

Conceptual problems and scale limitations of defining ecological communities: a critique of the CI concept (Community of Individuals)

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Abstract

Recently, Looijen & van Andel (1999) proposed a new definition of an ecological community by using two criteria: (1) restricting membership by taxonomic relatedness, and (2) defining boundaries by the intersection of the area of population range boundaries. I analyze the implications of their definition and explore the limitations of the approach. Overall, I show this definition to be highly scale-limited, to not encompass many ecological concepts developed for the community level, and to have hidden assumptions that are not met in natural systems. An alternative model of the ecological community is proposed as a contrast, a model based on the community of an individual, in which individuals and interactions are used to develop the larger entity of an ecological community. This alternative model illustrates that the principal problems Looijen & van Andel (1999) discussed about previous community concepts with respect to application to vegetation classification are not 'problems' but are characteristics of ecological communities. Any definition of an ecological community must be able to incorporate these characteristics as well as current ecological concepts used at the community level.

Key words: community concepts, population boundaries, scale limitation

Introduction

Ecological concepts at the community level have advanced during the last 25 years, e.g. by focusing on apparent competition (Holt 1977) or patch dynamics (Pickett & White 1985). Yet, specific developments of a community model that effectively incorporates these concepts remain incomplete. No agreed definition of an ecological community has arisen within the debate about the nature of plant communities (McIntosh 1985; Keddy 1987). In fact, a diversity of opinions exists about the community concept (e.g. Wilson 1991, 1994; Keddy 1993; Dale 1994; Mirkin 1994; Grootjans *et al.* 1996; Looijen & van

Andel 1999). Looijen & van Andel (1999), for example, suggested that multiple definitions of the concept of ecological communities have created problems for scientists aiming to advance ecology. As a solution to these problems, Looijen & van Andel (1999) developed an analysis of the community concept with the hope of an unambiguous definition. In this paper I reconsider their ideas. As an ecologist who works principally with the dynamics of ecological communities, I find their approach and definition to be excessively narrow and confining. Admittedly, Looijen & van Andel (1999) focussed on problems for

classification, but their extension to all of ecology demands a re-evaluation.

Looijen & van Andel (1999) suggested that three major problems exist in ecology resulting from multiple definitions of the concept 'community' and termed these 'the problem of ambiguity', 'the boundary problem' and 'the problem of heterogeneity'. The problem of ambiguity arises from a lack of agreement on the definition of a community, i.e. that 'community' is being used for various collections of organisms at different levels or combinations of trophic levels. The authors argue that boundary and heterogeneity problems result from definitions that incorporate populations rather than individuals because adjacent communities then would have considerable overlap. Following their analysis of the issues, Looijen & van Andel (1999) proposed two criteria as their definition of the community: (1) the restriction of membership to taxonomic groupings, and (2) the set of individuals of two or more species that occur in the intersection of areas occupied by populations of these species with boundaries defined by the range limits of the species.

The goal of the present article is to analyze conceptually Looijen & van Andel's (1999) model of a community in the spirit of Austin's (1999) plea for ecologists to evaluate more critically their concepts and models. The criteria of the 'Looijen & van Andel model' set a specific spatial and temporal scale, and in doing so, Looijen & van Andel (1999) isolated for their attention only a limited array of community level behaviours. Pragmatically, all ecologists set some type of scale in order to isolate behaviours of interest (Allen & Starr 1982; Allen & Hoekstra 1992; Pickett *et al.* 1989; Jax *et al.* 1998). What is different in this case is that Looijen & van Andel (1999) assert that their scale is *the* appropriate scale and that general ecological laws may arise from its application.

I will describe a number of shortcomings of the Looijen & van Andel (1999) definition, both for classification or as a model of an ecological community. The scale limitations of the Looijen & van Andel (1999) model create either ambiguity or conflicts with respect to what organisms are members of their community. Additionally, applying their criteria is unrealistic in high diversity communities or with populations of low density. The static nature of their community model stands in contrast to decades of research on the temporal heterogeneity and

dynamics of communities. Finally, the assertions of Looijen & van Andel (1999) concerning general ecological laws indicate that a number of unidentified assumptions must also apply. These assumptions, i.e. 'unique underlying processes', 'consistency of processes among replicate CI communities' and 'independence from other communities', are frequently, if not always, violated and limit their community model to few ecological applications. While I agree strongly with their intention of defining concepts adequately, I am disappointed in their approach and conclusions. Also, I feel that multidimensional concepts like the ecological community should not be constrained to only a limited portion of their functional domain (Brand & Parker 1995).

Finally, I develop an alternative model of the ecological community to contrast with the Looijen & van Andel (1999) approach. This model, based on the community of a focal individual, illustrates characteristics of the ecological community lacking in the CI approach. The most important aspects of this model are that (1) communities are continuous in time and space (Brand & Parker 1995), and (2) processes underlie composition and dynamics (Pickett *et al.* 1992). Fundamentally, this means that classification is arbitrary, even though there can be relatively clear and repeatable assemblages of some species that we can see easily across a landscape.

Communities are dynamic, historical entities (Parker & Pickett 1998) and their spatial expression results from a variety of processes of different spatial and temporal extents (Pickett *et al.* 1987; Wu & Loucks 1995; Parker & Pickett 1998). Climatic changes, for example, have influenced glacial and interglacial migrations of plants at large temporal scales (Davis 1981, 1983; Huntley & Birks 1983), while at smaller scales of around a century, for example, climatic flux is reflected in shifts in surface and canopy fire regimes exhibited by vegetation in western North America (Swetnam 1993). Patch dynamics continue in these systems at considerably smaller spatial and temporal scales shifting local site composition (Pickett & White 1985), often responding to short-term climatic shifts. In contrast to the set spatial and temporal scale of the Looijen & van Andel (1999) model, this range in the scale of processes underlying ecological communities is resolved only at a variety of scales and any community model must reflect this potential.

Introduction to the Looijen & van Andel model of ecological communities

Looijen & van Andel (1999) provided two criteria that are linked together as their approach to defining communities. The first of these could be called 'restricted membership'. Looijen & van Andel (1999) noted that researchers have defined communities as either intra-trophic level assemblages, like groups of plants or birds that overlap in their resource requirements, or inter-trophic level assemblages, e.g. incorporating plants, their herbivores, and the predators of the herbivores. Looijen & van Andel (1999) argued that the variety of combinations used to define communities is ambiguous, that this is "bound to create problems" (p. 213), and therefore they asserted that the term 'community' should be limited to taxonomic assemblages like plants, birds or insects; 'biocoenosis' should be used to refer to all of the species in an area (cf. McNaughton & Wolf 1973). Their second criterion they called 'CI' or 'Community of Individuals', and it is "the set of individuals of two or more (plant, bird, etc.) species that occur in the intersection of the areas occupied by populations of these species" (p. 218). Combined, the two criteria are believed to provide "discrete, non-overlapping spatial boundaries and within these boundaries, communities are homogeneous" (p. 218).

While the second part of their article, the CI definition, is lengthy and with considerable detail about its logical sequence, the practicality and potential of CI rests completely on the first decision to limit membership. Linkage between their two restrictions, first being the restriction of who could be considered a part of the community, the second being the definition of the boundary (CI), is necessary for this to be practical considering the variation in scale between soil organisms of a few millimetres vs 50 m high trees. In contrast to their approach on CI, the decision to restrict membership is rather ambiguous and even subject to some of the same criticisms they proposed for other definitions, for example, that taxonomic groups might be of different trophic levels (p. 213). Except for an argument concerning the competitive exclusion principle, no reasonable justification for this otherwise arbitrary restriction was provided. The failure of competitive exclusion to apply to communities

appears to lie not in definitional ambiguity, as Looijen & van Andel (1999) suggest, but in the diversity of life history traits (e.g. Grubb 1977; Parker *et al.* 1989) and in continuous temporal dynamics (e.g. Bormann & Likens 1979; Pickett & White 1985; Burrows 1990). Theoretical work on resource limitations even suggests that local depletion of resources by sessile organisms like plants will select for competitive equivalence (Pacala 1988); in circumstances with resource competition, variation in timing of establishment or other traits are more important than competitive exclusion (Grubb 1977; Keddy 1989; Goldberg 1997). The competitive exclusion principle should not be taken as an operational prediction but as a central idealization that is general and phenomenological rather than mechanistic (Pickett *et al.* 1994).

Scale issues of the Looijen & van Andel definition

The restrictions of the two decisions recommended by Looijen & van Andel (1999) result in a number of scale limitations and conflicts. Combining species of different sizes creates conflicts between the taxonomic criterion and the CI definition. Along scales of increasing diversity problems arise in determining boundaries. By setting a single and relatively small spatial scale (the aerial intersection of population distributions), Looijen & van Andel (1999) hope to achieve homogeneity. Homogeneity, however, also depends on the scale examined. Because boundaries enclose a limited array of species does not mean that each location is homogeneous for individuals within the community. The small spatial scale also forces the definition to be limited to small temporal scales as well, failing to incorporate the temporal dynamics inherent within communities. Scale limitations imposed by the Looijen & van Andel model are various, and not all would arise in every system. The following illustrates only some of these problems with their definition when applying it to actual plant communities.

Scale conflicts among species

In their restricted membership criterion, Looijen & van Andel (1999) provided no further guidelines other than taxonomy ("plants, birds or insects", p. 218). Ambiguity remains within

the guideline of "plants," as to whether all plants within an area should be considered, or whether we should restrict ourselves to certain life forms. They mention taxonomic relatedness (p. 214) but it would be unrealistic to limit a study to flowering plants, for example, and ignore co-occurring conifers, so relatedness must be fairly coarse. Because they provided no further clarification of this first part of their community definition, scale conflicts can arise. The term "plants", for example, applies to a considerable diversity of life forms, sizes and trophic types. Bryophytes are common in most communities, but the scale difference between the size of those organisms and their populations can sometimes be radically different from those of larger plants like trees. Nor is their definition restricted to organisms of the same trophic level because, for example, in the California floristic province over 200 parasitic, hemiparasitic, and mycotrophic plants are found and are widespread in every community type (Hickman 1993). The implications of this ambiguity lead to scale conflicts when applying both of their criteria for an ecological community as seen below.

The second restriction of communities as the spatial area delimited by the intersection

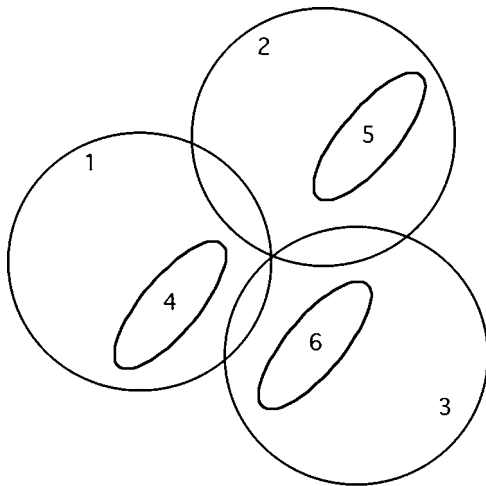


Fig. 1. Hypothetical array of species. In Case (A), each numbered shape represents a different species, as in the arrays of Looijen & van Andel (1999). The number of CI communities would be defined by the spatial intersection of distributional area of different species populations. In Case (B), circles 1, 2, and 3 represent three large individuals of redwood trees while shapes 4, 5 and 6 represent understory populations of different herb species.

of multiple population boundaries also leads to potential scale conflicts because of membership ambiguity. If we restrict our consideration to all higher plants, a variety of life forms and trophic levels can be found, for example, in coastal redwood forests (*Sequoia sempervirens*) in western North America. Large, long-lived redwoods coexist with a number of life forms from smaller trees (like *Lithocarpus densiflora*) to shrubs (*Heteromeles arbutifolia*), and parasitic or mycotrophic plants like *Corallorhiza maculata*. Understory perennial herbs like *Oxalis oregana* and *Viola sempervirens* can have extensive populations and distribution in some locations, but in most areas toward the southern end of their geographic range, their within-forest distribution can be limited to square meters. Consider Fig. 1 which shows the population distributions of six different species from this forest system. Using the same analysis as Looijen & van Andel (1999) applied in their hypothetical examples (their Figs. 1, 2), we might determine that there are nine communities (pure areas of species 1, 2, and 3, the spatial intersections or joint distributions of 1 & 2, 1 & 3 and 2 & 3, and the communities represented by the overlap of the first 3 with the species included in their ranges, 1 & 4, 2 & 5 and 3 & 6). Now consider a scale change, in which 1, 2 and 3 are actually the canopy boundaries of three individual redwoods, while 4, 5 and 6 are entire populations of different understory herbs. Adhering to a strict CI definition, a new community would be erected each time we encountered the boundaries of the range of these understory species' populations. In such a circumstance, a larger individual may encompass the entire distribution of another smaller species population. Yet, by all reasonable definitions of populations, for example distance between populations in relation to potential seed dispersal, amount of gene flow etc., these herbaceous plants will have numerous, but separate populations. When applying CI in a situation with large individuals encompassing the boundaries of entire populations, it is not clear whether the redwood individual is a member of the community created by the discrete population of herbs. If we include the whole redwood individual, then the community fails the homogeneity criterion, but if we do not, then each replicate 'community' of redwood and understory plant may or may not contain individual redwoods. The CI criterion already requires us to cut up species popula-

tions into various communities, but the definition clearly fails if we have to cut up individuals into various communities. While this may seem an extreme example, similar patterns exist in other communities containing substantially different life forms. For example, in shrub-dominated communities adjacent to redwood forests, small populations of herbaceous species like *Polygala californica* can be found beneath part of the canopy of one or two individuals of *Arctostaphylos glandulosa*.

The taxonomic criterion is thus an ambiguous approach to limiting membership in a community and not a clarification. What is contained of ecological relevance within the boundaries of a CI community as described above? Additional criteria would be required, such as a class of interactions (e.g. competition for mineral nutrients) or a type of life form (e.g. trees). Because different life forms compete for the same pools of mineral nutrients in the soil (bacteria, fungi, herbs, shrubs and trees), restricting life forms would be necessary for a practical, although functionally arbitrary, application of CI. As more criteria become added, the taxonomic restriction becomes similar to other terms referring to subsets of the community such as guilds or functional groups. In the context of their three problems of ambiguity, heterogeneity, and problem of boundaries, it appears that their taxonomic restriction combined with CI does not solve these issues in communities in which the size of individuals can be orders of magnitude different. When all plants in a habitat are the focus, an application of the CI definition yields conflicts resulting from the scale of size differences among its members and their population sizes.

High diversity, defining populations and the boundary problem

Looijen & van Andel (1999) recognized that diversity can create problems for ecologists applying their criteria that may make their approach unusable, but they felt that some type of new approach is needed and "one cannot have one's cake and eat it" (p. 219). Other than suggesting it would entail increased labour, Looijen & van Andel (1999) provided no further assessment. However, several issues are involved when working in a community of relatively high diversity. The most important of these issues is the difficulty of determining population boundaries for rarer

species. Because precise boundaries are required for their CI criterion, ironically, in systems of high diversity in which having precise boundaries is especially critical for appropriate membership and community delineation, determining boundaries is also the most ambiguous and difficult. I will consider only two issues here, i.e. the definition of populations and determining boundaries for uncommon species.

Defining a population on the landscape has as many difficulties as defining a community and is often subject to similar ambiguities. At one end of a spectrum, a population of a species may appear relatively aggregated, discrete and distant from the nearest conspecific population. In contrast, many populations exhibit decreasing density toward their margins or are widespread with extremely low densities (Pitman *et al.* 1999), and determining the boundary for one population *vs* another or whether two low density aggregations should be considered one or two populations is subject to arbitrary decisions. For those types of populations, Looijen & van Andel's criteria merely shift the ambiguity and boundary issues from the community level to the population level. While the problem appears solved for the community definition, now it becomes a multiple problem for the population level.

Looijen & van Andel (1999) also indicate that their solution may be to ignore arbitrarily some of the species within their communities. For example they state, "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' in a certain area, and, hence, to determine whether or not it is to be included in a community" (pp. 218–219).

The ambiguity of having a relative abundance threshold undermines the conceptual basis for their community model, it provides only a utilitarian approach to classification, and it contrasts especially with the hope that general laws might arise from examining "regularities in species co-occurrence patterns" (p. 221). Consider what a 1% threshold means. Typically, community dominance patterns reflect lognormal or exponential distributions from the most to least abundant species (Preston 1962; Whittaker 1975). For a community of only 30 species, over half the

species may fall below a 1% criterion. The total abundance of all these rare species still can be significant (well over 10% of the total number of individuals), but the imposition of a particular cut-off criterion introduces considerable ambiguity into what we might consider an actual community of species. An example like this is found in a study of two areas in east Africa (Maliondo *et al.* 2000). One forest type contained only 30 species with over 1000 individuals per hectare, yet 16 species (53%) were less than 1% of the total density (<10 ind. ha^{-1}). The second forest type had greater density (1606 ind. ha^{-1}) and a few more species (38 total) but 25 species (66%) were less than 1% of the density of the site (dominance patterns fit an exponential curve with an exponent of 0.925). In the first area, eight species (27%) were represented by only one individual ($<0.001\%$ relative abundance), while in the second, 12 species (32%) had only one individual (0.0006% relative abundance). This example is a forest of fairly low diversity compared to many areas of the tropics and even had 2–3 times the usual density (cf. Jones 1955; Richards 1963; Whitmore 1975; Anonymous 1978; Gentry 1992; Pitman *et al.* 1999). When considering forests that contain as many as 100 species, or 300 species, the proportion of species falling below 1% or even 0.1% begins to climb as well, until the vast majority of species are relatively rare.

Having a relative abundance criterion is an admission that setting boundaries to populations can be fairly difficult. When investigating communities with large organisms, for example forests, determining the boundary for any particular species population can be impressively difficult as their density declines to less than one individual per hectare. In the upper Amazon region of Peru, for example, Pitman *et al.* (1999) list over 88% of 825 tree species with less than one individual per hectare above a certain size in their 400 km^2 study area although most are geographically widespread; over 50% of the species never exceeded one individual per hectare in any plot. Looijen & van Andel (1999) would trade determining a community boundary arbitrarily for determining the boundary for hundreds of species, and by an equally arbitrary and difficult criterion. Critically, setting population boundaries in diverse systems appears to thwart solution to the boundary problem. In high diversity systems, even slight changes in the placement of

boundaries would result in significant shifts in species richness and the overall number of communities by the CI criterion.

Another issue concerning diversity is whether communities are homogeneous as diversity increases. Looijen & van Andel (1999) leave homogeneity in a community an undefined term, yet it is a characteristic of communities they expect would arise from their definition. My interpretation is that they mean that large samples taken in any one area would have the same combination of species as in another area. For there to be actual homogeneity within any of their communities species would have to have a constant age and density throughout, in contrast to the usual pattern of aggregation of individuals and variable age classes. As Looijen & van Andel (1999) wish to define communities by individuals rather than populations, consider homogeneity from the perspective of an individual. In a community with as few as two species of the same life form, there can be a number of biotic conditions from the perspective of an individual. Assume an individual, for example, is surrounded by only six other individuals, then a two species community system will have potentially seven different biotic environments from the perspective of individuals, because the six surrounding trees could be found in seven different combinations of two species. Even if one species were fairly dominant, e.g. 70% of the individuals and the second 30%, considerable heterogeneity would still exist in biotic environments, with no one combination being more than 32–33% of the total (determined by solving $a^6 + 4a^5b + 7a^4b^2 + 8a^3b^3 + 7a^2b^4 + 4ab^5 + b^6$). With increased diversity in a community, the possible combinations also increase at a greater rate.

Scale and temporal dynamics

Setting a relatively small spatial scale by the CI criterion also requires a small temporal scale. A strict compositional criterion means that the loss or gain of any single species changes the type of community (p. 220, Looijen & van Andel 1999). Because community composition changes constantly on a variety of temporal scales (Miles 1979; Davis 1981; Pickett & White 1985; Williamson 1987), the usefulness of the CI criterion is limited because the communities may not last long enough to finish any research. This lack of a temporal scale in the CI model excludes most

dynamic community concepts like patch dynamics, succession or fluctuations. Because of the extensive literature on temporal dynamics, I will raise only a few issues.

The persistence of any particular CI community will depend on environmental variation and turnover rates of species. Communities containing annual species will be subject to the greatest disruption in classification. Arid and semi-arid sites can have communities of great diversity (Axelrod 1977; Turner 1982; Mares 1992; Hickman 1993; Archer *et al.* 1999). The proportion of annuals in annual grasslands and in many desert communities can be well over half the species found in a community (Turner 1982; Turner & Brown 1982). The problem for the CI definition in these kinds of systems is the incredible dynamics of the species populations. Annual grasslands in California, for example, are subject to large and unexpected shifts in composition and dominance (Hobbs & Mooney 1995). In a desert community, the presence of an annual species, its abundance and distributional extent all depend on the pattern and amount of rainfall occurring in any one year (Beatley 1974). In these types of communities then, each year can result in significant changes in the distributions of species and even whether they are present (except in a dormant seed bank). The CI criteria do not incorporate appropriately the dynamics of annual species populations in any of these systems. Rather than understanding the range of compositional potential with annual environmental flux as a part of a dynamic community, Looijen & van Andel (1999) would have the number and extent of CI communities change radically with each year.

Communities also are subject to localized disturbances that initiate compositional changes for which the CI concept appears inappropriate. Often, species may be specialized to recruiting only after such disturbances. Communities characterized by fire, for example, often have a large number of species that re-establish only after a burn resulting in substantial compositional change (e.g. Keeley 1991; Keeley & Bond 1997). For many of these 'patch' species, their populations can be widely separated, and their distribution and abundance dependent on the disturbance regime of an area (Pickett & White 1985). In forests, trees that only recruit following disturbance tend to have shorter longevity than species able to recruit in the shade of closed canopies (Bormann & Likens 1979). In the

context of the CI criterion, a forest containing shade-intolerant patch specialists as well as shade-tolerant species, instead of having different functional groups within a single community, would be classified into a number of communities based on the size and composition of patches. Further, as these patches age and shade-intolerant species begin to decline, composition shifts. Each loss or gain of a species changes the CI classification. Along a range in sizes of potential disturbances, from single tree falls to large, landscape-altering wildfires, the response of the CI model is constant change in the number, extent and identity of community classifications. In the context of disturbance and patch dynamics or successional change, the CI criterion fails to incorporate the range of compositional potential for what ecologists otherwise describe as a single multidimensional community with temporal dynamics. The inability of the CI model to include a variety of functional groups that respond differentially to disturbances of different types, sizes or frequencies, suggests a remarkably static and ecologically irrelevant concept.

Reification of communities: are CI communities analogous to pure chemical substances?

The most radical extension of the proposal of Looijen & van Andel (1999) is their assertion that CI communities are fundamental entities. They propose that the CI approach yields a number of results, most importantly clear boundaries and homogeneity. From this result they claim that general laws about communities or species co-occurrences finally may be possible (p. 210, 213, 217, 221). The leap from spatially and temporally restricted assemblages to general laws is not obvious, but the insight comes from their analogy of CI communities with characteristics of organic chemistry. "One may compare this to developments in organic chemistry, where enormous progress was made once 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" (p. 220). Their analogy with chemistry, that rapid progress was made after chemists learned to use "pure substances," claims that the use of their community definition will generate a biotic parallel to pure chemical substances.

For their analogy to be appropriate their communities must have at least three other characteristics in addition to clear boundaries, 'homogeneity' and a 'constant and unique species list'. The pairing of 'pattern and process' reminds us of the fact that their 'pattern', unique composition and homogeneity, actually results from a history of underlying biotic and abiotic processes. The standard of a loss or gain of a single species for distinguishing communities also hypothesizes a shift in underlying processes with each species change. The CI species list must be representative of all processes influencing species composition, and each CI community must reflect a unique combination of processes or history. Replicates of each CI community across the landscape must reflect, just as accurately, the same set of processes, otherwise, each 'community' would be convergent in their species lists, but not in the underlying processes that influence, support, maintain, or enable that species list. If they do not represent the same set of processes, then the CI approach to communities will not accurately represent something analogous to chemical 'pure substances' because of their incongruity from one location to another. Like pure substances, each community must also be independent from one another. Processes arising in a given community must not significantly influence the composition of any other community. Therefore, for the CI communities of Looijen & van Andel (1999) to achieve anything like their goal in the chemical analogy, their communities must include three additional characteristics: (1) each CI community (species composition) must represent a different set of biotic and abiotic processes or thresholds from adjacent communities, (2) every replicate of the same community across the landscape must represent the same set of processes and thresholds, and (3) each community must be independent from every other.

For these three characteristics to be true, communities would have to be controlled completely by internal processes. Only assembly rules approach such a possibility (Drake 1991; Keddy 1992; Wilson 1994; Wilson & Roxburgh 1994): However, assembly rules may be lacking or unpredictable for any particular community (Drake 1991; Wilson 1991) and may work better when considering traits rather than species identity (Keddy 1992; Weiher & Keddy 1995).

The significant influence of contingency in ecological systems (McNaughton 1983; Berlow 1997; Parker & Pickett 1998; Lawton 1999) suggests that finding a single CI community in which one or more of these three characteristics are not violated would be difficult. Great heterogeneity exists in the dynamics of populations at a community level. The same processes may not produce the same pattern of species (Sutherland 1974, 1990; Petraitis & Dudgeon 1999) and under some circumstances radical compositional shifts can occur following events that normally reinforce that composition (Zedler *et al.* 1983; Haidinger & Keeley 1993). Suitable habitats where a species should be found but is missing, or sites where a species is found in unsuitable habitats both violate the first two characteristics. Considerable research indicates that it is rather common for species to have local extinctions and re-colonizations and to be absent from suitable sites (McCune & Allen 1985a, b; Hanski 1994, 1996; Kadmon & Pulliam 1993, 1995; Venable & Brown 1993) or for dispersal or reproduction to limit the ability of species to return to suitable sites (Venable & Brown 1993; Eriksson & Ehrlén 1992; Primack & Miao 1992; Eriksson 1996; Tilman 1997; Brunet & von Oheimb 1998; Clark *et al.* 1998). Empirical evidence also indicates that high dispersal rates can establish and maintain populations in habitats that cannot sustain them (Lidicker 1975; van Horne 1983; Kadmon & Schmid 1990; Pulliam 2000). The development of source-sink theory predicts that this may be a rather common occurrence (Holt 1985; Pulliam 1988, 1996; Pulliam & Danielson 1991), although sometimes weak (Kadmon & Tielbörger 1999). In some cases the majority of species co-occurrences may be in sink habitat (Pulliam 2000). Together this research establishes that combinations of species at a particular site as well as the processes that produced that pattern are not consistent among sites or across a landscape.

Because processes of various scales impact and maintain the composition of any particular location, the likelihood of any CI community being independent is small (Ricklefs 1987; Cornell & Lawton 1992; Ricklefs & Schluter 1993; Turner *et al.* 1993; Caley & Schluter 1997; Wu & Loucks 1995; Parker & Pickett 1998; Gaston & Blackburn 1999). The source-sink dynamics discussed above establish that preventing dispersal would sub-

stantially simplify the composition of any community (Pulliam 2000). Studies of fragmentation of habitats reinforce this conclusion even though processes may vary among locations (Saunders *et al.* 1991; Crooks & Soulé 1999). Following fragmentation, resident species are lost through time (relaxation or extinction debt; Diamond 1972; Saunders *et al.* 1991; Tilman *et al.* 1994; Loehle & Li 1996; Gonzalez 2000). The minimum dynamic area (Pickett & Thompson 1978) can be substantial for any particular community and for some communities even extremely large areas are thought to be well away from equilibrium (Wright 1974; Romme 1982; Baker 1989; Sprugel 1991; Turner *et al.* 1993).

Because CI communities lack these three characteristics of unique processes, consistency of processes among replicate CI communities, and independence from other communities, the search for general laws will have to start somewhere else. Even though Looijen & van Andel (1999) recognize the openness of communities and attempted to develop a neutral model with respect to processes, their intention of developing a fundamental entity for communities involved the very problem of 'reification' or 'objectification' (Palmer & White 1994; Parker & Pickett 1997) that they were trying to avoid.

Developing a conceptual basis for an ecological community

At this point I want to reconsider the *concept* of an ecological community. Looijen & van Andel (1999) provided a definition and a brief analysis of the diversity of current definitions and how their CI definition might resolve boundaries between communities and consequently reduce heterogeneity; but no development of a general concept resulted. Historically, ecologists have been interested in the distribution and abundance of species regardless of a focus on community classification or on interactions among species. Physical factors clearly influence composition, but so do biotic factors like trophic or mutualistic interactions. Species clearly differ in their adaptations to these influences. Because every location varies in its combination of physical and biotic influences, species sort differentially and have unique distributions. Temporally, composition changes as environmental shifts occur. A concept of community must be able

to incorporate all these characteristics as well as the ecological and evolutionary potential implied. Developing such a concept at length is beyond the scope of this paper, but to contrast with the Looijen & van Andel (1999) model, some kind of initial proposal is required.

An appropriate starting point is needed to develop a concept of a community. Definitions for 'community' often have no logical derivation other than the convenience and interest of the researchers and usually at some 'whole community' perspective. Conceptual arguments often focus on issues of boundaries (e.g. McIntosh 1985; Shipley & Keddy 1987; Looijen & van Andel 1999). When ecologists are interested in competition, they tend to restrict their definition to groups that might be competing for limiting resources. If the research tests trophic regulation of community structure, then species interacting among different trophic levels are included. These limited extents of a community help to focus research questions but exclude significant portions of any particular organism's total environment. Every individual organism is impacted not only by physical factors, but exists in an environment modified and influenced by an array of other organisms. To develop a community concept, rather than starting with a community assemblage, consider instead the community of a *single* individual. What other individuals are significant influences on the establishment, growth, survival or reproduction of this focal individual? – From this focal individual organism perspective, its community is other individuals of its own species with which it reproduces, and individuals of other species with which it interacts, for example individuals with which it competes or from which it obtains resources. In other words, the community of this individual is all other individuals with which it interacts (Fig. 2). Temporally, the particular composition of the interaction web will change as new individuals arrive, populations turn over or others die. Other individuals that influence the abundance and distribution of those directly interacting with our focal individual (Fig. 3) further modify interactions. The *concept* of community is this web of interactions, direct or indirect, that constructs the biotic environment of individuals. Developing ecological community concepts from interactions has a long (Haeckel 1866) and continuing history (e.g. Pickett *et al.* 1989; Menge 1995).

To scale up to the population level, a web of interactions is built with populations as nodes. The web summarizes interactions with individuals of the same focal population. Each individual of the population does not experience the exact same biological community,

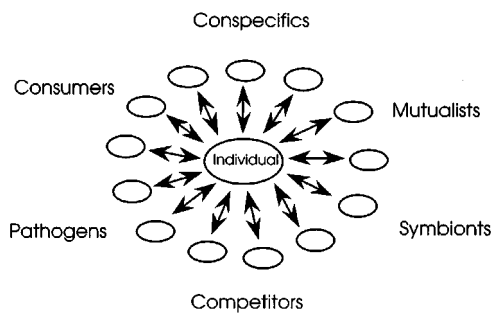


Fig. 2. Representation of a web of interactions from the perspective of a focal individual. Only direct interactions with the focal individual are illustrated.

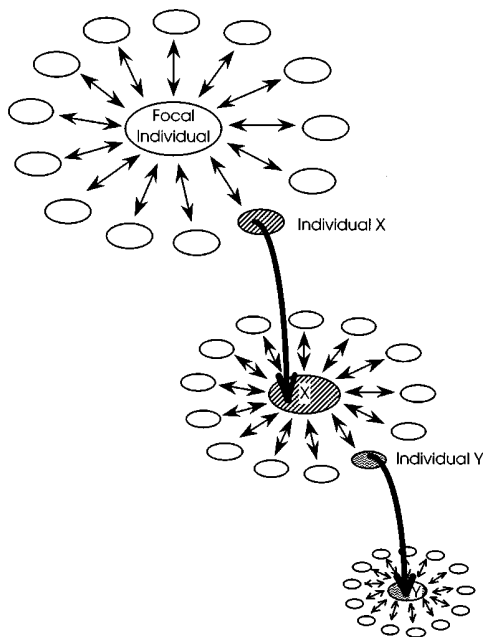


Fig. 3. Three individuals and their interaction webs are represented. All individuals interact with a large number of other individuals, each having their own unique web of interactions. Indirect interactions arise through influence on those interacting with the focal individual. Individual Y in the lower right of the figure, for example, interacts indirectly with the focal individual by its actions on Individual X which interacts directly with the focal individual.

but often there is rough concordance. For example, while some individual trees may differ in the collection of mycorrhizal fungal species associated with their root systems, they all do interact with symbiotic fungi and potentially any individual tree-individual fungus pairing is possible. As a consequence, we can describe probabilistically the potential community experience for a particular population and circumscribe the range of species with which it is likely to interact (Fig. 4).

To scale up to a spatial site, all individuals resident at the site become interconnected by their interactions (Fig. 5). The limit to this community web becomes difficult to determine, because the other organisms that interact with individuals at any site each have an interactive web themselves (Fig. 3), and a further group of species that modify the abundance and distribution of those web members. All species that exist within the spatial boundaries are incorporated and also the species with which they interact, including mobile species that may not currently reside at that site. This type of community web may be remarkably interconnected, such that species are separated by only a few links. Researchers investigating the structure of food webs, for example, have found that in trophically well-documented communities the num-

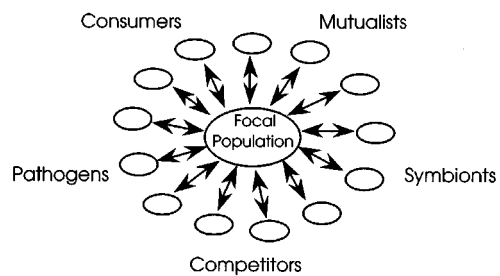


Fig. 4. Representation of the community of a species population. The circles represent different species populations and the links represent interactions. This community web is based on interactions that occur between individuals of the focal population with individuals of other species populations. The linkages represent a summarization of the slightly different interaction webs of the individuals comprising the population. Because not all individuals will experience the same web of interactions, the linkages actually represent probabilities of interactions among individuals of two populations. Only direct interactions with the focal population are illustrated.

ber of trophic links separating any pair of species averages two links (Williams *et al.* 2001). Incorporating other kinds of interactions takes this a step further, linking all species directly or indirectly with one another (Bender *et al.* 1984; Kerfoot & Sih 1987; Menge & Sutherland 1987; Menge 1995, 1997; Strauss 1991; Wootton 1994).

Contrasts between the focal-individual and CI models

The 'focal-individual model of the community' contrasts in a number of ways with the CI model of Looijen & van Andel (1999). Central to these contrasts is the reliance of the focal-individual model on interactions while Looijen & van Andel (1999) reject interactions as a definitional criterion. The focal-individual model uses a web of interactions to build a structure that incorporates direct and indirect

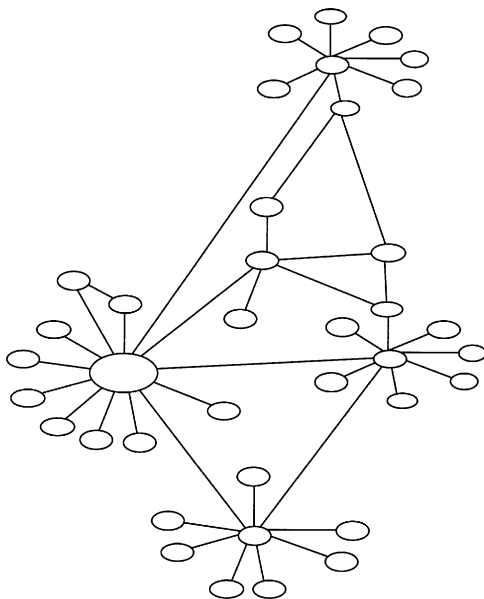


Fig. 5. A web of interactions connecting a number of individuals of different species representing only a small part of a community based on some spatial extent. All individuals are interconnected directly or indirectly with all other individuals. While not all individuals are shown, the essentials of individuals interconnected by interactions, of some individuals having more connections than others, and of the potential for shared predators or herbivores are all represented.

interactions, but one that is indefinite in the extent of the linkages. The structure involves the participation of all individuals at a site as well as by mobile individuals that currently may not be present. The focal-individual model, consequently, lacks specific spatial or temporal boundaries. These characteristics differ from the CI model, which specifies a restricted membership, boundaries, and consequently a limited spatial/temporal scale. Two issues, inclusive vs restricted membership and the absence vs the presence of community boundaries, reflect fundamental differences in emphasis and approach between the two models and are expanded on below.

Restricting membership of a community as proposed by Looijen & van Andel (1999) not only involves the ambiguities involved in determining what species belong to the particular taxonomic criterion, but also whether the excluded species influence the presence or abundance of the selected species. The ambiguity that Looijen & van Andel (1999) discussed as a problem for ecologists is how researchers define what they investigate. For the purposes of an investigation, an operational 'community' may be only a designated subset of the actual community of which ecologists will ask research questions. Looijen & van Andel (1999) also propose that ecologists work with a subset, but by using the taxonomic criterion. Because their subset is not an independent assemblage or functional component, but an arbitrary grouping by taxonomy and population boundaries, their CI subset does not isolate any particular ecological function. When ecological groups are not isolated, there can be substantial influence from outside the focal subset. A problem arises if the outside influence acts differentially on the focal subset.

When ecologists define the group on which they wish to focus, that does not remove those species from the overall community and does not prevent their interaction with species not considered (Fig. 6). For a particular research question, the inherent working assumption always exists that other community members do not impose a significant differential impact within the focal subset, such that experiments, observations or interpretations are invalid. The ambiguity is not in what the community actually is, or that ecologists use different operational definitions, but whether researchers recognize the existence of this assumption of no differential impact. Hierar-

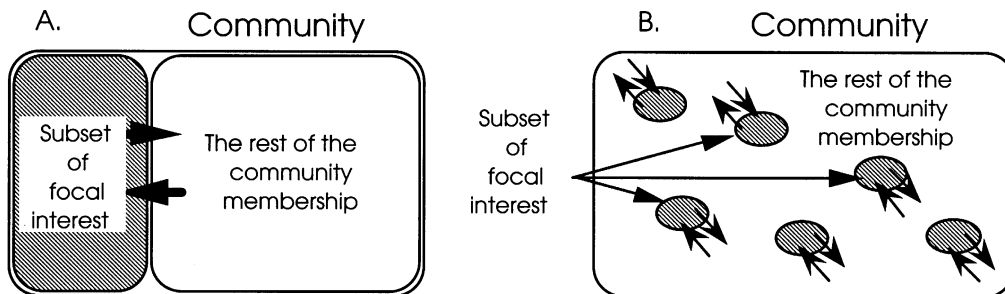


Fig. 6. Representation of all the species or individuals of a community separating out focal research assemblages from the rest of the community. A and B represent two different versions of the same concept, that ecologists usually choose to focus their specific research on a subset of species of the entire community. At the same time, other individuals of the community continue to interact with the subset of focal interest, and in some cases may differentially affect a portion of the focal group.

chical approaches have implied this assumption, the 'subset' community being thought of as the focal level, and the total community as the level above, or the context or constraining level (Allen & Starr 1982; Pickett *et al.* 1989; Allen & Hoekstra 1992), but the potential for differential influence is not clearly indicated. Differential influences by other members of the community potentially creates much of the biotic source of contingency in community research (Strong *et al.* 1984; Huston 1994; Lawton 1999). Restricting the definition of community to a taxonomic group as in the CI model of Looijen & van Andel (1999) is subject to the same error. Using 'community' for the subset studied and 'biocoenosis' for the entire assemblage of organisms (Looijen & van Andel 1999) does not solve the ambiguity but actually may continue to confuse the issue because of the pretense that a CI community is somehow independent within the biocoenosis.

Direct and indirect effects studied in a number of communities clearly indicate that the assumption of no differential influence can be violated. When competitors are defined as the 'community' of interest, the assumption is that predators or other community members do not impose a differential influence. Holt (1977), for example, distinguished between direct and apparent competition among species and developed a model in which abundance of two trophically similar species could be regulated by shared enemies. He deliberately set up his model so that the two 'competitors' would have no resource overlap in his first model, to be able to distinguish between direct and apparent competition. The

differential influence of shared enemies has been verified whether species do or do not share resources (Bonsall & Hassel 1998; Crooks & Soulé 1999; van Nouthys & Hanski 2000). In some cases the species at greatest abundance erroneously was interpreted as the better competitor (Tomkins *et al.* 2000). While studies have focused principally on trophic interactions, indirect interactions have been found to be significant in a variety of circumstances (Levine 1976; Vandermeer 1980; Walker & Chapin 1987; Abrams 1992; Sousa & Connell 1992; Wootton 1994; Menge 1995; Sinclair *et al.* 2000), including facilitation between competitors (Callaway & Pennings 2000).

Finally, the focal-individual and CI model differ on the importance of boundaries. The CI model suggests the potential for clear and unambiguous boundaries. In contrast, the focal-individual model lacks clear boundaries, spatially or temporally. Because any individual at any location is the focal-individual in its community, boundaries as interpreted by ecologists based on the distribution of one or several species generally are arbitrary with respect to the experience of any individual organism or ecological process. Interactions do not cease at a perceived boundary, and, in fact, what ecologists consider 'boundary regions' or 'ecotones' may represent very active areas of evolution (Smith *et al.* 1997; Schneider *et al.* 1999). If that is the case, then from an ecological perspective of interactions, ecosystem processes, evolutionary changes, or any class or specific mechanism considered, all can occur at any place and time.

The natural groups we think of as communities reflect spatial similarity in the distribution of processes linking together similar suites of species, yet communities do have ambiguous boundaries because processes, linking interactions, or mobile community members all rarely stop at a single spatial place (i.e. communities are 'fuzzy sets', Scheiner *et al.* 1993). Whatever criteria are used to determine communities, species composition or traits of the members such as life forms, or life history characters (Keddy 1992; Weiher & Keddy 1995), each shows independence from other criteria either spatially or temporally (Whittaker 1973). Finally, the goal of determining particular spatial boundaries for a community imposes a false spatial scale as it may only encompass the range of sessile members of the community. For the grassland systems of eastern Africa as one example, the long-ranging grazer populations would not be incorporated into a CI approach, yet the role they play in the overall distribution and abundance of plants in these grassland communities is fundamental (McNaughton 1983, 1985).

Conclusions

The concept of an ecological community incorporates the dynamics of populations in the context of interactions with multiple species. Any specific definition, therefore, must incorporate a large number of concepts to be ecologically relevant. These include species specific dynamics that occur on different spatial and temporal dimensions like metapopulation dynamics and source-sink dynamics. Multi-species dynamic patterns such as patch dynamics must also be incorporated, or response to disturbances like fire, drought or climatic fluctuations (e.g. El Niño events). A community concept must also incorporate other patterns of sorting or species dynamics such as succession or range extensions. Finally, the definition must be robust enough to incorporate conditions appropriate to evolutionary potential.

'Community' admittedly has been used often as a concept of convenience for ecologists and the implications of its structure rarely have been articulated. The multidimensional uses of the concept, however, reflect different approaches to investigate processes underlying its structure and dynamics. Processes that act on organisms arise at a vari-

ety of scales, some small enough or discrete enough that ecologists speak of metapopulation dynamics (Hanski 1994, 1996) or patch dynamics (Pickett & White 1985), but other processes are of regional scale like climate for which characteristics of life form are often more important rather than species identity, e.g. the convergence of life form and life history adaptations in mediterranean-climate regions (Mooney 1977; Keeley & Bond 1997).

Looijen & van Andel (1999) challenged current community concepts, and, because of perceived problems, developed their own definition. The 'problems' of ambiguity, boundaries, and heterogeneity are not actually problems of community definition, but are characteristics of communities. They reflect the reality of the ecological tableau. Rather than develop a scalable, multidimensional community concept, Looijen & van Andel (1999) proposed two criteria that limit the scale and dimensionality of ecological communities. The lack of independence and process consistency of their entities defeat their assertion that such entities might be the basis for the development of fundamental ecological laws. Their desire to clarify approaches for the classification of communities is admirable, but their specific approach lacks ecological relevance. Confining multidimensional entities to a single spatial-temporal scale is the arbitrary behaviour, not the ambiguity of boundaries between communities in attempts to identify or classify them.

The alternative focal-individual model of the ecological community, emphasizes a web of direct and indirect interactive linkages among individuals. Because this model has no specific spatial or temporal boundaries, it can be scaled to fit processes investigated. Source-sink dynamics, patch dynamics, succession or other ecological concepts may arise at different spatial or temporal scales depending on the community or the particular species involved, therefore, it is important that the community concept be scalable. This model also structurally indicates that when focal subsets are segregated for particular research questions, other species may have differential impacts. Additionally, is the recognition that only some community members are sessile, or as in the case of open water communities, no members may be sessile. Nonetheless, the proposed focal-individual community model permits all interacting members to participate.

Recognizing the multiple temporal and spatial dimensions that communities can assume is fundamental to successful advancement of ecology and its application. The issue that Looijen & van Andel (1999) draw attention to, the classification of communities, is an important issue, especially in light of its application to conservation. Nonetheless, it is circumscription and classification that is arbitrary. Boundaries between competitors would not be the same as between mutualists. For any process considered, a different system scaled to that process might be required. Finally, difficulties appear to arise whenever definitions constrain a multidimensional entity like the ecological community. Once constrained, spatial and temporal scale conflicts defeat the definitional limits.

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