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ABSTRACT: A survey of the literature on 'community evolution' reveals that this term has been used in at least three different contexts: 1) replacement of species assemblages over geological time; 2) development of community-level characteristics resulting from interactions and coevolution of species; 3) natural selection operating on species assemblages. To define community evolution therefore is to recognize three different perspectives, each depending on different scales and mechanisms of evolution. It is further argued that evolution defined as 'any change in genetic constitution' is relevant not only at the population level but also the community level. This follows from recognizing the genotype (in contrast to the species) as a relevant unit of community variation.

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INTRODUCTION

The term community evolution has been used inconsistently in the literature and there is also some confusion about the distinction between community evolution and succession in that both infer community change. Some have viewed succession as an evolutionary theory of the community (Lewontin 1969, Pickett 1976). Others, for example, Allee et al. (1949) have recognized a distinction and proposed that the two concepts are independently meaningful; they proposed that succession may be conceived as the "ontogeny" of the community, and that the evolution of "interspecific integration" may be thought of as the "phylogeny" of the species groupings within the community. Dunbar (1972) recognized a close association of the terms and stated that "... the two processes of ecological succession, ... and of ecological evolution ... are basically the same", but went on to endorse Allee et al.'s (1949) view.

The distinction between the two ideas is becoming more marked. In a recent volume of Benchmark papers on succession (Golley 1977), an evolutionary perspective is virtually absent (Johnson 1979). Conversely, only 2 of the 18 chapters in Cody and Diamond's (1975) "Ecology and Evolution of Communities" use the terminology of succession in discussion. Ecologists essentially share a common understanding about the meaning of the term succession. But what is community evolution? Community evolution has been a vague and loosely interpreted concept and the purpose of this article is to draw attention to the different usages of the term.

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PERSPECTIVES OF COMMUNITY EVOLUTION

In ecological theory, features associated with the phenomenon of change have been recognized at both the population and community levels of organization. Traditionally there has been little integration, in theory or approach, of the two levels in their common attempt to understand patterns and processes in nature. Changes of various sorts were independently recognized at the population and community levels but change in genetic constitution of a population was specifically called evolution and change in species constitution of a community was specifically called succession. Community ecologists, particularly botanists, although aware of the role of natural selection in the structuring and functioning of communities, were concerned largely with descriptions and classifications of vegetation. As evolutionary thinking pervaded all levels of biology however, more integration of population and community ecology emerged, bringing with it a newly synthesized term reflecting this integration - community evolution.

Attempts to integrate and define the relevance of evolution in the community context have resulted in three schools of thought. These are distinguished below.

A) Replacement of Species Assemblages (Community Phylogeny)

> "Three billion years of community evolution"
> (Simpson 1969)

The most obvious feature of community change is the replacement of groups of species. What seems to have been the original connotation for community evolution arose with efforts by paleontologists and paleoecologists to prescribe a community-level parallel for the origin of species. Community phylogeny is a macro-evolutionary theory of the community and describes past communities and their environments over geological time spans (Mason 1947, Ladd 1957, Olsen 1966, Simpson 1969, Boucot 1978, Gray *et al.* 1981).

B) Evolution of Community Characteristics (Community Character Development)

> "The evolution of a community must entail 'parallel' or coadaptive evolution of the community's species"
> (Whittaker & Woodwell 1971)

The processes operating in communities result in two kinds of products: 1) replacement of community types - called succession, and 2) change in community-level characteristics such as species richness, evenness, dominance, physiognomy, trophic structure, stability, spatial pattern, coadaptive associations or networks, etc. Community evolution in this school is a term used to define the evolution or change of these community characteristics in order to distinguish this from the traditional meaning of succession. The central characteristic here is that of coadaptive associations or networks and changes in this characteristic are reflected by changes in all the others. Authors presenting this view of community evolution include Dice (1952), Whittaker & Woodwell (1971), Richardson (1977), Cody & Diamond (1978) and May (1978). The basic tenets are best summarized by Whittaker and Woodwell (1971) who stated that, "The community is the context of species evolution ... The evolution of a community must entail 'parallel' or co-adaptive evolution of the community's species. The community is an assemblage of interacting and

coevolving species ... Through this evolution there will appear adaptation to environment for the community as well as the species. ... Community level characteristics also will evolve." This is not a group selection argument since the community is not regarded as a unit of adaptation in the sense of natural selection operating at the community level. Care is needed in discussing evolution of characteristics of communities as a process separate from the evolution of their species (Whittaker 1975) and the community need not be viewed as a super-organism to think that these emergent characteristics should correspond to those of organisms (Whittaker and Woodwell 1971).

Community evolution in this sense means that community-level characteristics will tend to follow certain deducible and recognizable trends through time dictated by the fact that they are "community-level products of evolution and interaction at the species level" (Whittaker & Woodwell 1971) and that "... the observed patterns in community structure are products of natural selection ..." (Cody & Diamond 1975). Various authors have used the term community evolution in this context when referring to different community-level characteristics, such as physiognomy (Whittaker & Woodwell 1971), stability (Hutchinson 1959, Levandowsky & White 1977), niche structure (Valentine 1968), diversity (Hutchinson 1959, Whittaker 1969, 1975) and patterns of interspecific association (Aarssen et al. 1979, Aarssen 1983).

C) Natural Selection of Communities (Community Selection)

> "... characters, individuals and populations have followed each other as the units upon which natural selection is deemed to act. Now the stage is set for the next step in synthetic evolutionism, the study of the evolution of biotic communities ..." (Baker 1966)

This school views Darwinian natural selection acting at the level of the community and so defines community evolution. Lewontin (1970) argued that, "At yet higher levels, the species and the community, natural selection obviously must occur ..." A number of authors have advocated the idea of natural selection of communities and ecosystems, for example Dunbar (1960, 1972), Emerson (1960), Darnell (1970). The idea of natural selection acting on the community level is equivalent to Clement's "super-organism" view of the community.

One of the most recent contributions to the idea of community selection/evolution has come from Wilson (1976, 1980). Wilson argues that if a spatial variation exists in community composition, organisms will differentially feel their own effects on the community and this will expose variations in indirect effects to natural selection leading ultimately to what Wilson regards as a "form of evolution on the community level" (Wilson 1976). His model of patch selection proposes that a mutant or variant which benefits other members of its patch (but not members of adjacent patches) can enhance the relative fitness of the whole patch so that the relative frequency of the patch may increase but that of the mutant itself need not.

Natural selection of a community (or community evolution) in this sense means that the community itself can acquire adaptations through the effect of its component species on it, which will in turn affect its component species and "... only those members that positively contribute to community welfare persist" (Wilson 1980). A similar view was proposed by Goodall (1963) in referring to community evolution but not community selection.

PROSPECTUS

Three different usages of the term community evolution have been used in the literature and this has left the primary meaning of the term uncertain. An alternative approach is to use more specific titles for each viewpoint, e.g. A) community phylogeny, B) community character development, and C) community selection. Using this terminology not only reduces confusion by distinguishing three different phenomena that have all previously been called the same thing, but also points more precisely to the scope and meaning of each perspective.

Each of these perspectives of community evolution is the counterpart of different perspectives of change or evolution at the population/species level. Change in genetic constitution is traditionally regarded as population evolution, but recent views in plant ecology recognize that a major part of community variation also exists at the intraspecific level (Antonovics 1976, Harper 1977). The precise unit of local adaptation in a plant community is clearly not the species, and the specialized genotype or ecotype representing a species in a certain area may not be the same even in closely adjacent regions (Jain & Bradshaw 1966, Snaydon 1970, Bradshaw 1972, Linhart 1974, Solbrig & Simpson 1974, Warwick & Briggs 1979). In the Darwinian view the most crucial forces of selection will come from the biotic pressures of neighbours within the constraints set by the abiotic environment. Only recently have cases been reported of fine-scale biotic specialization in response to competitors in plant communities (Snaydon 1978, Turkington 1979, Turkington & Harper 1979, Martin & Harding 1981, Aarssen 1983). The occurrence of differentiation at such a micro-scale depends on the existence of abundant intraspecific variation and multidirectional selection forces, both of which are amply displayed in many types of plant communities that have been studied (Bradshaw 1972, Antonovics 1976, Snaydon 1978, Burdon 1981a, b).

5.	COMMUNITY PHYLOGENY	'ORIGIN OF COMMUNITIES' - REPLACEMENT OF SPECIES ASSEMBLAGES OVER GEOLOGIC TIME SPAN
		↑
4.	SUCCESSION	REPLACEMENT OF COMMUNITY 'TYPES' (SPECIES ASSEMBLAGES)
		↑
3.	COMMUNITY CHARACTER DEVELOPMENT	CHANGES IN COMMUNITY-LEVEL CHARACTERISTICS REFLECTING COADAPTIVE EVOLUTION
		↑
2.	COMMUNITY SELECTION	GROUP SELECTION ON THE LEVEL OF OF THE COMMUNITY
		↑
1.	COMMUNITY MICRO-EVOLUTION	CHANGES IN GENETIC CONSTITUTION OF COMMUNITY OF 'INDIVIDUALS' BY INDIVIDUAL SELECTION

FIGURE 1. LEVELS OF COMMUNITY CHANGE OR 'EVOLUTION'

To the plant ecologist then, the genotype is a relevant unit of community variation. Hence, there is good reason to argue that the evolution of the community (as with the population) can be manifested by changes in genotype frequencies within the community (regardless of species) as a result of individual natural selection. MacMahon et al. (1978, 1981) have also adopted an approach to community phenomena that is centered on the individual. This view contrasts with traditional thinking in community ecology which treats the species as more of a taxonomically distinctive unit rather than as a wide ranging collection of ecologically different individuals. There is a growing interest to change this typological view of the species in community ecology (Harper 1982).

To summarize, if we include succession, there are at least five distinguishable levels of community change (Fig. 1) each of which might loosely be called community evolution. Doing so however has created semantic confusion. Each perspective of community evolution is recognized in current literature but clearly it is necessary for authors to specify which they are using, for each one depends on different scales and mechanisms of evolution. The literature indicates that the term community evolution refers to a much more broadly based concept than some authors may wish to convey.

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LITERATURE CITED

Aarssen, L.W. 1983. Interactions and coexistence of species in pasture community evolution. Ph.D. Thesis. University of British Columbia, Vancouver, B.C. Canada.

Aarssen, L.W., R. Turkington and P.B. Cavers. 1979. Neighbour relationships in grass-legume communities. II. Temporal stability and community evolution. Can. J. Bot. 57: 2695-2703.

Allee, W.C., A.E. Emerson, O. Park, T. Park and K.P. Schmidt. 1949. Principles of animal ecology. W.B. Saunders Co., Phil.

Antonovics, J. 1976. The input from population genetics: The new ecological genetics. Syst. Bot. 1: 223-245.

Baker, H.G. 1966. Reasoning about adaptations in ecosystems. Bioscience 16: 35-37.

Boucot, A.J. 1978. Community evolution and rates of cladogenesis. Evolutionary Biology 11: 545-655.

Bradshaw, A.D. 1972. Some of the evolutionary consequences of being a plant. Evol. Biol. 5: 25-47.

Burdon, J.J. 1981a. Intra-specific diversity in a natural population of Trifolium repens. J. Ecol. 68: 717-735.

Burdon, J.J. 1981b. Variation in disease-resistance within a population of Trifolium repens. J. Ecol. 68: 737-744.

Clements, F.E. 1916. Plant succession: analysis of the development of vegetation. Carnegie Inst. Wash. Publ. 242: 1-512.

Cody, M.L. and J.M. Diamond. 1975. Ecology and evolution of communities. Harvard Univ. Press., Cambridge, Mass.

Darnell, R.M. 1970. Evolution and the ecosystem. Amer. Zool. 10; 9-15.

Dice, L.R. 1952. Natural communities. Univ. Michigan Press, Ann Arbor.

Dunbar, M.J. 1960. The evolution of stability in marine environments; natural

selection at the level of the ecosystem. Amer. Natur. 94: 129-136.
Dunbar, M.J. 1972. The ecosystem as a unit of natural selection. In, E.S. Deevey (ed.). Growth by intussusception. pp. 113-130. Trans. Conn. Acad. Arts Sci., Vol. 44.
Emerson, A.E. 1960. The evolution of adaptation in population systems. In, S. Tax (ed.). Evolution after Darwin, Vol. 1, pp. 307-348. Univ. Chicago Press.
Golley, F.B. (ed.). 1977. Ecological succession. Benchmark papers in ecology. Vol. 5. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Penn. 373 pp.
Goodall, D.W. 1963. The continuum and the individualistic association. Vegetatio 11: 297-316.
Gray, J., A.J. Boucot and W.B.N. Berry. (eds.). 1981. Communities of the past. Academic press, N.Y. 640 pp.
Harper, J.L. 1977. Population biology of plants. Academic Press, London. 892 pp.
Harper, J.L. 1982. After description. In, Newman, E.I. (ed.). The plant community as a working mechanism. Spec. Publ. No. 1, Brit. Ecol. Soc. Blackwell Sci. Publ., Oxford pp. 11-25.
Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Amer. Natur. 93: 145-159.
Jain, S.K. and A.D. Bradshaw. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. Heredity 21: 407-441.
Johnson, E.A. 1979. Succession: An unfinished revolution. Ecology 60: 238-240.
Ladd, H.S. (ed.). 1957. Treatise on maine ecology and paleoecology. Vol. 2. Paleoecology Geol. Soc. Amer. Mem. 67: 1-1077.
Levandowsky, M. and B.S. White. 1977. Randomness, time scales, and the evolution of biological communities. Evolutionary Biology 10: 69-161.
Levins, R. 1975. Evolution in communities near equilibrium. In, Cody, M.L. & J.M. Diamond (eds.), Ecology and evolution of communities. pp. 16-50. Harvard Univ. Press, Cambridge, Mass.
Lewontin, R.C. 1969. The meaning of stability. In, Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22: 13-24.
Lewontin, R.C. 1970. The units of selection. Ann. Rev. Ecol. Syst. 1: 1-18.
Linhart, Y. 1974. Intra-population differentiation in annual plants. I. Veronica peregrina L. raised under noncompetitive conditions. Evolution 28: 232-243.
MacMahon, J.A., D.L. Phillips, J.V. Robinson & D.J. Schimpf. 1978. Levels of biological organization: an organism-centered approach. Bio Science 28: 700-704.
MacMahon, J.A., D.J. Schimpf, D.C. Anderson, K.G. Smith & R.L. Bayne, Jr. 1981. An organism-centered approach to some community and ecosystem concepts. J. Theor. Biol. 88: 287-307.
Martin, M.M. and J. Harding. 1981. Evidence for the evolution of competition between two species of annual plants. Evolution 35: 975-987.
Mason, H.L. 1947. Evolution of certain floristic associations in western North America. Ecol. Monog. 17: 201-210.
May, R.M. 1978. The evolution of ecological systems. Sci. Am. 239(3): 118-133.
Olsen, E.C. 1966. Community evolution and the origin of mammals. Ecology 47: 291-302.
Pickett, S.T.A. 1976. Succession: An evolutionary interpretation. Amer. Natur. 110: 107-119.
Richardson, J.L. 1977. Dimensions of ecology. Williams & Wilkins Co., Baltimore.

Simpson, G.G. 1969. The first three billion years of community evolution. In, Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22: 162-177.

Snaydon, R.W. 1970. Rapid population differentiation in a mosaic environment. I. The response of Anthoxanthum odoratum populations to soils. Evolution 24: 257-269.

Snaydon, R.W. 1978. Genetic changes in pasture populations. In, J.R. Wilson (ed.). Plant relations in pastures. CSIRO, E. Melbourne, Australia.

Solbrig, O.T. and B.B. Simpson. 1974. Components of regulation of a population of dandelions in Michigan. J. Ecol. 62: 473-486.

Turkington, R. 1979. Neighbour relationships in grass-legume communities. IV. Fine-scale biotic differentiation. Can. J. Bot. 57: 2711-2716.

Turkington, R. and J.L. Harper. 1979. The growth, distribution and neighbour relationships of Trifolium repens L. in a permanent pasture. 4. Fine-scale biotic differentiation. J. Ecol. 67: 245-254.

Valentine, J.W. 1968. The evolution of ecological units above the population level. J. Paleontol. 42: 253-267.

Warwick, S.I. & D. Briggs. 1979. The genecology of lawn weeds. III. Cultivation experiments with Achillea millefolium L., Bellis perennis L., Plantago lanceolata L., Plantago major L. and Prunella vulgaris L. collected from lawns and contrasting grassland habitats. New Phytol. 38: 509-536.

Whittaker, R.H. 1969. Evolution of diversity in plant communities. In, Diversity and stability in ecological systems. Brookhaven Symp. Biol. 22: 178-196.

Whittaker, R.H. 1975. Communities and ecosystems, 2nd ed. MacMillan, New York. 385 pp.

Whittaker, R.H. and G.M. Woodwell. 1971. Evolution of natural communities. In, J.A. Weins (ed.). Ecosystem structure and function, pp. 137-159. Proc. 31st Ann. Biol. Coll., Oregon State Univ. Press.

Wilson, D.S. 1976. Evolution on the level of communities. Science 192: 1358-1360.

Wilson, D.S. 1980. The natural selection of populations and communities. Benajamin/Cummings Publ. Co., Menlo Park, Calif. 186 pp.