

Seeing the Forest *and* the Trees: On the Very Idea of an Ecological Community¹

Jay Odenbaugh
Department of Philosophy
Environmental Studies
Lewis and Clark College
Portland, Oregon 97219

I. Introduction. Throughout the history of ecology, there have been many different views held about the nature of ecological communities. Some ecologists have argued that they exist mind-independently with discrete boundaries and others have contended that they are merely ephemeral collections of species with minimal interactions. In this essay, first I provide an analysis of the concept of *ecological community*; or better yet, *community* concepts. Second, I consider the most serious challenge to the reality of ecological communities; what is called gradient analysis pioneered by Robert Whittaker. I argue that many have misinterpreted the results of gradient analysis and that properly construed the existence of communities, and more specifically, community properties are not threatened. Finally, I sketch how the debate over the reality of communities matters to environmental policy.

II. Controversy and Concepts. Ecologists Frederic Clements and Henry Gleason disagreed vigorously over succession and the nature of ecological communities. Suppose a set of species in a particular place at a particular time is disturbed by some exogenous process like a forest fire. Clements argued that

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communities in response to such disturbances follow a very specific sequence of stages called “seres” and that there is a single climax community that is self-perpetuating and tightly integrated. Clements considered communities to be “superorganisms”:

The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies... The life-history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant (1916, 16).²

Gleason considered Clements’ views to be without empirical support and argued that succession results from individual species’ physiological requirements and local climatic conditions. He writes,

[I]t may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements (1917, 26).

Likewise, he did not think that there is a final climax community; communities are continually changing. Hence, Gleason’s views are considered “individualistic.” In effect, for Gleason there is no system but only a set of species reacting to disturbances relatively independently of the others.

Throughout the history of ecology, ecologists have conceived of communities in roughly three different ways.

- Communities are groups of species at particular places and times and nothing more.
- Communities are functionally interrelated groups of species.

² This passage is interesting since it is not clear why the study of how “vegetation” changes through time necessarily presupposes that it is an “organic entity”. That is, surely one can study how plant and animal species change through time without assuming they form some superorganism. However, if one contends that it is truly a developmental process - an ontogeny - and that only organisms have an ontogeny, then Clements would be correct. Of course, equating succession and ontogeny begs the very question at issue.

- Communities are groups of species that are organismic.

In the next section, I consider a framework for thinking about the nature of ecological communities and for clarifying different community concepts.

III. Metaphysics and Ecological Communities. Objects, except possibly for the simplest as described by current or future particle physics, are composed of parts which potentially interact. Objects can be classified by the type and intensity of the relations that exist between their parts. These different types of objects will be called *aggregates*, *wholes*, and *individuals*.

If an object is an *aggregate*, then its parts bear insignificant causal relations to one another at a time and over time. If an object is a *whole*, then certain causal relations exist between its parts such that it is causally structured at a time and through time. Finally, an *individual* is an object whose parts bear causal relations to one another such that the object is highly structured and integrated. The differences between aggregates, wholes, and individuals concern the causal relations amongst their parts and the strength of those relations and as such, there is a continuum between them.

Now consider the sort of community that Gleason had in mind:

Are we not justified in coming to the general conclusion, far removed from the prevailing opinion, that an association [i.e., community] is not an organism, scarcely even a vegetation unit, but merely a *coincidence*? (1926, 16).

Communities, according to Gleason, are composed of whatever species coexist in space and time. This we might call a *Gleasonian Community*.

A *Gleasonian community* is a group of species in a particular area at a particular time.

In effect, this type of community consists of *aggregates*.

Consider a group of n species at a particular place and time. If the group is a Gleasonian community, then we can properly ask why some other $(n + 1)$ -th species is *not* a member of the community. If we were taking one of the other approaches, the answer would be given by the causal interactions. The $(n + 1)$ -th species would be excluded from such interactions. Thus, membership in the community is not secured by mind-independent causal interactions but rather by the ecologist's choice about spatial and temporal boundaries.

It should be noted that this inference is valid only if we assume that community membership is secured by either mind-independent causal interactions among species or by the choices and conventions of ecologists. Of course, one might suppose that communities are the product of both and I will revisit this suggestion in the last section. However, in this section, I will consider those cases where the options are mutually exclusive. Given this supposition and assuming Gleason is correct, then it follows community membership is based on scientist's conventions or decisions. Nevertheless, one might suppose that there are non-causal mind-independent properties which are the basis of community membership. For example, consider the following contender - the Shannon Diversity Index. Let S be the total number of species and p_i is the proportion of species i in S . Thus, The Shannon Diversity Index is

$H = -\sum_{i=1}^S p_i \ln p_i$. This index combines the richness and evenness of a collection

of species into a single number. However, this need not be a genuine community-level property since *any* collection of species as separated in space

and time as you like can possess have a Shannon Index. As such, it is not a mind-independent property secured by the causal interactions of the relevant species.³

Thus, we are left with the following argument:

1. If Gleasonian communities objectively exist (i.e., are real), they must exist mind-independently.
2. These communities depend on ecologists' decisions – arbitrary or not – as to what species to consider members of the community.
3. Hence, they do not objectively exist.

This view is offered by ecologist Robert MacArthur:

Irrespective of how other ecologists use the term “community”—and there are almost as many uses as there are ecologists—I use it here to mean any set of organisms currently living near each other and about which it is interesting to talk... (1962, 189-190).

However, as we noted, the “ $(n + 1)$ -th problem” might not be a problem if groups of organisms can be distinguished in virtue of the causal interactions between their respective species populations. As Richard Levins and Richard Lewontin write,

The question of boundaries of communities is really secondary to the issues of interaction among species” (1980 [1993], 54).

Hence, the $(n + 1)$ th problem need not be a particular problem for “Hutchinsonian” and “Clementsian” approaches.

A whole is a set of species' populations that exist as a structured entity—there are causal relations that at least weakly integrate the species at a time and through time. This type of community concept is sometimes associated

³ I thank Sahotra Sarkar for forcing me to think more carefully about the nature of properties even though I cannot discuss the issue more fully.

with George Evelyn Hutchinson (see “Circular Causal Systems in Ecology”). Hutchinson thought of communities as having feedback loops that assure their self-regulation and persistence. What sorts of causal relations or “feedback loops” might bind species in a community?

One candidate is the various interspecific interactions that exist amongst organisms and populations. Between any two species, we can classify these interactions as either positive (+), negative (–), or non-existent (0) depending on how they affect the growth or abundance of the respective species. These relations include competition [–,–], predator-prey [–,+], mutualism [+,+], amensalism [–,0], and commensalism [0,+]. Between any three or more species, we can similarly distinguish between various indirect effects such as apparent competition and trophic cascades. If there are interspecific interactions between species that integrates the species into something more than an aggregate – a whole – then this community will be called a *Hutchinsonian community*.

A *Hutchinsonian community* is a group of species that at least weakly interact with one another and not others at a time and through time.

Finally, a *Clementsian community* is a tightly integrated group of species that bear various causal relations between its component species. The community forms an individual like that of a multi-cellular organism. So,

A *Clementsian community* is a group of species that strongly interact with one another at a time and through time.

Communities can exist as aggregates, wholes, or individuals.

It is certainly an empirical issue whether any of these community concepts apply to any group of species. Nonetheless, some progress has been made in understanding what ecological communities *might* be. Next, I want to consider an argument for the non-existence of Hutchinsonian and Clementsian communities.

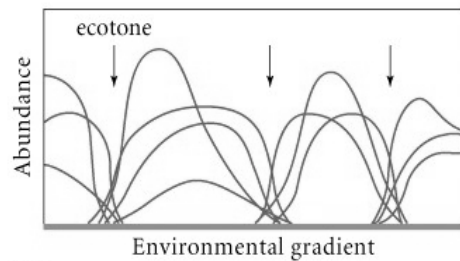
IV. Gradient Analysis and Community Boundaries. Here is an argument against the existence of ecological communities both in the Hutchinsonian and Clementsian senses:

1. Communities are real only if they have (possibly vague) boundaries.
2. However, many purported communities do not have distinct boundaries.
3. Hence, many purported communities are not real.

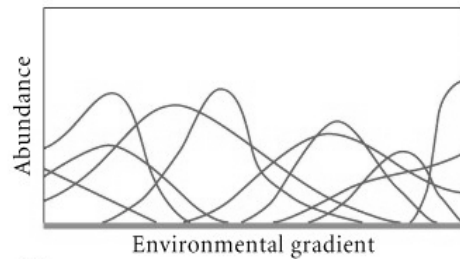
A fundamental philosophical assumption behind this argument is the following:
A system exists *only if* it has a (possibly vague) boundary.

Empirically one can portray changes in community structure by plotting species abundances along some continuous gradient of an abiotic variable. The gradient may concern moisture, temperature, salinity, exposure, etc. One samples the species' populations along the continua noting both the exact conditions and the abundance of the species. Cornell ecologist Robert Whittaker performed such gradient analyses in the 1950-60s in mountainous areas including: the Santa Catalina Mountains in Southern Arizona, the Siskyou Mountains in Oregon, and the Great Smoky Mountains in Tennessee. In mountains, moisture and temperature vary with elevation, slope, and exposure

Whittaker reasoned that if a group of species forms a Clementsian community, then it should have a “closed structure”. Similarly, if a group of species forms a Gleasonian community, then it should have an “open structure”. These possible structures are depicted in (a) and (b) respectively.

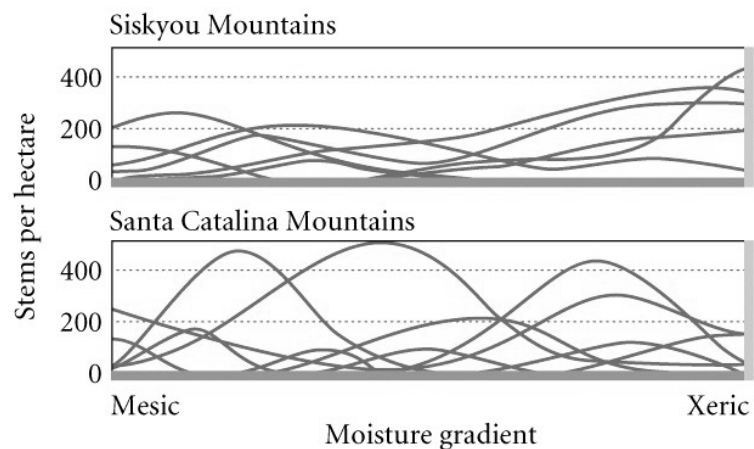


(a)



(b)

Whittaker’s results suggested that there are no community boundaries - the species vary continuously along the environmental gradients. He examined the distribution of plant species along moisture gradients with elevation held constant at 460 - 470 m in Oregon and 1,830 - 2,140 m in Arizona.



Whittaker's results have been interpreted in many ways, but there is a very common interpretation as found in the following:

If plants really did form tightly knit communities - "nation states of trees," is the ecologist Paul Colinvaux's felicitous phrase - then the distribution should fall into clusters. Instead, Whittaker found, each species behaved totally independently...What all this means is that there is no such thing, really, as a pine forest, or a mixed-hardwood forest or a tall-grass prairie or a tundra. These are human categories, not biological ones. They are simply names that we have applied in a rough attempt to impose intellectual order on the infinite diversity of landscapes that exist. (Budiansky 1995, 86)

There are no discrete communities of plants. The reality is endless blending as each individual Darwinian species finds its own range, jostling its neighbors, living in its own individual niche. (Colinvaux 1978, 72).

However, there are several problems with these interpretations.

First, ecologists and botanists using Whittaker's results have committed a fallacy of "hasty generalization". Given the continuum of causal interactions, there will be species' populations which do not belong to communities and some that do. Moreover, given the importance of habitat fragmentation and patchiness of landscapes, we should expect the existence of at least some Hutchinsonian communities. Thus, even if Whittaker's studies show that these specific collections of species do not form communities, this is insufficient to show that there are no such communities.

Second, Whittaker's data are correlative and his argument contains implicit interactive assumptions:

- ❑ Interactions among species should be similar at all points along environmental continua.
- ❑ Groups of species should be associated at all points on a gradient if interdependence is to be accepted.

However, we know this to be false. Species may be interdependent at some points on a gradient and not at others with respect to most interspecific interactions. In the Northern Rockies, *Pinus albicaulis* increases the mortality rate of *Abies lasiocarpa* at lower elevations. At timberlines in xeric areas, *A. lasiocarpa* “clumps” around *P. albicaulis* and has decreased growth rates as the latter’s mortality rate increases. Thus, fully overlapping discrete groups of species is not necessary for demonstrating interdependence.

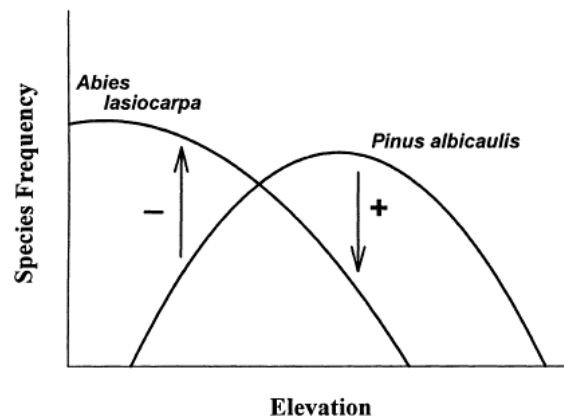


Fig. 1 Schematic continuum of *Pinus albicaulis* and *Abies lasiocarpa* on elevational gradients in the northern Rocky Mountains. Differences in the effects of *P. albicaulis* on *A. lasiocarpa* are denoted with arrows data from R.M. Callaway (submitted)

Third, when we consider Whittaker’s own explanation of the patterns, he argues that it is niche differentiation that leads to no boundaries. He writes,

It is of interest to ask *why* species do not evolve to form groups with parallel distributions... The two species are in close competition (in the same or closely related niches) within the same range of a habitat gradient, such as elevation or topographic moisture. Selection will increase the difference in mean adaptive positions along the habitat

gradient. As competing species evolve toward difference in niche, so they evolve also toward difference in habitat. (1975, 116)

Thus, community-level properties cause an absence of boundaries - no traditional boundaries is compatible with anti-individualism. Remember, a system exists *only if* it has a (possibly vague) boundary. Suppose there are few of the discrete communities ecologists have catalogued; nonetheless, there are community-level properties:

A community-level property is any causal biotic relation between two or more species.

Note that the relevant causal interactions are between *two or more species*. Intraspecific competition is an interaction between individuals of the same species that affects its rate of growth. As such, it is not a community-level property.⁴

By way of summary, we can see how we can respond to the worries generated by gradient analysis. First, not every species or every collection of species occurring in a place at a time is a member of a community or forms a community. This is consistent with the existence of some communities. Second, we have seen that interactions between species may not be similar at all points along a gradient and groups of species may not be associated at such all points even when they are interdependent. This implies that *proper parts* of species may form communities with other *proper parts* of species. In effect, communities may be much smaller mereologically than is often suggested. Third, processes such as interspecific competition along an environmental

⁴ I thank Greg Cooper for getting me to be clear on this point.

gradient amongst species allow for the existence of community-level properties without the existence of traditional discrete communities.⁵

So, after some conceptual clarification, we are left with the questions of community ecology:

- ❑ Do sets of species exhibit any interdependence, and if so, how interdependent are they?
- ❑ Do sets of species exhibit such interdependence that they are systemic?

These are empirical questions and as such must be left to the empirical investigations of ecologists as they should be.

V. Communities and Environmental Policy. Ecologists and conservationists are interested in the protection of communities in addition to that of species. The Nature Conservancy makes decisions about land acquisition based on the classification of communities present using the U. S. Natural Vegetational Classification System. In some cases, communities are included in laws - in Southern California - land development is regulated differently in “coastal sage scrub” than in “chaparral” communities. One might argue as follows though:

1. One can protect something only if it exists.
2. However, ecological communities by and large do not exist.
3. Hence, one cannot protect them.

⁵ I *am not* suggesting that there exist community-level properties without communities. Of course, for any community-level property, its bearers form a community. However this entails that communities may be much smaller (or larger) than the traditional communities that ecologists classify. For example, one type of community or biome is that of a temperate rain forest. However, in the Pacific Northwest such classification may include more than just a set of interacting species. I *am* suggesting that implications of adopting interactive community concepts have not been followed to logical extremes.

I have argued that premise (2) has often been supported by flimsy evidence. Nevertheless, if we grant this premises (1) and (2) are true, one can still argue for the protection of the bearers of community-level properties; that is, even if some community designations are artifactual.

Suppose that when the Nature Conservancy classifies a collection of species as a community they include a real interactive community as a proper subset of a set which has non-interacting members. That is, the set of species includes at least a Hutchinsonian community in larger Gleasonian community. Even if such a designation is ultimately artifactual as Gleason and MacArthur allege; nonetheless, by protecting community-level properties and their bearers:

- ❑ We can correct for the inadequacy of species-by-species protection and protect large suites of species and their interactions.
- ❑ We can preserve taxa other than charismatic megafauna like fungi and invertebrates and the ecological services they provide.

Conventional communities including real ones can serve as conventional surrogates for protecting community-level properties which might be invisible to current legislation like the United States' Endangered Species Act.

VI. Conclusion. In this presentation, I first provide an analysis of *community* concepts. Second, I argue that the individualistic hypothesis is not shown to be true by Whittaker's gradient analysis and is suggested false by empirical evidence on species interactions. Third, I contend the foremost issue in community ecology is species' interdependence not the existence discrete

boundaries. Finally, I suggested that the nature of communities matters to environmental protection and policy.

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