria do we have for lumping some organisms or populations as one community and others as another?

To discuss these questions I have selected, from a host of definitions of the term 'community', the following six, which I think are representative of different views of communities (box 1). They offer different criteria for community membership.

- C1: An assemblage of populations of plants, animals, bacteria, and fungi that live in an environment and interact with one another, forming together a distinctive living system with its own composition, structure, environmental relations, development and functions (Whittaker 1975: 1-2).
- C2: One or more populations with similar [life habits and] resource demands co-occurring in space and time (McNaughton & Wolf 1973: 550).
- C3: A group of interacting species that occur in the same area (Ricklefs 1973: 590).
- C4: A group of species living closely enough together for the potential of interaction (Strong et al. 1984: vii).
- C5: Any assemblage of populations [of plants and animals] in a predescribed area or habitat (Krebs 1972: 379).
- C6: Whatever lives in a habitat (lake, forest, sea floor) that some ecologist wants to study (Cohen 1989: 181).

**Box 1:** Various definitions of the concept 'community' in the ecological literature.

The differences between these definitions relate to the following questions: (1) Are communities to be regarded as distinctive living systems analogous to organisms? (2) Are communities groups of organisms or populations belonging to a single trophic level or to a

single phylum (such as vascular plants) or class (such as birds, mammals, etcetera), or do they comprise multiple trophic levels and multiple classes and phyla? (3) Is interaction, or the potential of interaction, a necessary and/or sufficient condition for community membership? and (4) Are communities spatially and/or structurally distinct entities and how can they be delimited? Questions 1, 2 and 3 relate to the problem of ambiguity, question 4 relates to the boundary problem and the problem of heterogeneity. I will answer these questions in the order of appearance.

### 9.2.2 Holistic and reductionistic views

As mentioned in chapter 8, the major controversy with respect to communities used to be whether they are to be regarded as a kind of superorganisms, as distinctive living systems having a physiological integrity, structure and development analogous to those of real organisms. Definition C1 is still a reflection of this Clementsian, holistic, approach to communities. It appears, however, that this approach has been definitively abandoned in favour of more reductionistic approaches (though it may still be alive with respect to ecosystems; see Simberloff 1980). The major reason seems to be the 'recognition' that communities are not discrete systems - and hence cannot have a physiological integrity analogous to that of organisms - but rather consist of diffuse sets of populations blending into one another, both in space and in time. In time, species constantly immigrate and emigrate or become locally extinct (though as far as plants are concerned they may remain dormant as a seed bank). In space, populations most often gradually merge into one another, whence community boundaries are vague (the boundary problem).

However, as also mentioned in chapter 8, not all holistic elements of the Clementsian approach have been abandoned. The controversy today is whether, nevertheless, communities have an emergent structure (species number and composition) which cannot be accounted for solely by relations between species and environments, and which must be explained in terms of interactions between species. This moderately holistic approach is opposed by the radically reductionistic approach in the tradition of Gleason, that communities are more or less coincidental assemblages of species populations and that their so-called 'structure' is the sole result of individual species' adaptations to local environmental conditions.

The moderate approach is reflected in definitions C2, C3 and C4 above. Of course, there are no definitions reflecting the radically reductionistic approach, because in this approach communities are denied an independent ontological status, but there are some definitions compatible with it, such as definitions C5 and C6.

This is not the place to argue in favour of either of these last two views, because the present aim is to define the concept 'community', not to describe or explain community structure. However, it may already be mentioned that the definition I will provide later on is compatible with both views, because it leaves aside whether communities have an emergent structure and how it is to be explained.<sup>52</sup>

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<sup>52</sup>Some ecologists seem to confuse definition and explanation. That is, they attempt to put part of the explanation of community structure into their definition of the concept 'community'.

### 9.2.3 Communities and biocoenoses

Most of the definitions listed above state (C1 and C6) or suggest (C3, C4 and C5) that communities comprise either more than one trophic level or more than one taxonomic class or phylum or both. McNaughton and Wolf (1973: 5) state, however, that the term "community is usually applied to organisms with similar life habits [and resource demands]" and that, therefore, they "will refer to tree communities, insect communities, or bird communities, rather than lumping such diverse organisms as a single community". The authors suggest that the term '*biocoenosis*' be applied to a group of populations belonging to various trophic levels and various classes or phyla, constituting the biotic part of an ecosystem ('community' as referred to by C1). This (that is, the biotic component of an ecosystem) is the usual definition of a biocoenosis. The concept 'ecosystem' is thereby usually left undefined, or, following Tansley (1935), is defined as the whole of a biocoenosis and its abiotic environment. In English, there is no other term than 'biocoenosis' to indicate the relevant difference with the (other meaning of the) term 'community' (or it must be 'living community'). In Dutch, one uses the terms 'levensgemeenschap' (biocoenosis) and 'gemeenschap' (community) to indicate the two concepts.

Though I agree with McNaughton and Wolff's proposition, it should be mentioned that the two criteria for community membership they suggest, namely same trophic level ("similar [life habits and] resource demands") and same taxonomic phylum or class ("tree communities, insect communities, or bird communities"), are incompatible. For example, such diverse organisms as rabbits, geese and grasshoppers all have similar resource demands (in the qualitative sense, that is) and hence belong to a single trophic level, while on the other hand such birds as warblers, geese and owls belong to different trophic levels. Since I fail to see the use, for the purpose of community membership, of lumping together such groups of insects, birds, mammals, etcetera, as belong to singular trophic levels, and because it is indeed quite usual to refer to plant communities, bird communities, etcetera, I assume the authors have in mind groups of populations belonging to a single taxonomic phylum or class when thinking of communities.

At first sight, it may seem as if no serious confusion or other problems could arise from applying the term 'community' to both levels of organization. Since for all purposes accurate descriptions of the structure of communities have to be provided, any particular community of study may always be specified as being a plant community, an insect community, etcetera, or a community in the sense of a biocoenosis. However, on the theoretical level and as far as explanations are concerned, the ambiguity is bound to create problems. The competitive exclusion principle (CEP) provides a good example.

What is usually called a biocoenosis (the biotic part of an ecosystem; and think of an ecosystem as, for instance, a forest, a meadow, a moor, a lake or a dune valley) most often includes not only different 'communities' in the sense of different groups of taxonomically or phylogenetically related species (that is, a group of higher plants, a group of insects, a group of fungi, etcetera) but also different 'communities' per taxonomic phylum or class (that is, for instance, different plant communities). This means that the species composition (plants plus other species) in one part of the total area occupied by a biocoenosis is often quite different from the species composition in another part of that area. In other words, biocoenoses are spatially often quite heterogeneous in species composition. As mentioned earlier, heterogeneity may be one reason for the lack of general laws and theories about

'communities'. The CEP, for instance, may be formulated as: "if two competing species coexist in a stable environment, then they do so as a result of niche differentiation (..). If, however, there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other" (Begon et al. 1986, p. 260). This principle can be used to explain (differences in) the structure of communities through explanations of the coexistence or non-coexistence of species. Suppose, however, that there are two plant species, S1 and S2, that have identical niches and belong to the same biocoenosis but occur widely separate in space, that is, belong to different plant communities. And suppose that there is ample evidence that this is the result of competitive exclusion. Now when we would use the term 'community' for the concept of a biocoenosis, we would be forced to say, in spite of this evidence, that the CEP is false, because then S1 and S2 would belong to the same 'community' and hence coexist.<sup>53</sup> Alternatively, when the term 'community' is used for both plant communities, etcetera, and for biocoenoses, we would be forced to say both that S1 and S2 coexist (because they belong to the same community in the sense of biocoenosis) **and** that they do not coexist (because they belong to different plant communities).

Such contradictions and 'falsifications', or at least the confusions preceding them, can be avoided only by applying the term 'community' to either biocoenoses or to groups of plants, birds, etcetera. In view of, among other things, the wish to save the CEP, which applies only to the latter concept, and also to prevent, in this respect, the problem of heterogeneity (which generally exists at the level of biocoenoses but not necessarily at the level of plant communities, etcetera), I think the problem is best solved by restricting use of the term 'community' to groups of taxonomically related species. Following McNaughton and Wolff, the term 'biocoenosis' may then be used, as previously, to denote the biotic component of an ecosystem.

#### 9.2.4 Interactions between species

The third question relating to the problem of ambiguity is whether interaction, or the potential of interaction, is a necessary and/or sufficient condition for community membership. Before discussing this question, it should be noted that most types of biotic interaction (all cases of herbivory and insectivory, most cases of mutualism, parasitism and commensalism, many cases of predation, and some cases of competition) occur between species belonging to different taxonomic classes or phyla. Therefore, given the conclusion of the preceding section, they are interactions within biocoenoses, not within communities. Within communities, the prevailing types of biotic interaction appear to be competition and (in animal communities) predation, and there are only relatively few cases of mutualism, (half) parasitism and commensalism (for example, epiphytes and scavengers).

One should not conclude from this that interactions which do not belong to interactions within communities, cannot be important in structuring communities. On the contrary. The effects of herbivores on the distribution and abundance of plant species, and hence on the structure of plant communities, is beyond doubt. The effects of predators, parasites and other

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<sup>53</sup>Of course, the principle would be falsified not on empirical grounds but on analytical grounds.

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consumer species on the distribution and abundance of prey or host species, and hence on the communities to which they belong, are more controversial, but there is no reason why such effects are to be precluded *a priori*. Such cases of what may be called 'downward structuring' should be distinguished, moreover, from cases of 'upward structuring': the dependence of predators, parasites and other consumer species, and hence of the communities to which they belong, on the presence and relative abundance of prey or host species.

The question is, however, whether or not communities are to be defined exclusively as groups of interacting populations. Positive answers to this question are implied by definitions C1, C3 and C4 above, while the other definitions are neutral in this respect (that is, compatible with the view that communities may consist of both interacting and non-interacting populations).

Ricklefs (1973) suggests that the term 'association' be used for a group of populations occurring together in a certain area, and that the term 'community' be applied only to groups of interacting populations (C3). This amounts to making interaction a necessary condition for community membership. The definition (C4) provided by Strong, Simberloff, Abele and Thistle (Strong et al. 1984) is less restrictive, requiring only that there be the potential of interaction, and implicating that interaction may be sufficient but not necessary.

Although the possibility of interaction should not be precluded, of course, there are several reasons why, in my view, interaction should not be considered a necessary condition for community membership. Firstly, it would preclude neutralistic species (that is, by definition, species that do not interact) from belonging to the same community, or to any community for that matter. Though a radical holist may deny that there are neutralistic species (since all things are related), it is likely that there are many neutralistic species, also within communities (though perhaps not within plant communities, since all plant species make demands on essentially the same resources and, therefore, are likely to compete). Within bird communities, for instance, it is likely that warblers do not interact with ducks, or ducks with owls.

Secondly, it would deny community membership to potentially interacting species which do not, however, for whatever reason, actually interact. Although this is (as with any definition) partly a matter of convention, I suspect that most ecologists would feel rather uncomfortable with these implications (because the standard practice is to include species in communities irrespective of their interactionist status). In addition, to document actual interactions between species may be a most difficult task in many situations, especially when the supposed interactions are competitive and of the exploitative (not directly visible) type, implicating that the criterion is also not easily made operative.

Thus, in my view interaction is not a necessary condition for community membership. It is not a sufficient condition either. For it may well be possible that two populations, which occur widely separate in space (and hence do not belong to the same community), still interact, for instance through seed dispersal or other dispersal processes. Communities are not closed systems. Suppose, moreover, that as a result of competitive exclusion two populations occur separately but adjacent to one another in space. Obviously, there could still be (the potential of) interaction between them along the border of the areas they occupy (settling boundary conflicts, as it were). The interaction criterion would then force us to say that these populations belong to the same community, whereas it is precisely in situations like this (competitive exclusion) that they are said not to coexist and hence to belong to different

communities.<sup>54</sup>

The additional requirement, that the populations must occur in the same area, is also insufficient. Why restricting community membership to interacting (or potentially interacting) populations which occur in area A and why not extend it to (potentially) interacting populations in area B encompassing A? In the next section I will argue that the solution lies in the condition that the areas occupied by the populations must intersect, since it is only within the intersection area that we can speak of a community. However, this condition is separately sufficient for community membership and it is neither necessary nor sufficient that species interact.

### **9.3 The boundary problem and the problem of heterogeneity**

#### **9.3.1 The boundary problem**

The final and toughest question is whether communities can be considered discrete, spatially and/or structurally distinct and homogeneous entities. As mentioned, it seems as if most ecologists today believe that communities are not discrete, spatially distinct entities but rather consist of diffuse sets of populations that gradually blend into one another. The major reason is that the environmental factors, to which species respond in their distribution, are rarely if ever discretely distributed but form continuous gradients. Populations are often distributed along such environmental gradients. However, since different populations generally respond differently to any such gradient, and hence may occur higher or lower on a gradient, they rarely if ever occupy exactly the same area in a landscape. As a result, the boundaries between communities, defined as groups of populations, are generally vague and gradual. This was, in fact, the crux of Gleason's (1926, 1939, 1963) critique of Clements' (1916) superorganism theory (see also Whittaker 1953). The boundary problem is a problem, of course, because it frustrates adequate descriptions of the structure of communities. Though it is best known for plant communities, the problem is exacerbated for most animal communities (excepting groups of animals on small islands, which are often treated as single communities), because of the motility of most animal species.

As argued above, the statement that communities are groups of populations which occur together in space and time is inadequate as a definition of community. However, a fair interpretation of 'to occur together in space and time' is that populations must occur simultaneously in a definite, restricted place or area in order to belong to the same community. This condition is stated explicitly in definitions C4 and C5, and in a certain sense in definitions C6 ('in a habitat') and C1 ('in an environment'). It does not offer a solution to the boundary problem, however, since this problem is precisely how to delineate the areas (or the 'environments' or 'habitats', see below) occupied by communities.

There are three basic ways in which (plant) ecologists have tried to recognize and categorize communities (McIntosh 1985, p. 130): according to (1) the environment (*cf.* C1), habitat (*cf.*

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<sup>54</sup>Of course, this depends also on the definition of the term 'coexistence'. I assume here that coexisting species belong, by definition, to the same community. Conversely, one could define a community as a group of coexisting species. The point of interest is that coexisting species may or may not interact.

C6) or biotope<sup>55</sup>; (2) the physiognomy of the vegetation based on the life form of the most conspicuous species; and (3) the taxonomic composition of the vegetation supplemented by some measure of the relative abundance of species.

The first approach is based on, and limited by, our ability to recognize different biotopes. Although the approach may work for communities in such clearly distinctive biotopes as lakes and forests, it is of no help in delimiting communities within most terrestrial or aquatic landscapes. For the major reason why communities are often blending into one another is that biotopes do, that is to say, that external abiotic and/or biotic conditions (in terms of which biotopes are characterized) are often connected by most gradual transitions (environmental gradients). Hence, when trying to delineate biotopes we are bound to run into the same sort of difficulties as beset the delineation of communities.<sup>56</sup>

It will be clear that the second approach, based on physiognomy, cannot solve the boundary problem either, since it allows only for the delineation of the area occupied by some conspicuous species but provides no criteria for the inclusion or exclusion of other species. There may be exceptions in cases where the structure of a community is largely determined by one or a few dominant species, such as in forests, but even then the criterion is adequate only when the population boundaries of the dominant species coincide with those of all other species that are considered to belong to the same community. Anyway, the criterion is not generally applicable.

The third approach has been more constructive. It starts by asking, not whether and how communities can be spatially delineated, but what sets them apart structurally. With structural differences one usually means species number and composition and relative abundances of species. Several methods, such as sampling techniques, cluster analyses and (dis)similarity measures, have been developed to categorize communities on the basis of structural differences between different areas in a landscape (McCoy et al. 1986). This has led to all sorts of classification systems of communities (see, among others, Raunkiaer 1934; Braun-Blanquet 1964; Müller-Dombois & Ellenberg 1974; Whittaker 1978). These are hierarchical systems in which one abstracts from concrete communities (phytocoenosa) as they occur in the field (or, better, in *relevés* or sample areas) to community types (phytocoena), which are subsequently grouped into higher units of abstraction (associations, alliances, orders and classes). The basic idea underlying these systems is that the distribution of species is determined in the first place by environmental conditions and that in different areas where more or less the same conditions occur, the same type of community is found.

This approach, which is called phytosociology or vegetation science, has in a sense been very successful. Still, I will show that the approach has not been drawn to its full consequences and that, therefore, in its present form, it too cannot solve the boundary problem. In fact, in its present form it rather creates boundary problems. These can be resolved, however, within the approach.

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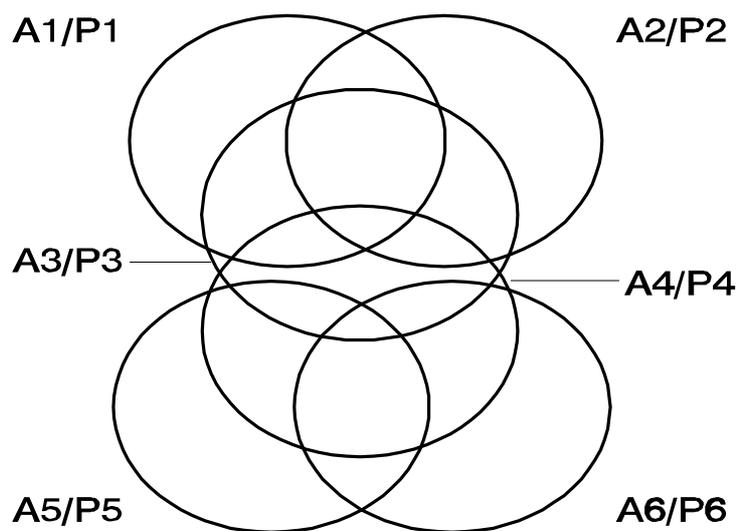
<sup>55</sup>In the next chapter I will argue that the term 'biotope' is best used for what is meant here: a particular suite of abiotic and/or biotic conditions in a certain area.

<sup>56</sup>It may be noted that there is also the danger of circularity here, since a biotope is often defined as the environment of a community (for example Whittaker et al. 1973; see the next chapter).

### 9.3.2 The problem: communities as groups of populations

Boundary problems result from a combination of two factors, one being 'factual' or empirical, the other being conceptual or theoretical. The latter is the view, shared by the majority of ecologists, that communities are groups of populations occurring together in space and time. The former is the empirical 'fact' that mostly, however, population boundaries of different species in a landscape do not coincide, that is, the fact that populations often do **not** occur together in space (and time). Boundary problems, as well as problems of heterogeneity, result from this remarkable discrepancy between 'theory' and 'fact'. Assuming that 'the facts' cannot be changed, clearly there must be something wrong with present theory.<sup>57</sup>

To illustrate what is wrong, consider the following, simplistic but not entirely unrealistic example. Let  $A_1, A_2, \dots, A_6$  be the areas occupied by populations of species  $S_1, S_2, \dots, S_6$  in a landscape, and assume that within (but not outside) each of these areas relative abundance criteria are met. Assume also that each of the areas overlaps with at least one other area and that total overlap is such that the intersections of  $A_1, A_2, A_3$  and  $A_4$ , and of  $A_3, A_4, A_5$  and  $A_6$ , are non-empty, but that the intersection of  $A_1$  and  $A_2$ , and  $A_5$  and  $A_6$  is empty (figure 6). That is, there are two distinct but overlapping clusters of populations, one of



**Figure 6:** Schematic representation of populations of species  $S_1, S_2$  and  $S_3$ , and  $S_4, S_5$  and  $S_6$  occupying areas  $A_1, A_2$  and  $A_3$ , and  $A_4, A_5$  and  $A_6$ , respectively. Because  $A_3 \cap A_4$  is non-empty, there is a boundary problem.

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<sup>57</sup>As I have argued in chapter 3, it is difficult to speak of 'facts' irrespective of 'theory'. 'Facts' generally appear to be 'facts-in-the-light-of-some-theory'. In the present case too, it is interesting how the 'facts' can change with a change of theory, perspective or conceptual scheme. See also section 9.5.2.

species S1, S2 and S3, and the other of species S4, S5 and S6. Suppose, in fact, that there is a classification system according to which S1, S2 and S3 belong to a community type X1, and S4, S5 and S6 belong to another community type X2. Then, given this typology and assuming that communities are groups of co-occurring populations, one may indeed take the two clusters of populations to be communities x1 and x2, of types X1 and X2, respectively. However, because the intersection of A3 and A4 is non-empty, there is a boundary problem.

Given that communities are groups of populations, it is very difficult, if not impossible, to resolve this problem in an objective, non-arbitrary way, that is, to draw an objective, non-arbitrary line separating x1 from x2. We might use the lower (southern) boundary of S3, but then parts of S4, S5 and S6 would come to belong to x1, making it no longer a community of type X1. Similarly, if we use the upper (northern) boundary of S4, parts of S1, S2 and S3 would come to belong to x2, making it no longer a community of type X2. Alternatively, to solve this problem, we might also take the upper boundary of S4 as the lower boundary of x1, and the lower boundary of S3 as the upper boundary of x2. This would have the advantage of x1 and x2 being 'pure' communities of types X1 and X2, respectively. However, the disadvantage would be that the interjacent area (the intersection of A3 and A4) would be left out of account. To solve that problem, or, rather, to diminish it, we could also use the lower boundaries of S1 and S2 and the upper boundaries of S5 and S6 as the lower and upper boundaries, respectively, of two different communities, x3 and x4. In that case, however, these communities would not be of types X1 and X2 but of, say, types X3 and X4, respectively, the former being comprised of species S1, S2, S3 and S4, and the latter being comprised of species S3, S4, S5 and S6. Moreover, there would still be an interjacent area left out of account: the area in between x3 and x4, containing parts of S3 and S4. To resolve this latter problem, we could also draw a line (separating x3 from x4, not x1 from x2) halfway across the interjacent area. We could even define the whole interjacent area as a transition zone or boundary zone between x3 and x4 (see section 9.3.3). Analogously, we could also define the whole intersection of A3 and A4 as a boundary zone between x1 and x2. Each of these options seems more or less arbitrary, and it is for this reason, I think, that at most (if not all) ecologists have come to accept the 'fact' that communities cannot but be defined somewhat arbitrary.

### **9.3.3 Boundary communities**

To be sure, one 'solution' to the boundary problem has been indeed, as indicated above, to use the upper boundary of S4 as the lower boundary of a community x1 (of type X1), to use the lower boundary of S3 as the upper boundary of a community x2 (of type X2), and to define the intersection of A3 and A4 as a transition zone or boundary area. (Alternatively, one might define the area in between the lower boundaries of S1 and S2 and the upper boundaries of S5 and S6 as the transition zone of communities x3 and x4.)

In addition, the observation that the species composition in such transition zones is always more or less different from the species composition in either of the 'main' communities they

'separate', has led to the creation of so-called boundary communities.<sup>58</sup> Two main types of such boundary communities are being distinguished, namely those occurring in so-called '*limes convergens*' or 'ecotone' situations, and those occurring in so-called '*limes divergens*' or 'ecocline' situations (van Leeuwen 1965; van der Maarel 1976, 1990).

A *limes convergens* is a more or less sharp boundary between communities resulting from a more or less abrupt change in one or more environmental variables leading to the convergence or coincidence of population boundaries. Boundary communities in *limes convergens* situations are generally less rich in species than the communities they separate. (Of course, if the population boundaries of all species in a community were to coincide - in a *limes coincidens*, so to speak - there would be no boundary problem and no reason to introduce boundary communities.) A *limes divergens*, on the other hand, occurs when there is a gradual change in environmental conditions and when, as a result, populations gradually merge into one another. In such cases, community boundaries are vague. In *limes divergens* situations, boundary communities are generally more rich in species than the communities they separate.

*Limes convergens* and *limes divergens* are considered extremes of a continuum and all sorts of intermediate boundary communities are possible (Whittaker 1967, 1978; van der Maarel 1976; Austin et al. 1984). The 'boundary community' in the 'transition zone' of x1 and x2 (that is, in the intersection of A3 and A4) would be more of a *limes divergens* community: it would contain all six species as against the three species of both x1 and x2 (but see note 60). On the other hand, the 'boundary community' in the 'transition zone' of x3 and x4 would be more of a *limes convergens* community: it would contain only two species (S3 and S4), as against the four species in each of the 'main' communities.

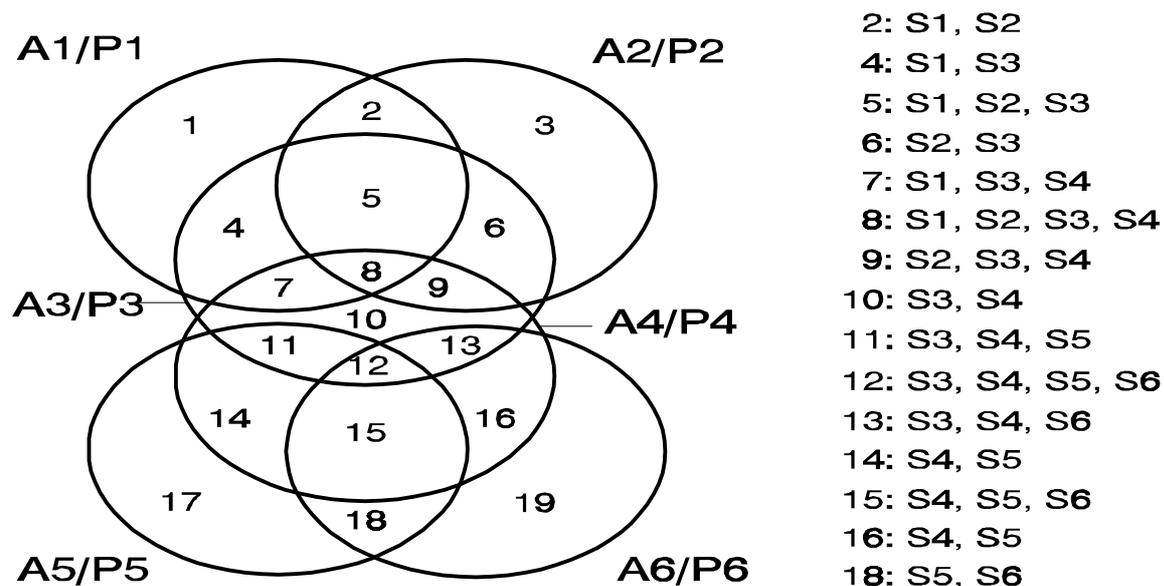
#### 9.3.4 The problem of heterogeneity

Of course, to define (and classify) boundary communities is not really to solve the boundary problem but to accept it as being irresolvable. This is not the only problem, however. In addition, if population boundaries do not coincide, then lumping groups of populations into communities will always create communities which are spatially heterogeneous in species composition.

Consider again the above example and let us take the case where communities x1 and x2 are separated by a boundary community (say x6) in the intersection of A3 and A4 (figure 7). Each of these communities is heterogeneous in the sense that the species composition in one part of the total area it occupies is different from that in another part. Within the boundaries of x1, for example, the species composition in area 2 (S1, S2) is different from the one in, say, area 5 (S1, S2, S3) or area 6 (S2, S3). Similarly, within x2, the species composition in area 15 (S4, S5, S6) is different from the one in, say, area 14 (S4, S5) or area 16 (S4, S6). In fact, each of the intersection areas in figure 7, including those within the boundaries of x6,

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<sup>58</sup>A recent trend in landscape ecology even shows a shift in the attention from 'main' communities to such boundary communities, or 'ecotones' as they have also come to be called, and some have even gone so far as to attribute special properties to these, such as conferring stability to the 'main' communities they separate (for example, di Castri *et al.* 1988; Naiman *et al.* 1988).



**Figure 7:** Same example as in figure 6. Each of the numbered areas has a different species composition. Areas 1, 3, 17 and 19 each contain individuals of only one species.

has a different species composition.

As mentioned before, heterogeneity of communities may be one reason for the present lack of (well confirmed or corroborated) general laws and theories about communities. Unfortunately, present classification systems provide a good example. The major criticism of these systems is that communities as defined by them are hardly ever found in nature, at least not in their 'pure', 'ideal' or typical form: concrete communities in the field (phytocoenosa) are almost always 'imperfect reflections' of the ideal types (phytocoena). Either some species are lacking which according to the system should be present, or others are present which according to the system should be absent, or both (some examples will be provided below in section 9.5). The chief cause of this seems to be that community types (phytocoena) are being abstracted from sets of concrete communities (phytocoenosa) whose members are often (1) heterogeneous, and (2) more or less variable, and hence different from one another, qua species composition (though not as different as they are from members of other sets). That is, both the sets and their members are often heterogeneous.<sup>59</sup> Both forms of heterogeneity disappear, however, in the abstract types (which are more or less fixed species combinations). As a result, upon (re)turning to the field, one finds that concrete communities generally deviate considerably, qua species composition, from the ideal types. This problem would not arise if community types were abstracted from sets of, qua species composition, homogeneous and identical communities.

<sup>59</sup>The former is probably a consequence of the latter, and of the fact that communities are being defined somewhat arbitrary. For if communities are (1) arbitrary and (2) heterogeneous, the chances of finding large numbers of communities with equal species composition would seem to be less than if communities were well-defined (well-delineated) and homogeneous.

### 9.3.5 The solution: communities as sets of individuals

For one reason or other, ecologists have never been able to solve the boundary problem, nor the problem of heterogeneity, and seem to accept them as being irresolvable. This is odd, because in my view there is a very simple solution to both problems. To arrive at that solution, recall that both problems result from the fact that communities are being defined as groups of co-occurring populations, whereas, actually, different populations seldomly co-occur in exactly the same area. As a result, there will always be populations that range over communities, no matter how community boundaries are drawn, whence communities will always be heterogeneous and community boundaries will always be vague. However, if populations range over communities, then *communities cannot be groups of populations!* Rather, populations are cut up into parts belonging to the one community and parts belonging to another community. (There is no way of defining two or more communities in figure 6 or 7 without cutting up at least some of the populations.) In other words, communities are comprised of only parts, that is, of only certain groups of individuals, of different populations.

To arrive at a more precise definition, let us take another look at figure 7. Strictly speaking, the set of individuals in the 'transition zone' of  $x_1$  and  $x_2$  (the intersection of A3 and A4) cannot be regarded as a community in the sense of either type X1 or type X2, since these types are defined as combinations of, respectively, species S1, S2 and S3, and species S4, S5 and S6, whereas the species composition in the 'transition zone' is S1, S2, S3, S4, S5 and S6 (but see note 60). This is, of course, the rationale behind the introduction of a boundary community. However, the solution to the boundary problem is not to define boundary communities but to take the rationale behind them more seriously. This rationale applies not only to the transition zone, but to each of the intersection areas in figure 7. That is, strictly speaking, a *community*  $x_1$  of species S1, S2 and S3 occurs only in the intersection of A1, A2 and A3 (area 5), and it is *not true* that a community of *these* species occurs in any of the other (intersection) areas. Similarly, a community  $x_2$  of species S4, S5 and S6 occurs only in area 15, and it is not true that such a community occurs in any of the other intersection areas. By the same reasoning, there is no such thing as a (boundary) community  $x_6$ , defined as a combination of S1, S2, S3, S4, S5 and S6, in any of the intersection areas 7-13 within the intersection of A3 and A4.<sup>60</sup>

The rationale is, of course, that we can speak of a community of two species, A and B, only in the intersection of the areas occupied by populations of these species, where individuals of **both** A and B occur, not in areas where individuals of only one of them occur, nor in areas where individuals of both A and B and of another species C occur.<sup>61</sup> This implies, however, that communities are to be defined, not as groups of co-occurring populations, but as groups of co-occurring individuals of different populations. More precisely, then, a community may be defined as:

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<sup>60</sup>Of course, such a community may be taken to exist in the intersection area as a whole, but this community would be extremely heterogeneous.

<sup>61</sup>Notice that, for the same reason, we cannot speak of communities at all in areas 1, 3, 17 and 19 in figure 7, since each of these areas contains individuals of only one species.

*the set of individuals of two or more species which occur in the intersection of the areas occupied by populations of these species.*<sup>62</sup> I will denote this definition as Ci (Community of individuals).

It will be clear that Ci resolves both the boundary problem and the problem of heterogeneity. What sets communities apart are differences in species composition. From these structural boundaries follow, given Ci, discrete, non-overlapping spatial boundaries and within these boundaries, communities are homogeneous. On Ci, each of the intersection areas in figure 7 contains a different community, each of these communities is homogeneous, and community boundaries are discrete and well-defined: they are defined by the lines of intersection of population boundaries.

Of course, one will still have to use some relative abundance criterion to determine population boundaries. More generally, one will still have to use some criterion to determine whether or not a species is sufficiently abundant to be considered 'present' (that is, 'interesting' or 'worth counting') in a certain area, and, hence, to determine whether or not it is to be included in a community. However, that is a problem besetting any attempt to define *population boundaries*, not community boundaries. It is not peculiar, therefore, to the approach suggested here. What counts in favour of the approach is that, once population boundaries are fixed, community boundaries follow automatically and unproblematically.

The major operational difference between the present approach and 'classical' approaches to communities is that, on Ci, one uses the lines of intersection of population boundaries, not population boundaries themselves, to define community boundaries. It is only when all the relevant population boundaries coincide that community boundaries as defined by Ci are identical with population boundaries.

It should be noted that to view communities as groups of individuals is not entirely new. Formerly, Westhoff (1951), Westhoff and den Held (1969), and Müller-Dombois and Ellenberg (1974) also recognized that communities are 'associations' of individuals. According to Westhoff and den Held (1969, p. 20), a (concrete) plant community (phytocoenosis) is "a certain vegetation (English: 'stand'; German: 'Bestand; French: 'groupement végétal') consisting of mutually influencing plants or plant individuals (..)". Later, however, the definition was changed by Westhoff and van der Maarel (1973) to "a part of the vegetation consisting of interacting populations (..)". In recent years, van Andel, Bakker and Grootjans (1993), Grootjans, Fresco, de Leeuw and Schippers (1994) and Palmer and White (1994) have come to view communities as groups of individuals. The main difference between Ci and the definitions provided by these other authors is that Ci is more explicit. It points explicitly to the group of individuals occurring in the intersection of the areas occupied by different species populations.

#### **9.4 Possible objections to the solution**

There are three objections likely to be raised against Ci. The first one is that application of Ci will lead to many more (types of) communities than are recognized in 'classical'

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<sup>62</sup>I cannot help noticing the significance of the word 'the' starting this definition, as it is so much more definite than the words 'an' or 'any' in former definitions of community (such as C1-C6).

approaches, so many more, in fact, that the approach is unfeasible. The second objection may be that application of Ci requires one to establish all the population boundaries in a landscape in order to define community boundaries. This too could make the approach unfeasible, especially in species-rich situations. The third objection may be that the approach based on Ci is too static and doesn't account for changes in population boundaries. Population boundaries may change from year to year, whence no community as defined by Ci will last longer than a season. I will first deal with the former two objections, which have to do with the structure of communities, and then with the third objection, which has to do with community dynamics.

#### 9.4.1 Structure and classification of communities

As to the first two objections, it should be noted, first of all, that one cannot have his cake and eat it too. That is, one cannot solve the above problems with respect to communities and go on studying them as before. If the approach based on Ci will be more laborious, and if it will lead to the recognition of more (types of) communities than are recognized in classical approaches, then so be it.

In the second place, though detecting community boundaries on the basis of Ci may be more laborious, it is never impossible. Londo (1971), for example, drew population boundaries of all species occurring in a transect across a dune lake shore. Grootjans, Fresco, de Leeuw and Schippers (1994) had no trouble in applying the view that communities are groups of individuals to species-rich *Calthion palustris* communities in Dutch hay meadows. In section 9.5 I will show, moreover, that (implicit) applications of Ci turn out to be not as uncommon, and hence not as unfeasible, as one might think.

In the third place, the fact that application of Ci will lead to the recognition of more (types of) communities should be seen as an advantage rather than a disadvantage. On Ci, community membership is both better defined and more limited, communities are homogeneous, and community boundaries are non-overlapping. All of this should facilitate both the task of providing accurate descriptions of (differences in) the structure of communities and the task of explaining them. The latter comes closer to explaining the coexistence of (pairs of) species. Moreover, because on Ci, communities are homogeneous, the chances of discovering regularities in species co-occurrence patterns are increased. One may compare this to developments in organic chemistry, where enormous progress was made when chemists started to work with pure substances instead of mixtures, leading to, among others, the laws of Lavoisier and Proust and Dalton's atomic theory.

In the fourth place, it is important to note that Ci is in itself very well compatible with (present) classification systems of communities. For Ci pertains to concrete communities as they occur in the field (phytocoenosa), whereas classification systems abstract from them to form community types (phytocoena) and higher units of abstraction. The relevant difference is that, on Ci, concrete communities are groups of individuals, whereas community types and higher units of abstraction are defined as combinations of *species*. Though Ci will generally lead to the recognition of more community types than are recognized in classical approaches, the former will generally encompass the latter (see figure 7: the community types {S1, S2, S3} and {S4, S5, S6} as defined by the view that communities are groups of populations, are encompassed by the community types as defined on the basis of Ci). And if and in so far as this is not the case, it is always possible to group the types as recognized on the basis of Ci

into higher units of abstraction corresponding to the types distinguished in classical approaches.

In the fifth and final place, it depends, of course, on the aim of study whether one may consider to apply Ci. If, for instance, the aim is to describe or map large vegetation complexes, one need not go into such detailed operations as are required by Ci. However, if the aim is to discover regularities in species co-occurrence patterns, or to describe or explain differences in the structure of communities, it seems to me that application of Ci stands a good chance of leading to interesting results.

#### **9.4.2 Community dynamics**

The third objection to Ci may be that population boundaries may change from year to year and that, therefore, no community as defined by Ci would last longer than a season. This is true in so far as population boundaries change and in so far as they change so extensively that they no longer overlap. Firstly, however, not all population boundaries change all the time, and not all changes of population boundaries are so extensive as to lead to the disappearance of (Ci-)communities. There are various ways in which population boundaries may change. A common type of change is that populations extend their areas. In that case, present communities do not cease to exist, though new communities may be formed. If, for instance, the population of S5 in figure 7 were to extend its area upwards (northwards) and came to overlap with the boundaries of S1 and S2, the communities in areas 11, 12, 14, 15 and 16 would remain to exist as before, but new communities of types {S1, S3, S4, S5}, {S1, S2, S3, S4, S5} and {S2, S3, S4, S5} would come into existence in the (new) intersection areas of the populations of these species. Or if, for example, the population of S3 were to extend its area downwards (southwards), the communities in the areas 4-13 would all remain to exist as before, but new communities of types {S3, S4, S5}, {S3, S4, S5, S6} and {S3, S4, S6} would arise in the former areas 14, 15 and 16, respectively (implicating that the former community types in these areas would indeed cease to exist).

Another common type of change is that populations decline and eventually even become extinct. If a population declines slowly, at first the community or communities to which it belongs will remain to exist, though the areas they occupy will be decreasing. Of course, if the population eventually becomes extinct, the community or communities to which it belonged cease to exist. If, for instance, S6 in figure 7 would slowly decline over a period of years or even decades, the community of type {S4, S5, S6} would remain to exist for many years (or even decades), though the area it occupies (15) will slowly become smaller, until eventually it will cease to exist when the boundary of S6 no longer overlaps with those of S4 and S5.

Thus, surely, community boundaries change with changes of population boundaries and communities may even cease to exist, just as they may arise or extend their areas. There is nothing strange about that. If population boundaries are not stable, then neither are community boundaries. If species co-occurrences are not stable, then neither is community structure. In my opinion, this is just as important as the stable coexistence of species in communities. If there were no stability at all, there would be no reason to study community structure. If there were no change, there would be no reason to study community dynamics.

In the second place, changes of population boundaries affect every approach of communities, irrespective of whether they are defined as sets of individuals or as groups of

populations. Ever from the start, ecologists have had to face the problem of how to combine theories about community structure with the apparent dynamics of communities (turnover of species, succession). In my opinion, the view that communities are groups of co-occurring populations has not particularly helped to solve this problem, precisely because population boundaries may change all the time. I have never really understood how Clements was able to combine his superorganism theory (assuming the 'same' community to continue to exist) with the ongoing changes in community structure (succession) he described (but see below).

In my opinion, precisely because population boundaries may change all the time, communities should not be defined as groups of co-occurring populations. This is incompatible with the fact that populations mostly do not co-occur in exactly the same area. It is even less compatible with the fact that population boundaries may change. If population boundaries change in the sense of moving into or out of a particular area occupied by a community, then the species composition of that area changes, and hence the type of community occurring there. In the most literal sense, then, the (former) community of that area ceases to exist and is replaced by (or 'turns into') another community of another type. This holds irrespective of whether communities are defined as sets of individuals or as groups of populations. If, for instance, species S6 in figure 7 were to change its boundary to the extent that it no longer overlaps with the boundaries of S4 and S5, and especially if S6 were to become locally extinct, then the community of type {S4, S5 S6} as defined by  $C_i$  would cease to exist. However, it would cease to exist also if it is defined as the group of populations of S4, S5 and S6 occurring in the union of A4, A5 and A6; in the first place because this union would change, and in the second place because the species composition in what is left of the union would change (S6 becoming locally extinct). Thus, in this respect, there is no difference between  $C_i$  and definitions of communities as groups of populations.

The main difference, in this respect, between the approach based on  $C_i$  and other, classical approaches of communities is not between viewing communities as groups of populations or as sets of individuals. It is rather that on  $C_i$ , community types are fixed and singular species combinations, whereas in classical approaches they are allowed a considerable degree of variability (heterogeneity) in species composition. In the Braun-Blanquet approach, for example, one distinguishes between so-called character species, differential species, faithful species and accompanying species. In order for a concrete community to belong to a certain type, at least the character species and some differential species must be present but the other species need not (though often one also allows the former to be absent; see section 9.5). Thus, concrete communities may differ considerably in species composition but still be taken to belong to the same type. As a result, also, the species' composition in a particular area may change considerably in time without forcing one to say that the community type has changed. This is indeed the classical way of combining theories of community structure with community dynamics. It is also the only way of allowing one to say that the same (type of) community remains to exist in a particular area in spite of population boundaries moving into or out of that area. The only way of allowing one to say that the same (type of) community remains to exist, or, alternatively, that 'the' (same) community has changed 'its' structure, in spite of changes of population boundaries, is by allowing community types to be more or less variable in species composition. For then, one or a few populations moving into or out of an area need not force one to say that a new type of community has arisen in that area.

The approach has always had to face two difficult problems, however. In the first place, one must decide how variable (heterogeneous) one should allow community types to be, or, put

## Chapter 9

differently, how much variation in species composition one should allow in order for different communities to belong to the same type. This means that one must also decide how 'impoverished' or 'enriched' a concrete community may be in order to still belong to a particular type. This often leads to difficulties in the classification of communities, even to the point where classification fails (see the next section for some examples).

In the second place, though from year to year changes of population boundaries need not be so extensive as to lead to drastic changes in species composition in a given area, over a long period of years they generally are. In the long run (succession) they certainly are. Thus, even within classical approaches, there will come a time, sooner or later, when the species composition in a given area has changed so extensively that one must conclude that the one type of community has disappeared (ceased to exist) and has been replaced by (or turned into) another type. On each occasion, the problem is to decide when this time has come.<sup>63</sup>

Given  $C_i$ , these problems do not occur. On  $C_i$ , community types are homogeneous: each species combination defines a separate community type. Therefore, there can never be classification problems, nor can there be problems in deciding whether the same community type still exists or has been replaced by another.

On  $C_i$ , when population boundaries change, community boundaries change accordingly. This may, but need not, lead to communities becoming extinct. In time, however, all communities become extinct and are being replaced by other communities. This holds also when communities are defined as groups of co-occurring populations, and it holds also when community types are allowed to be heterogeneous. Thus, the claim that communities as defined by  $C_i$  change or even cease to exist with changes of population boundaries certainly holds, but it holds also for other definitions.

### 9.5 An empirical example

In this final section, I will show the empirical adequacy of  $C_i$ . In doing so, I will also deal with a major complication of the above arguments in favour of  $C_i$ , namely the enormous discrepancy between present theory and actual research practice with respect to communities. For though in theory one holds that communities are groups of co-occurring populations, it appears that in practice populations are split up into parts belonging to the one community and parts belonging to other communities, more or less in accordance with  $C_i$ . Nevertheless, boundary problems and problems of heterogeneity occur all the time, in spite of my claim that  $C_i$  solves these problems. The reason is, of course, that  $C_i$  is not being applied explicitly and consistently.

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<sup>63</sup>Notice that the more heterogeneous one allows community types to be, the less difficult these problems become. In the most extreme case, when we define only one community type consisting of all species on earth, there will never be a classification problem and, forgetting about evolution, one will never have to decide about changes in community structure. We would then be back with one big superorganism, and nothing for community ecologists to study.

### 9.5.1 Salt marsh plant communities

In order to show the empirical adequacy of Ci I will discuss different plant communities at the Oosterkwelder salt marsh on the Dutch island of Schiermonnikoog, where I did some research myself (Looijen 1983; Looijen & Bakker 1987; Looijen et al. 1984). I will concentrate on a section of 32 hectares of this salt marsh, which was grazed by young cattle for many years prior to 1958, then was abandoned until 1972, when grazing was resumed (average stocking rate since 1972: 1.6 animal per hectare).

According to the present classification system (Westhoff & den Held 1969), nine plant community types (at the level of associations) occur in this section, each of which is represented by several up to a large number of concrete communities (phytocoenosa), together forming a mosaic of patterns. These types are, on the lower salt marsh and mud flats (-35 up to 35 cm above mean high water, MHW): *Salicornietum strictae typicum*, BC *Puccinellia maritima* [*Puccinellion maritimae*] (representing the grazed counterpart of the *Puccinellietum maritimae*), and *Plantagini-Limonietum*; on the higher salt marsh (35-85 cm above MHW): *Artemisietum maritimae* and *Juncetum gerardii typicum* (variants with and without *Juncus maritimus*); on the upper salt marsh and at the feet of low dunes (85-125 cm above MHW): *Sagino maritimae-Cochlearietum danicae* and a *Armeria maritima/Carex arenaria* community type classified as a transition of the *Armerion maritimae* and the *Galio-Koelerion* (which cannot be given a more detailed classification due the absence of character species); and, on the low dunes (125-205 cm above MHW): a *Ammophila arenaria* community type which is also assigned to transitions of the *Armerion maritimae* and the *Galio-Koelerion* (also lacking character species).<sup>64</sup> Complete species lists of these community types, including frequency of occurrence and mean coverage, can be found in Bakker (1989: 188-192).

To discuss the boundary problem, it suffices to restrict ourselves to the dominant species of these communities (which are not necessarily character species or differential species). In the following, figures between brackets denote frequency of occurrence and mean coverage, respectively (where + = 1-5%, a = 6-10%, 1 = 11-20%, 2 = 21-30%, etcetera).

*Salicornietum strictae* communities are dominated by *Salicornia europaea* (100/a); BC *Puccinellia maritima* communities by *Puccinellia maritima* (100/+) and *Salicornia europaea* (100/+) (as well as *Suaeda maritima*: 100/+); and *Plantagini-Limonietum* communities by *Puccinellia maritima* (100/4). The dominating species of *Artemisietum maritimae* communities is *Artemisia maritima* (100/3); that of *Juncetum gerardii typicum* communities (variants without *Juncus maritimus*) *Juncus gerardii* (100/3). Variants of *Juncetum gerardii* communities with *Juncus maritimus* are dominated by *Juncus maritimus* (100/1) and *Festuca rubra* (98/1). *Sagino maritimae-Cochlearietum danicae* communities are dominated by *Festuca rubra* (100/2), as are *Armeria maritima/Carex arenaria* communities (100/1), while variants of the latter type with *Ammophila arenaria* are dominated by *Armeria maritima* (100/+) and *Ammophila arenaria* (80/+). The dominating species of *Ammophila arenaria* communities, finally, is *Ammophila arenaria* (100/a).

Even if we consider only these eight dominant species - the argument holds much stronger if other species are also involved - it is easy to see that, contrary to present theory,

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<sup>64</sup>Communities of the latter two types are clear examples of the empirical inadequacy of the present classification system. In other words, they are counter-examples to this system.

communities are not groups of co-occurring populations. For none of these species is restricted to a single community (of only one type) but each occurs in more than one community (of more than one type). This means that the populations (or sub-populations) of these species are cut up into parts that belong to communities of one type and parts that belong to communities of (an)other type(s), more or less in accordance with Ci. In fact, if we were to produce an abstract map of the (sub-)population boundaries of these species, something very much like (an extended version of) figure 6 would result, with areas A1,..., A6 representing the areas occupied by populations of, respectively, *Salicornia europaea*, *Puccinellia maritima*, *Artemisia maritima*, *Juncus gerardii*, *Armeria maritima* and *Ammophila arenaria*. The map would contain two additional areas, A7 and A8, representing the areas occupied by populations of, respectively, *Festuca rubra* and *Juncus maritimus*. The former (A7) would intersect all other areas (*Festuca rubra* co-occurs with all other species, though only rarely with *Salicornia europaea*), and the latter (A8) would intersect all other areas but A6 (*Juncus maritimus* never co-occurs with *Ammophila arenaria*). Apart from these additional areas, the only difference with figure 6 would be that A5, representing the population of *Armeria maritima*, should now intersect both A1 and A2, as *Armeria maritima* co-occurs with both *Salicornia europaea* and *Puccinellia maritima* (though only rarely with the former).<sup>65</sup>

Thus, if communities were groups of populations, there would be only two types of communities in this section of the salt marsh, namely communities with and communities without *Ammophila arenaria*. Since this is not the case, and presuming that the present example is not exceptional, this points to an enormous discrepancy between theory and practice in vegetation science (and community ecology general). That is, theory dictates that communities are groups of populations, whereas in practice, communities turn out to be defined as groups of individuals belonging to different populations. (Of course, the communities which **are** recognized in this section of salt marsh are set apart by the abundances of these eight species relative to one another, and by the occurrences and relative abundances of other species.)

### 9.5.2 Conceptual schemes

This conclusion leads to a nagging question, however. For if, in practice, communities are defined as sets of individuals, more or less in accordance with Ci, then why are vegetation scientists still facing boundary problems, and why are the communities they describe

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<sup>65</sup>One should not conclude from this that all or most of the species co-occur in every concrete community: sometimes they do, sometimes they don't. The most extreme example is *Salicornia europaea* which co-occurs with no other species but *Puccinellia maritima* in *Salicornietum strictae* communities, with only *Puccinellia maritima* and *Juncus gerardii* in BC *Puccinellia maritima* communities, and with only *Puccinellia maritima*, *Juncus gerardii*, *Festuca rubra* and *Artemisia maritima* in *Plantagini-Limonietum* communities. The species (co-)occurs only rarely (with other species) in *Juncetum gerardii typicum* communities, and it does not (co-)occur (with other species) in communities of the upper salt marsh and of the low dunes. That is to say, *Salicornia europaea* actually has an almost exclusive distribution relative to most other species. The other species, however, co-occur in many more (types of) communities.

nevertheless often heterogeneous, contrary to my claim that Ci resolves these problems?

I think the main reason is that vegetation scientists simply do not think of communities explicitly as groups of individuals, in accordance with Ci, and therefore do not explicitly use (all) the lines of intersection of population boundaries to define community boundaries. Instead, their conceptual scheme dictates that communities are groups of populations, whence they are inclined to use (only some) population boundaries as community boundaries. As a result, Ci is generally met only halfway or partially. That is, the empirical fact that population (or sub-population) boundaries often diverge forces vegetation scientists to delineate communities in accordance with Ci, but only up to a certain point (that is, with respect to only a subset of all the populations involved). Beyond that, their conceptual scheme forces them to end up delineating communities in other ways (for instance, by using the population boundaries or high performance boundaries of some dominant species, physiognomically conspicuous species, character species or differential species as community boundaries).<sup>66</sup>

One of many possible examples to illustrate this may be found in van der Maarel (1976). Van der Maarel writes: "Plant community boundaries involve patterns, either of a single plant population, or of groups of populations with coinciding population boundaries" (p.424). His paper is called "On the establishment of plant community boundaries", however, because most communities occur in situations where there is no (complete) coincidence of population boundaries (whence van der Maarel's discussion of *limes convergens* and *limes divergens* communities). Referring to the study of Londo (1971), who drew population boundaries of all plant species occurring in a transect across a dune lake shore, van der Maarel (1976: 423) remarks that "although there appear boundaries everywhere in the transects, clear concentrations [i.e. convergences or coincidences, RL] are found, which usually coincide with phytocoenose boundaries detected earlier in that study". This should come as no surprise, because the only cases where community boundaries coincide with population boundaries is when population boundaries coincide. In such cases, it makes no difference to community boundaries whether communities are defined as groups of populations or as groups of individuals, because then the lines of intersection of population boundaries are identical to the population boundaries. Consequently, no boundary problems arise. However, as soon as population boundaries diverge (that is, in *limes divergens* situations and to a lesser extent in *limes convergens* - as distinct from '*limes coincidens*' - situations), community boundary problems are bound to arise when one still uses (some) population boundaries as community boundaries. Notice also that, as another consequence of this view: "Many observations (...) suggest the occurrence of population patterns and boundaries within phytocoenoses" (van der Maarel 1976, p.423/424), that is, that communities are heterogeneous.

More in particular, boundary problems and problems of heterogeneity may arise because of (1) the distinctions which are being made in classification systems between, on the one side, character species or differential species, and, on the other side, accompanying species and other species, and (2) the use of population boundaries or high performance boundaries of such character species or differential species, or of some other, dominant or physiognomically conspicuous, species, as community boundaries.

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<sup>66</sup>Generally, communities appear to be delineated on the basis of a mixture of taxonomical and physiognomical characteristics as determined partly by visual inspection of the vegetation, and partly by the relevant typology or classification system.

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The former may be illustrated by what are supposed to be *Plantagini-Limonietum* communities on the island of Schiermonnikoog. According to Westhoff and den Held (1969), the character species of the *Plantagini-Limonietum* are *Plantago maritima* and *Limonium vulgare*. According to Bakker (1989: 188, table VII.1), however, both species occur in only 49% of the (97) *relevés* in what are supposed to be *Plantagini-Limonietum* communities (mean coverage 1-5% and 6-10%, respectively), and both species occur also, and *Plantago maritima* even more frequently and in equal or higher relative abundance, in communities of other types (in particular of the *Juncetum gerardii*). Clearly, there is either a problem of empirical inadequacy (falsification) of the classification system or a problem of heterogeneity (at the level of the community type) in communities where either one or both species are lacking. There are boundary problems both when either one or both species are lacking, and when both species are present. When both species are present, there are boundary problems because both species occur also (and *Plantago maritima* with even higher frequency and relative abundance) in adjacent communities (of the *Juncetum gerardii*). When either one or both species are lacking, there are boundary problems because then the boundaries of what are supposed to be *Plantagini-Limonietum* communities have to be established on the basis of the occurrences and relative abundances of other species, which, however, not being character species, occur also in other, adjacent communities. Both problems can be resolved only by consistently applying Ci. This implies that one should accommodate the classification system by introducing more community types (viz. types with and without *Plantago maritima* and types with and without *Limonium vulgare*).

Similar problems may (but need not) arise when the population boundaries of a physiognomically conspicuous species are used as community boundaries. This may be illustrated by communities of the *Juncetum gerardii typicum* variant with *Juncus maritimus*. These communities are easily recognized and delineated by simply taking the boundaries of *Juncus maritimus* clumps (sub-populations) as community boundaries. However, the boundaries of *Juncus maritimus* clumps are often run across by population boundaries of other species, most notably *Elymus pycnanthus* and *Artemisia maritima*. In these cases, communities of this type become heterogeneous if one continues to use the boundaries of *Juncus maritimus* clumps as community boundaries. In addition, boundary problems arise, because the parts of *Juncus maritimus* clumps with, say, *Artemisia maritima* create a boundary zone between, on the one side, a community of the *Juncetum gerardii typicum* variant with *Juncus maritimus*, and, on the other side, an *Artemisietum maritimae* community. Again, both problems can be resolved only by consistently applying Ci (which implies, in this case, the introduction of another community type with both *Juncus maritimus* and *Artemisia maritima*).

Perhaps the most common type of boundary problem arises because the relative abundance criteria which are used to delineate communities are different from the criteria used to delineate populations (that is, because high performance boundaries are used as community boundaries). This may be illustrated by *Juncetum gerardii typicum* and *Artemisietum maritimae* communities and their respective dominating species, *Juncus gerardii* and *Artemisia maritima* (the latter also being a physiognomically conspicuous species). According to Westhoff & den Held (1969), the differential species of *Juncetum gerardii typicum* communities with respect to *Artemisietum maritimae* communities (both associations belong to the same alliance *Armerion maritimae*) is *Juncus gerardii*. However, according to Bakker (1989: 189, table VII.2), *Juncus gerardii* occurs in 49% of the (95) *relevés* in what are

supposed to be *Artemisietum maritimae* communities. In fact, the species composition of these two types of communities is almost identical. What sets them apart, however, is that *Artemisia maritima* has a mean coverage of 31-40% in *Artemisietum maritimae* communities as against a mean coverage of 1-5% in *Juncetum gerardii typicum* communities, and that *Juncus gerardii* has a mean coverage of 31-40% in *Juncetum gerardii typicum* communities as against a mean coverage of 1-5% in *Artemisietum maritimae* communities. This means, however, that there is a boundary zone, and hence a boundary problem, in between communities of these types, where both *Artemisia maritima* and *Juncus gerardii* have a mean coverage of 5-30%. Applying Ci in this case involves a shift of community boundaries from high performance boundaries to the lines of intersection of population boundaries, as well as the introduction of another community type with both *Juncus gerardii* and *Artemisia maritima*.

## 9.6 Animal communities

As mentioned in the introduction, because of the motility of most animal species, the boundary problem is even more serious with respect to animal communities as it is with respect to plant communities. Therefore, animal communities are even less to be considered groups of co-occurring populations than are plant communities. In fact, in animal ecology the boundary problem is so evident that it is not even recognized as a problem. Also, therefore, in animal ecology there is no tradition of trying to set up classification systems of communities, and community studies are much more studies of species' coexistence patterns than they are in plant ecology. Thus, as a final note to this chapter, it should be mentioned that Ci applies all the more to animal communities. As a matter of fact, I think that in animal ecology Ci is being applied, implicitly or explicitly, even more than in plant ecology. Of course, in animal ecology too, the problem is to determine population boundaries but, again, that is a problem besetting every approach of communities and it is not typical of Ci. As an alternative one might consider determining the home ranges of individuals (as is often done) and to map them on top of each other to determine community boundaries.

## 9.7 Conclusion

The purpose of this chapter was to provide a conceptual clarification of the term 'community' and to define it unambiguously. I have done so by arguing, first, that the term community is best used only for groups of coexisting species belonging to a single taxonomic group (class or phylum) in the sense of plants, birds, insects, etcetera, where the term 'biocoenoses' may be used for groups of species belonging to different taxonomic groups and comprising the biotic component of an ecosystem. Also, I have argued that, although species within communities may interact with each other, interaction is itself not a necessary nor a sufficient condition for community membership. Finally, I have argued that communities should not be seen as groups of coexisting populations of different species, but as sets of coexisting individuals of different species, occurring in the areas of intersection of populations of these species. This definition resolves, at least in theory, both the boundary problem and the problem of heterogeneity in community ecology, thus providing a better chance of discovering regularities in species co-occurrence patterns in communities. Though the definition was developed with a special view to plant communities, it is, because of the motility of most

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animals, even more adequate with respect to animal (bird, reptile, etcetera) communities.