

## Convergence or divergence: what should we expect from vegetation succession?

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**Summary.** The idea of successional convergence is reviewed to show that there are at least four groups of factors influencing the apparent or real convergence/divergence of successional seres in an area. They are: (1) the differentiation of young and late successional communities is determined by different environmental variables; (2) early and late successional species have different niche widths; (3) between-habitat heterogeneity changes in the course of succession; (4) there is often a different range of habitats available for analysis of early and late successional communities. It is concluded that there is not any simple answer to the convergence – divergence question and that it is useful to investigate more specific questions rather than to decide in general terms whether or not successions are convergent.

The hypothesis of convergence was inherent in the early concept of succession as formulated by Clements (1916). It states that all successional seres in the area with the same climate will *eventually* converge toward only one final community – climax. [One may wonder whether the concept of “equifinality of restitutions” invented by German biologist and philosopher Hans Driesch (1908) was not – together with Cowles’ (1901) generalizations – behind Clements’ idea]. As it is, the idea is *not* a testable hypothesis. Because it includes the term “eventually”, the non-convergence can always be explained by shortage of time for climax to develop. Step by step, the monoclimate theory has been largely abandoned and it is generally accepted that terminal communities are determined by global climate, relief, and soil parent material. The operational definition of convergence could be (Hanson 1962): the similarity of different seres increases as succession proceeds from early to late stages. However, to make this definition work, the time scale still has to be specified (temporal divergence does not disprove eventual convergence),

and the measure of similarity has to be defined. The latter is most often defined in terms of species composition, but characteristics of physiognomy and other structural characteristics have also been used.

One possible test of convergence assumes a continuous shift in composition toward that characteristic of the climax (Christensen and Peet 1984). However, this test assumes there *is* a unique climax in the area and that we know its characteristics; so, strictly speaking, there may be logical difficulties with this approach. Moreover, the fact that an earlier successional stage is more similar to the expected climax than the later stage does not exclude the possibility that the succession will eventually “converge” to the climax. For example, in our study on old field succession (Osbornová et al. 1990), we noted some species of forest understory (e.g. *Cephalanthera damasonium* (Mill.) Druce, *Viola mirabilis* L.) in a newly abandoned field adjacent to the forest during the first two years of succession. These species were out-competed later on by competitively stronger species of open sites, but they will very likely reappear later in the understory of a successional advanced forest community.

In field studies, both convergence (Fukarek 1961, Prach 1985, Boerner 1988) and divergence (Olson 1958, Pineda et al. 1981, Osbornová et al. 1990), as well as mixed patterns (Waldemarson-Jensen 1979, Rejmánek et al. 1987, Inouye and Tilman 1988, Rydin and Borgegård 1988) have been reported.

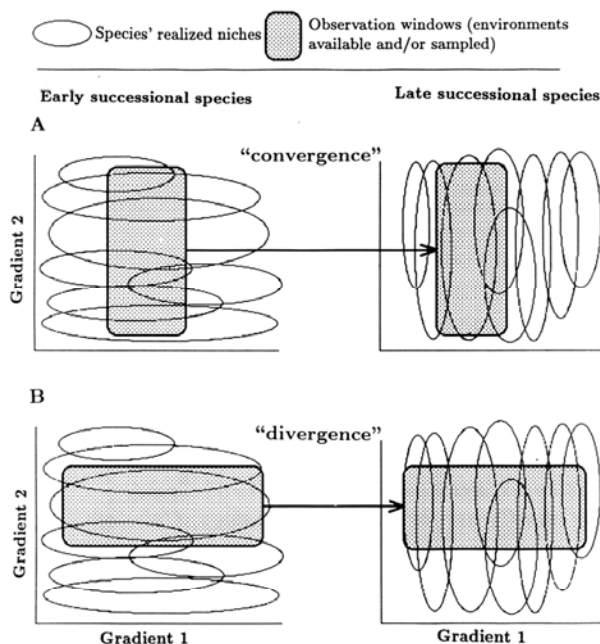


Fig. 1. Whether results from field studies of succession are interpreted as convergence or divergence depends on differences in distribution of early and late successional species along major environmental gradients and on the shape of the "observation window" (habitats available and/or sampled). If Gradient 2 is more important in differentiation of early successional communities and Gradient 1 is more important in differentiation of late successional communities, then data from a "vertical" observation window yield "convergence" (A) and data obtained through a "horizontal" window yield "divergence" (B).

## Circumstances which make a difference

There are four important questions which are relevant to the matter of real or apparent convergence/divergence of succession in an area:

1. Is the differentiation of young successional communities determined chiefly by other environmental variables than mature ones?
2. Does the average niche width (ecological amplitude) of early and late successional species differ?
3. Does the between-habitat heterogeneity change in the course of succession?
4. Is the same range of habitats available for analysis of both early and late successional communities?

(1) If the differentiation of young successional communities is primarily determined by environmental variables different from those of mature ones, the convergence/divergence depends on the range of environments available and/or sampled (Fig. 1). For example, if we follow succession on gravel bars in river beds in a region, the succession will very probably appear as divergent. The gravel bars in river beds are rather ex-

treme habitats and initial stages of succession there host relatively uniform vegetation (e.g. *Myricaria germanica* (L.) Desv., *Salix purpurea* L. in Central Europe), whereas the corresponding 'climax' communities differ considerably (Ellenberg 1988). Even Clements (1916) was already aware of this possibility. However, if we follow succession after various disturbances (fire, clear-cutting, windthrow) within a beech forest, the succession will very probably appear as convergent – various initial community types will finally be overgrown by beech forest.

Early species in succession behind retreating glaciers are less sensitive to an elevational gradient than late successional species. If we follow the succession over a wide range of elevations (in this case the long side of the "observation window" in Fig. 1B is parallel with the elevational gradient), successional "divergence" may be the result. An example is the study by Matthews (1979).

One of the most important environmental "gradients" in initial stages of old-field succession is usually the distance from successional more mature communities (sources of propagules), whereas in more advanced stages of succession, other factors, e.g. soil depth, create the most important gradient. Position and shape of the "observation window" (Fig. 1) then determines whether successional changes are interpreted as convergence, divergence, or a mixture of the two.

(2) If the differentiation of early and late successional communities is determined by the same gradient, but the average niche width with respect to this gradient (the realized niche or ecological amplitude) of early successional species is greater than that of late successional species (see Bazzaz 1987, Kullberg and Scheibe 1989), then divergence can be expected.

It should be noted that the realized niche width is influenced by the number of species available in an area (compare with van Leeuwen's (1966) concept of "limes convergens" characterized by species poor vegetation and "limes divergens" characterized by species richness). If important "climax" species are missing in some areas because of historical reasons (e.g., Hamilton 1981), the fewer "climax" species present are expected to have wider realized niches. Successional seres in such areas will more likely be "convergent".

(3) The convergent development of the abiotic environment, particularly of soil, leading to a convergence of vegetation, was one of the basic constituents of classical theory of primary succession. There is some indirect evidence for this point. For example, in mountains of Central Europe, acid soils often develop on both acid (granite, gneiss) and carbonate bedrock (limestone, dolomite) – see, e.g., Sillinger (1933). Both soils are covered by very similar plant communities dominated by dwarf pine ("Pinetum mughi" – Pawłowski et al. 1928, Aichinger 1933), yet they developed from considerably different pioneer plant communities. This is reflected in the Zürich-Montpellier vegetation classification: pioneer communities on these two different

kinds of substrates (acid and carbonate) are different on the level of classes and orders (*Juncetea trifidi* vs *Elyno-Seslerietea* on wind-exposed shallow soil stands, *Androsacetalia alpinae* vs *Traspetalia rotundifoliae* on screes) but mature communities on developed deep soil are only distinguishable on the level of associations or sub-associations (subassociations “silicicolum” vs “calcicolum” of *Pinetum mughi*). Such a convergence is probably not a general feature and can be expected mainly in places with rather extreme climate (e.g., high annual precipitation). In addition, floristically very similar peat bogs often develop from very different initial plant communities. On the contrary, the peat bog development could amplify small differences in environment with resulting pronounced divergence at a finer scale (Sjörs 1980, 1990, Zobel 1988).

Unfortunately, there is very little *direct* evidence for the long-term changes of the abiotic environment. Processes of soil development are very slow (Jenny 1980, Savina 1986) and the time needed for changes to be detectable exceeds not only the average duration of ecological projects, but often several human generations.

(4) In the modern landscape, “climax” communities are often restricted to rather special habitats which have not been suitable for agriculture or other human activities. There is ultimately a danger that succession viewed through this shrinking observation window will be interpreted as “convergence”. We believe that Cooper’s (1922) conclusion about chaparral with *Adenostoma fasciculatum* H. et A. being a climax community of the northern part of the Sacramento Valley in California is due to this kind of interpretive error (climax communities other than chaparral had grown on more suitable habitats that were used for agriculture).

## What are “chance factors”?

The popular question in this context is: to what extent is species composition along a successional gradient determined by site characteristics rather than by chance factors (e.g. Christensen and Peet 1984)? Usually, it is found that the role of chance factors decreases with successional age. However, what are site characteristics and what are chance factors? McCune and Allen (1985) use the term “historical factors” (instead of chance factors), claiming: “Site factors may be considered to be those environmental factors that are measurable on a given site over the span of data collection during typical research project (<5 years?). ... Historical factors, however, influence the vegetation but usually leave little or no direct, independent, and measurable evidence on the site”.

The type and intensity of disturbance that initiated succession and the availability of propagules (colonization potential) are usually more important in early

stages of succession (e.g. McClanahan 1986, Tsuyuzaki 1989, McLendon and Redente 1990, Myster and Pickett 1990); “site characteristics”, such as soil moisture are more important in late successional stages. These first-mentioned factors are more difficult to measure (or quantify) and therefore they are often considered to be “chance factors”. Consequently, the composition of successional more advanced communities appears to be more “deterministic”.

Undoubtedly, some factors influencing succession are more, and some are less predictable, and many short lasting “unpredictable” events can have a strong influence on the succession. An example of a single event that changed the course of succession is given by Osbornová et al. (1990: 25, 155): in one part of a 17 yr old abandoned field, all small invading shrubs (*Prunus spinosa* L., *Crataegus* sp. div.) were cut off at their base. At this time, shrub height was ~0.5 m and cover was ~5%. The shrubs were not able to re-colonize the plot and this part of the field was after 12 yr dominated by perennial grasses, whereas the unmanipulated part was covered by a nearly continuous shrub layer (cover 95%, height 3 m).

It can be misleading to call all the unexplained variability “random” or “result of a chance event”. For example, it is well known that one of the most important determinants of mountain communities is the depth and duration of snow cover (Hadač et al. 1969, Štursa et al. 1973, Uemura 1989, Barbour et al. 1990). The spatial pattern of snow depth in mountains is fairly consistent from year to year (e.g. Sýkora et al. 1973). However, the survey of vegetation and habitats, performed during the growing season only, will probably lead to an exaggeration of the importance of “chance factors”.

## Conclusions

There is no simple answer to the convergence – divergence question. Our discussion indicates that the results of field tests depend on the spatial and temporal scales considered and these can be influenced by the sampling design. Apparently, it would be more useful to investigate more specific questions rather than to attempt to decide in general terms whether the successions are convergent or not. More appropriate questions are: (1) What are the determinants of composition of early successional communities and what are the determinants of late successional communities? (2) what are the mechanisms of convergence/divergence in a particular case (specific area and specific time interval)?

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