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India's first satellite-tagged Ganges Softshell Turtle

What is wrong (and right) with community ecology?

- Shivam Shrotriya

Recently (April 2026), I taught a class on 'Statistical Methods in Community Ecology' to the new batch of PhD students at the Wildlife Institute of India (WII). I tried to cover the progression of methods in the field, beginning with the familiar territory of species richness and diversity indices, moving through compositional analysis and ordination, and ending with modern predictive approaches such as generalised linear models, machine learning, and hierarchical Bayesian frameworks. This is a sensible and typical statistical journey of modern community ecology, from counting species to asking how communities assemble, how they differ, how they interact, and how they may change. I have been teaching such classes to M.Sc. and PhD students from time to time. But whenever I prepare for these classes, I always grapple with a rather fundamental question before the statistics even begin - what exactly is a community?

Textbooks provide us with a starting point for any topic. Krebs *(Ecology: The Experimental Analysis of Distribution and Abundance*, 6th edition, 2013) defines a community as "an assemblage of populations of living organisms in a prescribed area or habitat", while Smith & Smith *(Elements of Ecology*, 9th edition, 2015) describe it as "species that [interact and] coexist within a given area or habitat". These are reasonable definitions to start with, but aren't these quite rudimentary and deceptively simple? What the textbooks agree upon is that the field deals with multiple species living within a defined area, usually assumed to be interacting with each other. In practice, both fundamental elements of these definitions are troublemakers. The first problem is how the area is defined, and I will come to that later. The second is which species are counted as part of the community.

A bird ecologist may study all birds in an area as a single community or may treat granivorous and insectivorous birds as two separate ones. For a plant ecologist, the community on one aspect of a mountain slope may differ from the community on another aspect, and a grassland community is something else altogether from a forest community. A carnivore ecologist may work on a large carnivore community or a mesocarnivore community, including some species and excluding others. We recently completed the dissertation defences for the 20th batch of M.Sc. in Wildlife Science and the 1st batch of M.Sc. in Freshwater Ecology at WII. It was exciting to see that about half of the studies dealt with communities of one kind or another - plants, insects, birds, amphibians, intertidal organisms, and even diatoms. In many of these studies, the community was confined to a particular taxonomic group. In some, it cut across flora and fauna and was tied instead to a spatial boundary.

So how do we find defining criteria for an ecological community? Most studies appear to take taxonomic closeness as the primary criterion, but grouping by spatial, trophic, functional, methodological, or even managerial units is common enough. Plant ecologists usually keep species growing together in a shared space at the centre. Animal ecologists frequently add another layer on top of the shared space with diet, behaviour, movement, detectability, or trophic role. Which species make it into a particular community, it seems, is somewhat artificial.

There also seems to be an underlying assumption in identifying a community that the species we have grouped together are interacting with one other. This is why our results of community ecology studies so often feature clustering, food webs, and interdependent population dynamics. What is usually left unstated is that the interaction we have in mind is, in my experience, mostly competition. Community ecology studies rely on the presence, abundance, and distribution of multiple (arbitrarily selected) species as their primary data. And we ecologists, for sure, understand well that the abundance and distribution of a species are not governed by competition for resources alone. A mesocarnivore community is also shaped by its prey, its parasites, its habitat, disturbances, and by carnivores both larger and smaller, yet a study reporting the structure of a mesocarnivore community may omit these influences. A plant ecologist would not treat all the plants eaten by a granivorous bird community as one community if those plants do not grow together. Which tree species are dominant and which are rare, may be the key question in a plant community study, while interactions with seed dispersers and pollinators, rarely included in the community at all, could be the stronger drivers of its structure.

This brings up a question I have not seen answered anywhere. If a community is considered a valid unit because the interactions within it are more important than the interactions with species outside of the community, then this must be measured. Are the interactions among plants in a patch stronger and more significant than the interactions between those plants and their pollinators in the same space? Is an insect community more tightly bound internally than it is to the vegetation on which it feeds? The justification is often asserted but almost never tested.

Let us now examine the other keyword, the 'defined area'. A waterbird community may be defined as all the birds sharing a waterbody, although many of them depend on terrestrial areas well beyond it for nesting, roosting, or feeding. Species from a forest community may be foraging in adjacent croplands and urban habitats. Even apparently distinct spatial boundaries turn out to be practically blurry.

Community, in this sense, is a fluid concept whose boundaries flex according to the needs and capacities of the ecologist. This fluidity is not a small inconvenience. It dictates what will be studied and what questions can be asked. Fauth *et al.* (1996) treated this problem as one of semantics and tried to separate community from the words used alongside it - assemblage, guild, and ensemble. Following that line of argument, Stroud *et al.* (2015) recommended that 'community' should refer to interacting species populations occurring together in space, 'assemblage' to a taxonomically related group of species occurring together, and 'guild' to species exploiting the same class of resources in a similar way. 'Ensemble' had been used so infrequently and so inconsistently that they proposed dropping it altogether. Useful as these distinctions are, they bring us back to the same place– where interactions matter more than others, and where we agree to place a convenient cut-off.

Here is what troubles me most about all of this. Cardou & Cadotte (2023) called this the scale problem. At a finer scale, when we focus on a single population of a single species, we are in the domain of population ecology. At a coarser scale, if we study ecological patterns that could apply to all species across a larger landscape, we are in the domain of macroecology. Community ecology sits in the awkward middle. The whole reason for moving from population ecology to community ecology is that a single species does not exist in isolation. It interacts with others, and so we must study those interactions. But whatever small set of species we then define as a community does not exist in isolation either. It interacts with everything else we left outside the box we just defined. We escaped one fiction of an isolated population and immediately built another of an isolated community, one level up. And if we say that community ecology is simply the study of interactions among co-occurring species, then it is hard to see where community ecology ends and ecology itself begins.

The community, then, lies in the eyes of the researcher. This is not a comfortable thing to teach, nor is it a small admission, because it means that the object of our study is partly an artefact of our decisions about it. Secretly, I feel more at ease teaching methods, mainly because dealing with these basic questions in community ecology is much harder. I think this goes some way towards explaining the most prominent criticism the field has faced.

In 1999, J. H. Lawton asked whether there are general laws in ecology and concluded that the answer depends on the level of biological organisation at which one is working. Population ecology can simplify the world to one species and its births, deaths, movements, and other limiting factors. Macroecology can zoom out and look for broad regularities and patterns in range size, species richness, latitude, or area. Community ecology, occupying the messy middle, is too large for the population abstractions to hold and too small for the broad patterns to drown out the noise. Lawton found that there are hardly any general patterns in ecology and concluded that the rules "are contingent in so many ways ... as to make the search for patterns unworkable". His judgement of community ecology, in particular, was not gentle. Community ecology, in his view, should be set aside so that ecology could get on with the scales that work better. Cardou & Cadotte (2023), reviewing this history, state that ecology's reputation as a soft science was largely due to the overwhelming emphasis on community ecology.

Cardou & Cadotte (2023) also make the point about definition quite sharply. A community defined as a group of interacting populations in a given area requires us to know both the precise extent of each population and the degree to which they interact, which they call "simply implausible". In reality, they write, ecologists do not study communities as such. They study "an arbitrary area that they believe captures an adequate representation of the types of interactions and mechanisms structuring species abundances and diversity within it".

There is an older version of this problem worth noting. As early as 1909, V. M. Spalding watched desert plant communities shift in composition from year to year and saw fluctuations. At almost the same time, F. E. Clements was working in Nebraska, where succession appeared so orderly that he thought of plant communities as superorganisms with each species playing its part like an organ in a body. Both of them generalised from what they saw, and what they saw depended on where they were standing. Contingency in ecology is not only a property of the systems we study; some of it belongs to us, the observers.

Cardou & Cadotte cite Kuhn (the philosophy of science guy) to make a wider point that scientific progress is not assured and that a discipline can sit in a pre-paradigm state for a long time without moving forward. Oksanen (1991) had put it more bluntly. He compared ecologists to skiers in a snowstorm who believe they are advancing because they cannot see their own old tracks and showed that most of the central ideas of modern community ecology were already present in an essay by A. K. Cajander written in 1905. His concern was not that the field lacked ideas, but that the field kept rediscovering old ones under new and flashier names. A reason why I also started writing these articles is to examine the history of ideas in ecology and conservation and to ask what has really advanced.

Let's now turn to how the field of community ecology has responded and advanced since Lawton's very strong critique. The interesting thing is that the useful responses have not tried to fix the 'boundary of community' problem. They have tried to dissolve it or at least made an honest admission of the limitations. Vellend (2010) sidesteps the argument entirely by defining a community as organisms of multiple species living in a specified place and time, deliberately bypassing the question of whether communities are coherent natural entities at all, and then organising everything the field studies under four processes borrowed from population genetics – selection, drift, speciation, and dispersal. Leibold *et al.* (2004) went the other way and made the boundary permeable on purpose, treating local communities as patches linked by dispersal within a metacommunity, so that the species sitting outside the community box are now part of the model rather than an inconvenience. McGill *et al.* (2006) argued that community ecology had "lost its way" by focusing on pairwise species interactions independent of the environment and proposed that we stop asking which species are present and start asking what trait distributions exist, how they vary across environments, and how they affect performance. Traits are measurable across taxa, so who belongs to the community matters rather less. This led to quite rapid growth in a branch called functional ecology; however, concerns exist about the robustness of the current statistical methods used to study trait-based ecology. And in a quite new approach, Ovaskainen *et al.* (2017) built a statistical framework, Hierarchical Modelling of Species Communities, in which the associations between species are estimated from the data rather than assumed at the outset. But it is worth reading Ovaskainen *et al.* (2017) carefully, because they themselves clearly understand the limits of their own tool and mention that their framework is correlative. Residual associations between species are hypotheses about interactions, not evidence of them, and variation the model cannot explain is not automatically attributable to drift.

This, overall, represents real progress, although leading in multiple directions rather than advancing community ecology as a unified field. Which brings me to the most sobering paper I have read on the topic. Charles J. Krebs, whose textbook definition of a community I quoted at the beginning of this article, and his colleagues published a review of a century of population and community ecology in 2024. In it, they list "What is a community?" among the questions the field keeps asking that remain "descriptive, vague, and/or untestable". The person whose book taught many of us the definition also finds himself thinking that the question was never properly answerable.

If you can read only one of the key readings listed below, I suggest reading the 'The Kluane project' passage of Krebs *et al.* (2024). The project in the boreal forest of southern Yukon began in 1973 with a simple survey of how many small rodent species lived in an area proposed as a national park. It grew into an attempt to understand the snowshoe hare cycle, and then into an experimental analysis of the whole food web, with large-scale manipulations and decades of monitoring. Fifty years and roughly 500 person-years of work later, they write that "so much is known but much is still missing from our understanding". Large mammals went unstudied due to the lack of funding. Weasels, passerines, and insects went unstudied due to the lack of expertise. For one of the better-studied and structurally simpler food webs on the planet, they have data on lynx kill rates only in winter. Their warning to the rest of us is worth quoting: "If you think that community and ecosystem ecology can be done quickly or simply, you will be very surprised at the necessary effort."

So, what do we do if the community cannot be fully known and its boundaries partly depend on how we draw it? Here are a few pointers that might help. The first thing, perhaps, is to admit that we are working with a study-specific community, clearly stating what boundaries we define—spatial, taxonomic, trophic, or sampling boundaries. And we may also add clarity about whether the study object is a community, an assemblage, a guild, a network, or simply an operational sample. A methodological convenience is not a natural unit, and there should be no pretence about which unit we have. The second thing is to let the question guide the method rather than the other way round. Begin with what process could have generated this data. Richness is a count, abundance is usually overdispersed, community matrices are sparse where shared absences are misleading, sites are often nested or hierarchical, and sampling effort varies. These are not statistical/analytical nuisances that we need to tidy up neatly. This is ecological information about how we encountered the system. The third point is to treat species and trait metrics and null models as the assumptions they are. Bray-Curtis, Jaccard, Euclidean distance, functional dispersion, ordinations, phylogenetic clustering, and every null model we build are decisions about what counts. Null models do not reveal truth; instead, they reveal assumptions. Integrated models, such as those of Ovaskainen *et al.* (2017), look promising for future studies. They are powerful precisely because they borrow information across species and connect environment, traits, phylogeny, and spatial structure. However, they are also correlative, and a model that fits the data well is not thereby an explanation. As Krebs reminds us, models are tools for thinking, not substitutes for evidence.

Community ecology may never be as neat and structured as we would like it to be. Its central object – the community – is itself partly natural, partly conceptual, and partly a decision made by the researcher before fieldwork begins. Students often start with a one-line definition as theoretical

understanding, then begin sampling an arbitrary subset of an open system and report its structure with more confidence than the textbook definition itself can support. The methods in this field have evolved quite fast in the past few decades. The concepts, however, have not kept pace with them. What is wrong with community ecology is that we never get clarity about anything. We are only able to study a part of the whole picture. What is right about it is that we keep striving for that clarity anyway and keep fighting the fog of war. The questions it asks, though, are unavoidable, because conservation almost never deals with one species at a time, and every partial answer tells us a little more about the system than we knew before.

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Key references:

Cardou, F. & Cadotte, M.W. (2023). From pattern to process in the search for generality. In: Cousens, R.D. (ed.) Effective Ecology: Seeking Success in a Hard Science. CRC Press, Milton Park, pp. 151-172.

Krebs, C.J. *et al.* (2025). Population and community ecology: past progress and future directions. Integrative Zoology 20: 2-14.

Lawton, J.H. (1999). Are there general laws in ecology? Oikos 84(2): 177-192.

McGill, B.J. *et al.* (2006). Rebuilding community ecology from functional traits. Trends in Ecology and Evolution 21(4): 178-185.

Ovaskainen, O. *et al.* (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters 20(5): 561-576.

Vellend, M. (2010). Conceptual synthesis in community ecology. The Quarterly Review of Biology 85(2): 183-206.

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