

## Forum

# The concept of the ecological community and a clash of perspectives: A reply to Looijen and van Andel

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## Introduction

At any location, the assemblage of resident organisms is continuously changing. Whether considering a temporal scale of less than a year or more than a thousand years, natural systems are dynamic. Looijen & van Andel (1999) developed a definition of an ecological community that would impose such constraints on the concept as to render it impractical for many ecological questions. With respect to the history of most research conducted at the community level of organization, their definition is irrelevant. I critiqued this approach in a number of ways (Parker 2001), to which Looijen & van Andel (2002) find exception.

Looijen & van Andel (2002) have responded to my critique of their CI concept of the community (Parker 2001) by redescribing much of it, providing further background on phytosociology, modifying their CI definition, contending that I have confused description with explanation, but generally failing to respond to the principal issues. Ultimately, we apparently can come to no logical common ground because our perspectives of communities are too different. Looijen & van Andel (2002) continue to view the dynamic community as a static object that can be understood only by an extreme reductionist approach. They view their Community of Individuals concept (CI) as a solution to perceived problems although in their recent response focused on phytosociology rather than ecology more generally. I remain unconvinced that their approach will yield any useful insights, even for community classification, and, in fact, consider it as a model of something outside of mainstream community ecology.

One issue appears to need clarification. They indicate that their objective is to explicitly separate the concept 'community' from that of 'biocoenosis'. They correctly note that I do not appear to make this distinction. Biocoenosis is simply a redundant term to community. This was a critical distinction for them because of their perception that ecological communities require two characteristics, clear boundaries and homogeneity. Their philosophical puzzles appear rooted in an essentialist philosophy that does not apply to community ecology. I will contend, again, that a more effective ecological perspective is that the organizational level above 'the individual' is 'all individuals of all species.' Ecologists usually focus on subsets of these, for example, populations of a particular species or some different subset like guilds or functional groups. Nonetheless, as I indicated previously, any focus on a subset (a logical decision for studying a particular issue) requires an assumption that the context (those individuals not in the study) does not have a differential influence (Parker 2001). Ecologists generally assume that multiple sites, randomly chosen, take into account any potential differential influence.

I will respond first to their recent article by discussing some of the issues not resolved by their approach or their response, specifically, issues of scale, problems in determining boundaries because of rarity or low population density, and temporal dynamics. Finally, I think a more fruitful resolution to this debate is to clarify the differences in the perspectives between myself and Looijen & van Andel as I perceive them.

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The final part of this article addresses these differences.

## Scale

Looijen & van Andel (2002) assert that their model has no problems with scale because they believe that they are using one level of scale, which to them means one cannot have a scale conflict. What they mean, perhaps, is that they are using one level of organization, populations in the first article. While they suggest that I was confused about level of organization and scale, the confusion appears to lie with their own argument. Looijen & van Andel fail to see that individuals can be of substantially different sizes (*scale*), even though they are a part of the same *level* of organization. My question was simple. When applying the Looijen & van Andel "intersection of population boundaries" criterion, one may capture only a portion of a large individual from one population (*Sequoia sempervirens*, redwood) 'intersecting' with the entire population of a smaller plant (*Oxalis oregana*, redwood sorrel). Looijen & van Andel attempt to escape this ambiguity of whether part of the 'canopy' belongs with the *Oxalis* by reasserting their criteria and describing the main stem of the redwood as being 'inside' the population of the *Oxalis*. I remain curious about the bookkeeping terminology when the *Oxalis* population does not surround the main trunk of the redwood, a far more frequent occurrence. The principal point seems to have been ignored, however, which is what the value is of such a 'community' definition in systems with substantial difference in the *scale* of the organisms involved. Far from being irrelevant, size differences impact the practicality and value of the whole approach and call attention to the conceptual narrowness of their definition.

## High species diversity and low population density

In the frequent case of many species being relatively rare and the boundaries of their populations being difficult to determine, Looijen & van Andel have agreed with the substance of the criticism I suggested previously. In agreeing with the ambiguity of attempting to define a community boundary by the equally difficult problem of defining a population boundary, however, they have chosen to modify their original definition now to the intersection of local distributional areas rather than areas occupied by populations (Looijen & van Andel 2002). However, 'local distributional areas' is an undefined term that may mean many things to different ecologists. Looijen & van Andel do not clari-

fy this term any further when they indicate that rare species with low density (one individual per hectare) may have a local distributional area 'so large' that this species may intersect or encompass many other population boundaries. Local distributional area becomes a troublesome and ambiguous term. The solution suggested is to not worry about the population boundaries of uncommon or rare species, and simply count them inside the intersectional areas (CI) of other populations that are easier to interpret, and assume their local distributional area is large. While this seems a practical solution, it contrasts greatly with their interest in solving the 'great' problems of communities, boundaries and homogeneity, because by ignoring the population boundaries of all the rare and low density species or avoiding how to define those ambiguous boundaries rigorously, they become conceptually contradictory because in some cases determining clear boundaries is critical (especially for their type-token distinction and the generation of ecological laws) but in other cases it does not matter.

## Probabilistic distribution of individuals and application of CI

Another example of differences between our perspectives concerns the probabilistic distribution of individuals. Individuals are likely to be missing from sites they should be found, because of vagaries in temporal processes (Pickett & White 1985; Hanski 1994, 1996; Wu & Loucks 1995) and similarly individuals can be found in sites within which they cannot maintain themselves (Pulliam 1988, 2000; Wu & Vankat 1995). Problematically, the association of any set of individuals and any set of processes is probabilistic; using the philosophical terminology Looijen & van Andel embrace, the *explanans* may not explain the *explanandum*. Looijen & van Andel (2002) are excited about individuals not being in sites they should or being found in places they should not. They feel such circumstances represent examples of classification systems being falsified. Their conclusions about falsification represent a decision to ignore the probabilistic nature of ecological phenomena, such as the particular distribution of individuals, and instead to develop a framework about the ecological world within a historical philosophical model. Additionally, their reification of CI communities in their earlier publication, their embracing of the 'necessity' of types and their refusal to incorporate the significant influence of contingency in ecological systems supports this interpretation. The probabilistic distribution of individuals and species means that CI is not relevant. Their discussion of falsification and of 'types' for their CI communities indicates that they embrace an essentialist philosophical tradition.

### Application of CI beyond classification: Temporal dynamics

Looijen & van Anandel (2002) respond to issues of understanding temporal change in a community by simply indicating it was their intention to incorporate no temporal change. If temporal change occurs, then the 'type' changes. Rather than providing an insight into how communities may change and the range of spatial and temporal scales at which change may occur, Looijen & van Anandel would have no community experience change, but rather, have ecologists involved in extensive bookkeeping to describe replacement of types spatially and temporally. For example, rather than an understanding of how a forest canopy disturbance may shift constraints to permit shade-intolerant tree species a differential opportunity to establish, we would only recognize community type replacement; should a new invasive species appear, we would only recognize community type replacement. Their response (Looijen & van Anandel 2002) is that their definition creates distinct entities and it does not matter that temporal dynamics must be termed changes in community types. No intellectual gain in understanding occurs with the application of the CI model. In my opinion, the narrowness of the conceptual scale and framework of CI renders it a useless, irrelevant concept. Change is ultimately what ecologists study, the 'types' are more often the functional groups involved and not the particular composition of a stand. The name of the community is a convenience and the particular composition is simply an example community.

### Application of CI beyond classification: Different collections of species

In practice, using separate terms for the entire biological system (biocoenosis for Looijen & van Anandel) and arbitrary taxonomically-restricted subsets (CI for Looijen & van Anandel) can be problematic because it is only one way of conceiving ecologically relevant organization. Looijen & van Anandel erect a philosophical structure within which they insist it is logical and necessary to restrict communities taxonomically, rather than as an epistemological choice of the investigator for a particular question. An ecologist that wishes to study, as a group, plants and their dispersal agents (birds and mammals), or perhaps above-ground food webs of an area, is left with a terminological conundrum using CI. Neither CI 'communities' nor an entire biocoenosis would represent these sets of organisms. Do we need to derive an alternative terminology (and definitions) that can accommodate these types of circumstances? The first criterion of Looijen & van Anandel (taxonomy) provides an arbitrary and unnecessary constraint on our

ecological approaches and understanding. No general application of CI exists for ecologists that study something other than only plants or only birds. We only gain ambiguity and confusion from being forced to consider the interactions between *some* of the members of a *series* of plant and animal CI communities just to focus a research question on dispersal or material/energy flow.

### Concept of the ecological community: The philosophical divide

The fundamental differences between the community concepts of Looijen & van Anandel versus myself lie in the scale and perspectives that we hold. Looijen & van Anandel (1999, 2002) are focused on the issue of plant community classification and attempted to erect a framework of specific definitions (CI communities, biocoenosis) to achieve their goals. That is an acceptable research agenda as far as it goes. Depending on the research question, ecologists define an assemblage spatially and temporally appropriate for the question. My problem with their framework was their assertion of generality and the expectation of ecological laws flowing out of the use of their definitions. The focal definition, the CI (community of individuals), abandons the current usage and direction of how communities are conceived (e.g. Underwood 1986; Drake 1991; Polis & Winemiller 1996; Williams & Martinez 2000; Hubbell 2001; Kinzig et al. 2001). They desire taxonomic and compositional homogeneity with clear boundaries as their requirements, but there exists no linkage to clear or homogeneous ecological processes or phenomena.

In contrast, I understand the core concept of the 'ecological community' as an interacting group of individuals representing different species. This is an unbiased and inclusive definition that is scale independent. The focal individual model developed previously (Parker 2001) is consistent with this core concept and had the goal of illustrating several features. One was that the characteristic of 'multiple species' is not restricted taxonomically and that any individual may interact with a broad diversity of species types. Thus the immediate community of any individual is comprised of conspecifics, but also pathogens, mutualists, competitors, etc. (Fig. 2, Parker 2001). Secondly, a goal was to illustrate the persistent contextual influence of indirect interactions because each individual is a 'focal-individual.' This indicates both the arbitrariness of focusing on any assemblage that restricts membership and of the potential differential influence on some of the focal group by the context. Finally, an objective was to indicate the extent of differences in life span and mobility among species within any system and consequently the ambiguity of boundaries. The focal-

individual model does not suggest that there is no clear model for ecologists to use, however, because the trend in ecology is to recognize these kinds of issues as well as the spatial context involved (e.g. Bender et al. 1984; Kerfoot & Sih 1987; Menge & Sutherland 1987; Menge 1995, 1997; Strauss 1991; Wootton 1994).

The principal conflict between our community models lies in the use of interactions as a criterion. In their first article, they suggested that interactions would not be a useful criterion because interactions would cross any boundary (Looijen & van Andel 1999). Because I do not feel that strict boundaries represent a useful ecological concept, I have no problem with interactions crossing human-imposed, arbitrary boundaries, and in fact that was one of the illustrations of my focal-individual model. Looijen & van Andel have difficulty with my model because it offers no criterion for distinguishing different communities from one another. Of course, that was one of the points, that criteria for distinguishing different communities are arbitrary decisions of the researcher, dependent on the question being posed. Whatever criterion is used will diminish the information contained in the system. In the second article, however, they suggest that interactions may play a role in the explanation of the structure and dynamics of communities and therefore should not be included in the definition of the concept (Looijen & van Andel 2002 – however, they then contradict themselves and indicate that interactions can be used to characterize communities or biocoenoses and give the example of food webs).

The critical issue here is their insistence on the separation of 'explanans' from 'explanandum' or explanatory processes from the community concept in the context of how they interpret the concept 'interactions.' Looijen & van Andel fail to distinguish between different dimensions of the concept 'interactions.' One dimension of 'interactions' is structural, in other words, a description of the network of interactions that exist in an ecological system. Another dimension is the nature of particular interactions, or their type, direction, magnitude, frequency and other characteristics that would, in fact, influence the existence, distribution and abundance of species within a community. The first characterization of interactions permits its use as a criterion for determining what individuals are relevant members of an ecological community; the second characterization of interactions would be used for investigating differences in frequency, abundance or dynamics. It seems obvious that the criterion of 'does an interaction exist' is different from the nature of an interaction, but only the latter would be the basis for any 'explanation' in their philosophical sense (explanans). Their failure to make this distinction suggests an over-idealized approach to ecology.

Given the distinction between the characterization of interactions as both a structural feature at one level and underlying processes at another level, then interactions provide a significant insight into the organization of ecological systems from a community perspective. That insight is that the level of ecological organization above that of the 'individual' is 'all individuals of all species.' All types of species influence other types of species directly or indirectly. Of course, research on all individuals in any spatial and temporal extent is rare. Ecologists generally focus on a subset of the community because of the nature of the question asked. Most ecologists realize this and attempt to limit the constraints on this type of approach by using multiple randomly-chosen sites and controls. A limited array may be used to study a particular set of processes, for example, 'guilds' may be examined to determine the extent of competition among members, or 'trees' may be examined to determine competition or interference processes for entering the canopy of a forest, or 'food webs' may be studied for material/energy flows among a collection of autotrophs and heterotrophs. But in each case these are subsets of the community and care must be taken to account for potential differential influences on the array of individuals investigated in any particular study.

## Summary

Ecology needs definitions that are not only clear and appropriate, but that are flexible for scaling to the variety of phenomena that we study. The focal individual model is consistent with the core definition of the ecological community, that of interacting individuals of more than one species; it represents one approach toward such a flexible model. The focal-individual model reflects the potential influence of any individual on another individual, regardless of species, and further incorporates the probability of indirect effects. The approach represents a broad framework, able to represent the level of organization of all individuals, but also able to accept the study of subsets of individuals (with certain assumptions), and can scale appropriately to whatever phenomena are studied. Rather than appealing to philosophy as an authority, the focal-individual model permits epistemological choices by the investigator.

Looijen & van Andel (1999, 2002) have developed a narrow and exclusionary approach, particularly striking when ecology otherwise appears to be embracing a broader approach and the merging of former disciplines (e.g. Jones & Lawton 1994). Their implied appeal to authority by their embracing of essentialist philosophy may sound logical, but really represents a significant and erroneous departure from ecological theory. Are

they really developing a new ecological paradigm with their definitions and recognizing a new logical type? If, within a forest, one disturbance yields the invasion of one new species while a second disturbance yields the invasion of two species, do these two results represent distinct ecological communities (different CI types), or rather different examples of the same ecological process? From my perspective, Looijen & van Andel abandon the core concept of ecological communities. Because of that, absurd structures such as tiny CI communities of redwood sorrel in a larger extensive CI community of redwoods can be created, or even the lack of terminology for other combinations like simple food webs, or plants, their seed predators and their seed dispersal agents. While they hope to achieve homogeneity and clear boundaries, these are only classification issues if one is rooted in an essentialist philosophy, but not otherwise of ecological significance. Classification is an approximation because of the historical variation in physical and biological processes that characterize any spatial extent and the probabilistic distribution of individuals. Taking a CI approach can be a decision of a particular researcher, but not in the sense that some essential 'type' is being described and that these are more than a subset of the level of ecological organization being investigated.

The seeming irreconcilable differences between the Looijen & van Andel versus my own approach represent differences in perspectives, and perhaps in our acceptance of human subjectivity. I appeal for breadth as well as rigor in ecology, and along with it better understanding of context and contingency, and how structure arises and interacts with and reflects function. I conclude with a quote from Allen & Hoekstra (1992, p. 286):

"The fact that one can make it fit the data is beside the point, for there is a hidden cost. The neat fit is deceptive, for one thinks one is finding out something about nature, when in fact all that is happening is the study of an arbitrary human-scaling decision."

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## References

- Allen TFH & TW Hoekstra (1992) *Toward a unified ecology*. Columbia University Press, New York.
- Bender EA, Case TJ & Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. *Ecology* 65: 1–13.
- Drake JA (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist* 137: 1–26.
- Hanski I (1994) Patch occupancy dynamics in fragmented landscapes. *Trends in Ecology & Evolution* 9: 131–135.
- Hanski I (1996) Metapopulation ecology. In: *Population Dynamics in Ecological Space and Time* (eds Rhodes OE Jr, Chesser RK & Smith MH) University of Chicago Press, Chicago.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Jones CG & Lawton JH (1994) *Linking Species and Ecosystems*. Chapman & Hall, New York.
- Kerfoot WC & Sih A (1987) *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover.
- Kinzig AP, Pacala SW & Tilman D (2001) *The Functional Consequences of Biodiversity; Empirical Progress and Theoretical Extensions*. Princeton University Press, Princeton.
- Looijen RC & van Andel J (1999) Ecological communities: conceptual problems and definitions. *Perspectives in Plant Ecology, Evolution & Systematics* 2: 210–222.
- Looijen RC & van Andel J (2002) A reply to Thomas Parker's critique of the CI community concept. *Perspectives in Plant Ecology, Evolution & Systematics* 5: 131–137.
- Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21–74.
- Menge BA (1997) Detection of direct vs. indirect effects: were experiments long enough? *The American Naturalist* 149: 807–823.
- Menge BA & Sutherland JP (1987) Community regulation: variations in disturbance, competition and predation in relation to environmental stress and recruitment. *The American Naturalist* 130: 730–757.
- Pickett STA & White PS (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, San Diego.
- Parker VT (2001) Conceptual problems and scale limitations of defining ecological communities: a critique of the CI concept (Community of Individuals). *Perspectives in Plant Ecology, Evolution and Systematics* 4: 80–96.
- Polis GA & Winemiller KO (1996) *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York.
- Pulliam HR (1988) Sources, sinks and population regulation. *The American Naturalist* 132: 652–661.
- Pulliam HR (2000) On the relationship between niche and distribution. *Ecology Letters* 3: 349–361.
- Strauss JY (1991) Indirect effects in community ecology: their definition, study and importance. *Trends in Ecology & Evolution* 6: 206–210.
- Underwood AJ (1986) What is a community? *Patterns and Processes in the History of Life* (eds Raup DM & Jablonski D), pp. 351–367. Springer, Berlin.
- Williams R & Martinez ND (2000) Simple rules yield complex food webs. *Nature* 404: 180–183.
- Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology & Systematics* 25: 443–466.
- Wu J & Vankat JL (1995) Island biogeography, theory and applications. *Encyclopedia of Environmental Biology* 2: 371–379.
- Wu J & Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly Review of Biology* 70: 439–466.