A Century of Community Ecology: How Much Progress?

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Much of the apparent progress in community ecology amounts to little more than re-inventing the wheel, albeit with technical improvements. Many central ideas in the field were stated by A.K. Cajander at the turn of the century. Thereafter, community ecology has moved back and forth between competition-centered and individualistic views of community structure. The chief problems have probably been inappropriate methodology (lack of rigorous formulation and/or critical experimental testing of theories) and a tendency to work only on subcommunities that are delimited by taxonomic criteria. Although these problems are beginning to be remedied, a new one has emerged: ignorance of history and a tendency to re-invent old ideas under new, flashy names. This problem is potentially as dangerous as the old ones and must be tackled by improving our first-hand contact with the classics in our field.

A look at recent literature on community ecology gives an impression of rapid progress. New concepts are created, models are built and in the lists of references, recent publications prevail heavily. We obviously move rapidly, but do we also make progress? Or are we rather like skiers in a snowstorm, who believe that they advance while moving in a circle, because they cannot see their old tracks? Fortunately, with a little patience, we can back-track our way and find out where we stood in the beginning of the century. This gives some standard for judging the extent of genuine long-term progress. As an example of our point of departure, I choose A.K. Cajander's essay from 1905[1], which I have translated from the Finnish, and edited by deleting lists of latin names and obscure geographic references (Box 1).

Cajander's approach was surprisingly modern and without a trace of clementsian superorganistic ideas. For Cajander[1–3], communities were products of a darwinian struggle for existence, organized by the principle of competitive exclusion[4]. As well as this principle, the essay also contains other glimpses of ideas central to modern community ecology: a markovian view of succession[5], the idea of *r* and *K* strategies[6] and the view of symmetric competitive interactions that force species towards the central parts of their fundamental niches[7,8]. Even the possibility of asymmetric competition and centrifugal community organization[9,10] was recognized (the French pines growing on limestone).

The paper also displays the most persistent fallacies of equilibrium community ecology. The recurrent disturbance by huge ice blocks during breakups had no place in Cajander's discussion on Siberian floodplains. Thus, he did not recognize the diverse rose–dogwood scrub as a product of intermediate levels of disturbance[11,12]. All replacements were attributed to competition, though the supposed competitive superiority of brown bent-grass over tufted hair-grass does not square with the autecology of these species[13]. The possibility that old meadows were grazed by cattle, which favored rhizomatous bent-grasses, was not considered. Cajander also failed even to mention the problem of fitting the gradual transition from spruce to larch taiga to his 'winner-takes-all' principle.

We can thus claim some genuine progress, especially in our ability to deal with disturbance[11–16] and consumer-mediated indirect interactions[17,18]. Also, the processes discovered by Cajander can today be discussed with much greater rigor[19,20] and new exciting perspectives have emerged, especially with regard to sessile organisms with mobile propagules[15,21,22]. Yet, considering the time that has elapsed since the publication of the German-language version of Cajander's theory[2], the rate of progress is not impressive.

Some of the problems can be attributed to the priorities of continental European ecologists, including Cajander himself. Their common preoccupation was with classifying the vegetation. Cajander's theory was thus treated as a rationale for the existence of discrete communities rather than as a hypothesis to be tested. However, the classification bias does not apply to Walter[23] (see, for example, the discussion on grass–tree antagonism in arid areas) or Ellenberg[24], whose arguments on alpine timberlines provide a splendid example of what could be called neocajanderian thinking and whose competition experiments[25] still stand out as classics of the field. Yet, even Walter and Ellenberg were fixed on equilibrium and competition and paid little attention to disturbance and grazing, except in the context of humans and domesticated grazers.

The spreading of the continuum view of vegetational gradients[26] amounted to a severe blow to neocajanderian thinking. If species indeed sorted themselves out individually along environmental gradients, then plant communities could not be structured by competitive exclusion as previously thought. Some Europeans responded to the challenge by documenting vegetational gradients, where subordinate species seemed to respond in concert to changes in the abundances of dominant species[27,28], but these studies could not turn the tide.

Cajander's ideas were, at least to a degree, products of Russian naturalism, characterized by keen and open-minded observing. As Finland was a part of the Russian Empire, it is likely that the impact went both ways. Russian naturalism flourished again during the 1930s when Gause[4] backed the theory of competitive exclusion with elegant experiments. Although the whole tradition was soon thereafter destroyed by Stalin, Gause's work profoundly influenced the thinking of British and American animal ecologists, and much of the modern theory of community ecology[7,8,29,30] has been built on the foundations laid by him. However, the theory has faced recurrent challenges from critics who maintain that the predicted patterns are not supported by available data and that an individual species-by-species approach is a more fertile way of looking at communities[31–33].

The broad picture thus displays circular movements between emphasis and de-emphasis of competition and competitive exclusion. At least in part, these movements seem to be attributable to three

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Box 1. 'The struggle between plants in nature', by A.K. Cajander: an edited translation of Ref. 1.

The life and distribution of plants depends on a great variety of factors. In order to survive, a plant needs warmth, moisture and light. The existence of a plant is also dependent on soil quality and on the action of animals and humans. Many distributional limits of plants are determined by climate, while some plants have their ranges limited by soil conditions or by the range limits of their insect or bird pollinators. It is also common to see plants extending their ranges as a consequence of human activity.

However, none of these factors, alone or in combination, suffices to explain the occurrence of plants in nature. We know, for instance, that the northern limit of the oak runs through southernmost Finland, at about 60° 30'N, and we can be fairly certain that this limit is caused by climatic factors. Yet, we find planted oaks up to 66°N. The western limit of the larch lies in the White Sea area, where larches have grown since ancient times. The westward march of larches must thus have been stopped by a natural obstacle that they have failed to overcome. Nevertheless, planted larches do not only thrive in our forests but form the most spectacular piece of woodland in the whole country, with trunks up to 40 meters tall. Many orchids and other forest-floor herbs only occur on lime-rich soils, but nothing prevents us from growing them in our gardens without adding any lime to the soil. In other words, external factors are far from sufficient to explain the occurrence of plants in nature. One crucial factor needs to be included: the war of everything against everything. That is what everywhere really determines the occurrence of plants, if a human hand is not there helping the weaker ones.

We can get a grasp of this tremendous competition by looking at the vegetation of a recently denuded piece of land, for example a recent forest burn. New plants of all kinds immediately invade such a place. These immigrants mainly represent those species whose seeds or spores happen to be available in great quantities. Usually, the first ones to come are club mosses and cup lichens. Almost simultaneously, fireweeds and certain grasses also invade. Small tree seedlings also appear, usually representing species with light seeds that can cover long distances (e.g. the aspen and the birch). To start with, everything has an opportunity to grow. However, the site soon becomes crowded and thus the struggle for existence begins, in which the weaker helplessly succumbs. The initially diverse vegetation becomes more regular as the plant cover closes.

An abandoned cropfield usually becomes a meadow. However, the meadow does not normally emerge at once. Initially, the site is occupied by a diverse mess of crop weeds. Among the weeds, some perennial meadow plants can also be found. The weeds are mainly annuals or biennials, and as they die, the perennials spread over the bare ground, which becomes inhospitable for the seedlings of the annuals. Weeds succumb one after another and the struggle now goes on between the perennials. The tufted hair-grass quickly emerges as the initial winner, converting the cropfield into a hair-grass meadow. However, amongst the hair-grass, shoots of brown bent-grass start to show up. As the meadow gets older, this species starts to be victorious and the community gradually changes into bent-grass meadow. However, those changes do not take place peacefully and in mutual agreement, but only after a tough struggle in which blood is shed for every square centimeter.

The most obvious way to discover this struggle is to compare the situation in our country, where human activities always create places in which there is a temporary relaxation of the struggle, to conditions in areas without human disturbance. I thus take the reader for a moment to the shores of Lena River in Siberia. North of 62°N, the Lena Valley is almost completely a wilderness. Along a stretch of 1100 kilometers, there are no human settlements whatsoever. Consequently, nature is very regular. The alluvial lands along the river are chiefly covered by forests. On lower shores, whether on islands or on the mainland, willow thickets prevail. On slightly more elevated shores, a kind of mixed forest or scrubland, chiefly formed by willows, roses, alders, birches and dogwoods, grows. On still more elevated land, spruce forests prevail. Further up, in areas only seldom reached by floods, there is a mixed spruce–larch forest, while outside the reach of floods, you see an endless, primeval larch forest wherever you look. Only along creeks and in moist depressions can you see stands of spruce, while pine forests are encountered on dry south-facing slopes.

Such directly boring regularity is never encountered in cultivated regions. In our country, quite similar hills can here support pines, there spruces and there again alders or birches. No rules exist: whichever tree that has first arrived prevails, or the forest is composed of those tree species that have been rejected by the lumberman. The same applies to all cultivated regions: the vegetation is always much less regular than in primeval nature, where there have been thousands of years for the mutual struggle to go on, forcing every species to areas and habitats of its own. If human influence were suddenly to cease, allowing an undisturbed struggle for existence, even our country would become covered by a primeval taiga as monotonous as the one that today prevails in Siberia and that, before the onset of large-scale agriculture, did indeed cover Finland, too.

There are many factors determining which plant will emerge as victorious in the struggle. Longevity is often decisively important, especially in habitats where plants form dense stands. In many cases, light relations settle the outcome. A plant that manages to cut off light from its neighbor thrives, whereas the neighbor will die. In order to be thus capable of overcoming its neighbors, the vigor of the plant is important. Normally, a plant is maximally vigorous in a habitat where all its requirements are well satisfied. In the optimum of its range, a plant can thus more easily exclude its neighbors than in a place where the plant does not thrive well. For example, it is impossible to create a mixed beech–spruce forest around Vienna by mixed sowing or planting, because the beech inevitably outcompetes the spruce. In the Bohemian highlands, such a mixed forest is equally impossible, but for the opposite reason. The spruce outcompetes the beech and a pure spruce forest is born. In our country, the pine, and even more so the spruce, outcompete the larch, whereas on the alluvial islands of Lena River, the converse happens. The spruce forests become mixed spruce–larch forests and finally pure larch forests if the islands rise out of the reach of the floods.

If only a small number of plant species existed, they would certainly cover enormous regions. If, for instance, pine were the only tree species in the world, then a continuous pine forest would cover the greater part of Europe and northern Asia. But, in fact, there are hundreds of other tree species dividing the area amongst themselves. Every one finds its habitat, where it is not outcompeted by stronger neighbors. Yet, it is not always so that a plant ends up growing where it thrives best. Far from that. For example, pine grows poorly on limestone. Nevertheless, there are parts of France where limestone areas form the only natural habitats of pine. This does not warrant the statement that pine is a lime plant in France. Indeed, it thrives better in other habitats but is outcompeted by other species there.

What is said above does not, in any way, diminish the crucial importance of external factors in shaping the vegetation. Usually, even small changes in temperature or moisture cause changes in the vegetation. However, there is no direct relation between the changes in external factors and the response of the vegetation. Large changes in external factors may cause but minor changes in the vegetation and vice versa. When looking at the vegetation of an alluvial meadow, one immediately observes that different species form their separate patches, so-called stands. Within such a stand, soil conditions can vary greatly without notable changes in the vegetation. Then, suddenly, the vegetation changes entirely, without any corresponding change in soil conditions. The explanation is simple. Up to the border, the dominant species of the patch is stronger than its neighbors, while right on the border, the relation changes: another species becomes mightier and an abrupt change in the vegetation ensues.

Thus, the importance of the struggle between plants in determining the distribution and local occurrence of plants on the surface of our earth is very great. If we ignore this struggle, we will not understand nature at all.

persistent problems that are already visible in Cajander's essay. First, ecologists have accepted loose, verbal formulations of theories that foster ambiguity and prevent detection of discrepancies between theories and data. Second, arguments are bolstered by amassing evidence of cases that seem to support them, rather than by subjecting them to critical comparative and experimental tests. Third, ecologists have chiefly worked on taxonomically defined subcommunities. Consequently, the

focus has been heavily on competition, whereas much less attention has been paid to direct and indirect impacts of predation and herbivory.

Fortunately, these problems are beginning to belong to the past. Since MacArthur's[7] work, modelling has become an established practice in ecology. Simberloff's group[33], in turn, has stressed the importance of controlled field experiments and rigorous treatment of comparative data. Paine[34], Crawley[18] and the Carpenter–Kitchell group[35] have increased our awareness of predation and herbivory and shown that these impacts can 'cascade' over long stretches of food webs, while Abrams[36,37] has explored indirect effects of herbivory and predation.

We have thus finally removed some of the old obstacles as our methodology has improved and the integrity of biotic communities has been realized. However, a new risk has emerged. The new generation of ecologists has little patience with the lengthy hand-waving arguments of our predecessors. This is psychologically understandable but professionally dangerous. In spite of their methodological shortcomings, the old classics amount to lots of bright people who knew their plants and birds and did some quite original thinking. It is a tremendous waste of time if we lose contact with their ideas and are forced to reinvent them, which is already happening at an alarming rate. No matter how busy we feel with our current projects, there can never be anything more urgent than to check that what we do covers new terrain and is not just another round along an old track.

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