OIKOS 104: 27–34, 2004

The community of an individual: implications for the community concept

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Parker, V. T. 2004. The community of an individual: implications for the community concept. – Oikos 104: 27–34.

The concept of the ecological community is examined from the perspective of its criteria and domain. The multiple definitions and uses of this concept indicate a variety of scales and approaches. In this paper, a core definition of the minimal criteria and domain is proposed. Using those criteria, a model of the ecological community is developed based on a focal individual and its interactions with other individuals. In order to increase the scale of the domain of this approach, additional criteria are required. This model is used to explore characteristics of the minimum domain and larger scales of the community concept. The structure that emerges emphasizes context dependency and the potential for indeterminacy for most types of interactions. A prominent historical argument, the nature of boundaries between communities, has no relevance in this model.

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Among the concepts ecologists use, one of the most problematic is the community concept. The ecological community is defined vaguely and the upper and lower boundaries of its domain are unclear. Current ecological textbooks indicate the uncertain boundaries of this concept, usually offering only general definitions, for example, "an interactive assemblage of species occurring together" (Putman 1994), "an assemblage of species populations that occur together" (Begon et al. 1996), or "a collection of species found in a particular place" (Morin 1999). These definitions express co-occurrence and interaction, but offer no further development. Examining how ecologists use the concept indicates a diversity of approaches. These multiple uses imply that several concepts are merged together, or that the concept has several dimensions that need to be made explicit. In this paper, I propose minimal criteria for this concept. These criteria suggest a simple model that I develop at the finest scale possible to illustrate assumptions and characteristics that may vary with expectations. My purpose is to explore minimal limits to the domain of the concept as a step in understanding its dimensionality and structure.

Problems with the community concept evolve from a history of different uses describing local assemblages. One approach assumes distinct 'natural types' of communities, designated by the differences in composition and abundance of their members. These ecological communities are thought bounded in space and time and characterized by an assemblage of persistent species (reviewed by McIntosh 1985, Underwood 1986, Schrader-Frechette and McCoy 1993, Morin 1999). While many assume communities exist as natural types, extreme versions of this perspective viewed communities as analogous to organisms (Clements 1916, 1936, Phillips 1931, 1935). Even when we admit that communities fail to persist at some time scales (Davis 1981), the assumption of persistent dominant species at shorter temporal scales also supports the notion of relatively unchanging natural communities. Belief in distinct communities can result in extreme and rather peculiar approaches to determining their boundaries (Looijen and van Andel 1999).

A historically distinct usage considers the 'community' as interacting individuals and the community is

Accepted 15 May 2003

ISSN 0030-1299

considered structured by biotic interactions. Whether the community is a 'unit' or not matters little because research is focused on interactions structuring composition and abundance among a focused subset of species. The community is treated only as the context of the study, although results from the study are often extended to the structure or dynamics of the whole community. This represents the classic experimental approach that has been successful in revealing connections between particular processes and aspects of community organization such as competition or disturbance (Connell 1961, Brown and Davidson 1977, Harper 1977, Sousa 1979, Pickett and White 1985, Brown 1998).

Recent research has also expanded the scale at which interactions may influence community structure and dynamics. The larger context involves temporal, spatial and interactive dimensions (McNaughton 1983, Walker and Chapin 1987, Pickett et al. 1989, Abrams 1992, Wooton 1994, Menge 1995, Parker and Pickett 1998, Sinclair et al. 2000). Contextual processes influence how particular species may or may not persist in patches and how their interactions with other species may be modified. Source-sink dynamics, for example, predicts populations sometimes are found in habitats in which they cannot persist (Lidicker 1975, Pulliam 1988, 2000), and regionally these sink habitats may be critical for the persistence of some species (Holt 1997b, Frouz and Kindlmann 2001). The extension of metapopulation models to multiple, interacting species shows the potential for context in the dynamics of populations (Nee et al. 1997) including indirect interactions among species that do not coexist in the same patches (Holt 1997a).

Such dynamics indicates the domain of the community concept requires a number of spatial and temporal scales (Brand and Parker 1995, Brown 1995, Lawton 1999, Gaston and Blackburn 1999, 2000), in contrast to classical views of communities as locally adapted, relatively persistent assemblages bounded in time and space. The ambiguity of the community concept has not constrained any of these developments, but because of the increasing importance of 'communities' in conservation, I feel the criteria we use for the concept deserves review at this point. For this paper, I develop a general model of the ecological community using interactions linking individuals. Rather than using populations as the smallest unit, I start by examining the community of a single individual (Parker 2001). This approach focuses on interactions, yet differs in characteristics and emphasis from the traditional focus on populations. Generally, no spatial and temporal boundaries are apparent, and an emphasis on context dependency emerges. My objectives are to further develop this model and examine some of its implications for the community concept.

The core concept of the ecological community

The core concept of ecological communities is that ecological organization and function result from individuals of different species interacting with one another. No other conceptual recipe defining a community seems to exist other than a collection of individuals from more than one species population (Schrader-Frechette and McCoy 1993) and interactions dependably occur among these individuals (Putman 1994). Interactions are diverse and include one dimensional interactions like herbivory by a leaf miner to those that are more complex, such as a hummingbird pollinating a plant while also dispersing mites, or a frugivore dispersing a host plant's seed while simultaneously bringing mistletoe seed onto the host. Interactions among diverse individuals creating ecological organization or structure is the one consistent characteristic of communities throughout the world, even though some ecologists may deliberately reject interactions as a defining criterion for communities (Looijen and van Andel 1999) because of the diversity, frequency and ubiquity of interactions.

Several conceptual models exist that propose an explicit topology for communities. One that is consistent with the general definition of communities being structured by interactions among individuals of different species is that proposed by Pickett et al. (1989). In their Minimum Interactive Structure (MIS) model, larger ecological entities (e.g. a guild) result from interactions or other processes linking together smaller ecological entities (e.g. species populations). A special case of this model, for example, would be a food web (Cohen 1989, Martinez 1991) in which entities would be defined as species populations and linkages as trophic interactions.

If the minimal structure of a community is defined by interactions among entities (the MIS of Pickett et al. 1989), what remains is to define both entities and interactions. The most inclusive definition of the ecological community, therefore, would be all individuals and all interactions. While this definition is consistent with a conceptual definition of the ecological community, clearly its domain (the biosphere) exceeds our traditional understanding of a community, as well as having too many individuals and linkages to make sense of at that scale of definition. We can, however, explore a variety of definitions for these two terms and examine the characteristics of the community that results.

The community of a single individual

The smallest ecological entity I want to consider is an individual organism. If interactions among individuals from different species represent the core concept of the ecological community, then the lower limit of the domain of this concept would be the community associated with a single focal individual. Although the concept of an ecological individual may also have ambiguities (is a lichen and its algal symbiont the individual or are they separate?), for the purposes of discussion in this paper, individuals will be considered broadly. Earlier I have suggested the community of a single, focal individual as part of an exploration of the community concept (Parker 2001). To construct this model, the entities are defined as individual organisms and linkages are defined as all biotic interactions. No constraints are placed on the interactions because research now suggests that any possible interaction can be significant for community structure or dynamics.

For a single individual, its community would incorporate conspecifics with which it is involved in reproductive activity, and other individuals of its own and other species with which it interacts. These would include individuals with which it competes, individuals with which it has symbioses, or individuals that might consume all or part of it. In other words, the immediate community of this individual is all the other individuals with which it interacts (Fig. 1). This type of web is inclusive of all direct ecological interactions among organisms that have been found to influence the performance, abundance or distribution of species. Conceptually, an individual-focused web can be constructed including all interactions. This inclusiveness and completeness has other implications that will be discussed later.

Individuals that exhibit considerable differences in size, location, or mode of nutrition among life history stages may experience substantially different stage-relative 'communities' during development. This would be particularly true for many invertebrates with complete metamorphosis between stages, or large plants in which the processes acting on seeds or seedlings may

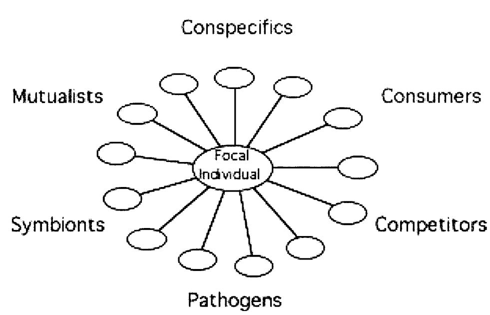

Fig. 1. This illustrates conceptually the community of an individual. Circles represent individuals and lines connecting individuals represent interactions. The community of a focal individual emerges from all the interactions it has with other individual organisms. This would include the conspecific mates of the focal individual, as well as its competitors, mutualists, parasites and others with which it interacts. This figure is modified from Parker (2001).

differ radically from those interacting with adults. Therefore, each individual potentially has a continuously changing set of individuals with which it interacts at different time periods. Organisms that substantially change size may also increase in the number of individuals with which they simultaneously interact. For a focal individual, therefore, communities are represented by a dynamic turnover of individuals with which it interacts that may represent various and changing species populations. This characteristic certainly does not seem familiar to the research questions generally asked of communities.

The net impact or direction of any particular interaction is context specific. There are two aspects of context; one of these is the influence of varying abiotic conditions. In other words, changes in physical environmental factors can shift the net outcome of biological interactions; for example, competitive dominance may switch from one individual to another (Christie and Detling 1982, Austin 1990). This provides the basis for explanations of changes in community structure along spatial or temporal environmental gradients (Austin and Austin 1980, Tilman 1982, 1988, Pennings and Callaway 1992). Performance of individuals based on environmental conditions can be incorporated in the links of this model altering individual performance as a variable influencing frequency, magnitude or direction of interactions.

The second contextual influence is that each individual interacting with the focal individual is itself a focal individual. The universe of other interactions with which it is involved influences the performance of any individual. Because this can be extended to linkages further and further away from our focal individual, the model also illustrates the frustration ecologists sometimes experience when trying to make reliable predictions. While influences on a focal individual clearly will weaken with the number of linkages involved, the role of context is explicit when individuals are involved in loops of interactions, for example when competitors share predators. Others have emphasized the contextual role of indirect interactions, for example, apparent competition, apparent mutualism, and other indirect interaction concepts (Levine 1976, Holt 1977, Menge 1995).

The intricate web of interactions, direct or indirect, current or historic, that constructs the biotic environment of an individual represents the minimal domain of the concept of an ecological community (Parker 2001, 2002). Linkages represent a diversity of interactions. The type of link; its frequency, intensity or magnitude; its extent; and its biotic and abiotic context determines the net impact of any particular link. These are concepts developed in a number of disparate field and theoretical studies but rarely brought together (see Pickett et al. 1987 for a framework for plant succession). Modeling all the individuals of any community and their interactions may not be practical currently, but this model conceptually is instructive because of some of its implications that I will consider later.

Scaling up an individual-based model to a spatial extent

Increasing the scale of a focal-individual model requires adding one or more criteria. For example, ecologists focusing on sessile species tend to examine a community as a spatial extent and if focusing on mobile species tend to examine appropriate spatial patches. The model can be retained as an individual-based model but described for a spatial extent; however, the number of individuals and their interactions increase rapidly with increasing area. The community now appears as a complex web or network with some richly connected nodes (usually species that are the principal sources of energy) and with other nodes less well connected (Fig. 2). Such a structure is reminiscent of figures produced by scale free random models in graph theory (Strogatz 2001).

Several characteristics of spatial models remain consistent with the focal-individual model, including the lack of clear boundaries and the influence of mobile species. Individuals along any of the spatial boundaries have interaction links to individuals outside the boundaries, for example, a boundary between shrub and forest communities. With respect to interactions, boundaries generally are arbitrary. Unless a physical discontinuity is present at a site that prevents potential interactions, individuals will compete for resources at the boundary area (Dunne and Parker 1999, Royce and Barbour 2001) or share mutualists in common (Horton et al. 1999). Also, many of the individuals involved in interactions are mobile, and may or may not be present at any sampling period. For any particular set of individuals or species within a defined spatial extent, including all their interactions with other individuals or populations additionally means including those that may not be currently present in the area. Mobile species interact in different ways and at different frequencies with sessile species, for example, as food for filtering species like barnacles, or as herbivores or dispersal agents for terrestrial plants.

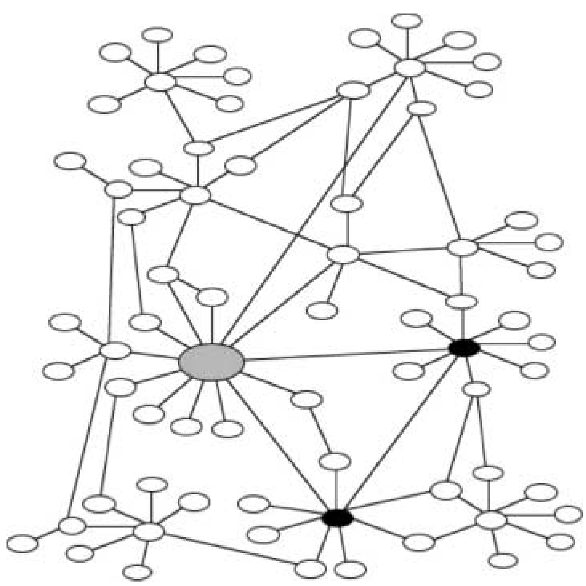

Fig. 2. A hypothetical illustration of interactions among individuals at a location. Because of the number of individuals and linkages possible, the purpose of this figure is to illustrate a few conceptual ideas. For any spatial area, a topology of interactions among individuals indicates a complex network. Some individuals interconnect more richly than others, due to their size, longevity, mobility, or resource interactions. Linkages to individuals outside the area are not shown.

Including mobile species, however, requires decisions about temporal extent. If a spatial area is analyzed for too brief a period, then many critical mobile species may not be included, reducing reliability of models or predictability. For example, analyzing any community only for a single time period may miss the impact of seasonal or migrating individuals, such as sampling a grassland community once may miss the impact of grazers on the system, resulting in a naïve view of the community (McNaughton 1983, 1985). Temporal variation in the net impact of mobile species is itself a dimension to which other species may demonstrate differential responses (Gaston and Blackburn 2000). This suggests that for any specified spatial extent, a further criterion will be needed to specify a temporal extent, with the recognition that any boundary may be inadequate. As an extreme example, current North American terrestrial communities lack most of the megafauna that were characteristic influences only a few thousand years ago; our understanding of these communities rarely considers any residual influences they may have on contemporary structure or dynamics.

Changing the definition of the entities

So far the entities of the community model have been individuals. Communities, however, generally are described as composed of species populations, even though this structure contains some disparities or ambiguities (Allen and Hoekstra 1992, Schrader-Frechette and McCoy 1993, Looijen and van Andel 1999). This organization derives from the traditionally assumed natural hierarchy in which communities are composed of populations of species (Begon et al. 1996) and are nested into larger ecosystems or landscapes.

Replacing individuals with species populations for the entities of the model changes a number of features. On the one hand it would provide a structure more typical of research and textbook perspectives. Redefining the entities to populations requires spatial-temporal criteria similar to the spatial model to define where and when to look for these collective entities, with the additional criterion of summarizing individuals into conspecific populations. Scaling up an individual-based model to a population-based model and to include all populations within a specific area changes the nature of the entities and linkages while leaving other aspects similar. Linkages now become probabilistic because, for any population, not all individuals necessarily will interact with any individual from another population to which they are linked. The diversity of linkages depends on the spatial extent of populations. Further, because entities are represented by populations, strength of interaction, frequency and other process characteristics are influenced directly by the sizes of interacting populations, their age or size class distributions, and whether they are mobile or not. A community model using populations would now require additional, familiar characteristics like relative abundances, spatial compartmentalization, or diversity, to be predictable. At the same time, regardless of specified spatial or temporal boundaries, interactions cross those boundaries and so they remain arbitrary to some extent.

Using populations also creates several ambiguities in conceptual models of communities. One is the disparity between any defined spatial or temporal extent of a community and that of 'component' populations. This is an issue that has been considered at length by others so I will only mention it briefly (Looijen and van Andel 1999). Spatially, populations that are found together may have very different ranges. Three different circumstances may result in any spatial-temporal designation. One is that an extensive or mobile population of a species may encompass more than one presumed community. For other species, the 'population' may be equivalent to the sum of all individuals for many species. Finally, for small individuals or patchily distributed species, the same spatial-temporal extent may summarize together multiple, distinct populations of the same species that may be experiencing substantially different biotic or abiotic interactions. Thus, any claim for a spatial-temporal extent for a community will likely encompass three different types of populations, a subset of a larger population, realistic populations, and combinations of multiple populations of the same species.

More critically, interactions both structurally and functionally link individuals together but using populations in some cases may increase the ambiguity of interpreting functional characteristics of communities. Populations are convenient to use because they are recognizable groups of individuals with similar ecological functions. For any particular ecological function or process, however, individuals from different species may perform similarly. Thus, when focusing on one ecological function, some other type of 'entity' may be more appropriate. The functional combination called 'trophic species' is one example that, although controversial to some, performs better in food web analyses than do separate populations (Martinez 1991, Dunne et al. 2002a, b, Williams et al. 2002). When functional groups are used rather than species populations, questions about the role of diversity and community function are better resolved (McCann 2000, Kinzig et al. 2002). This results from individuals from different species behaving similarly for a particular function. A different combination of individuals and species might be necessary for another ecological function (Collins and Benning 1996). Consequently, different configurations of species populations may produce similar ecological results, and the same pool of species can yield a variety of relatively stable communities (Drake 1991).

These varieties of combinations suggest that the concept of ecological community can have a variety of structures depending on the questions being asked. Because communities or ecosystems are structures in which a number of different individuals from different species functionally operate together, defining entities from a functional perspective when pursuing particular research questions makes more sense.

Temporal and spatial scales of a community

Community members participate from different temporal and spatial scales. This results in considerable variation in frequency, intensity or magnitude of interactions. Definitions, however, tend to constrain communities to a limited extent of their temporal or spatial potential (Brand and Parker 1995, Parker 2001, 2002). The multidimensionality of biotic as well as physical processes indicates that dynamics are continuous temporally and spatially (Brand and Parker 1995). Thus, patterns and their underlying processes can be observed on a variety of temporal or spatial scales (Ricklefs 1987, Holt 1993, 1997a, Brown 1995, Lawton 1999, Gaston and Blackburn 1999, 2000). Boundaries or other patterns reflect a particular temporal and spatial scale and a particular set of organisms. Biotic discontinuities often arise at some scale only if community membership is highly restricted (usually only to sessile stages of species) and patterns are summarized for populations.

Developing a model of a community based on interactions among its members reveals that the temporal or spatial extent of any community is essentially unbounded. For the community of a focal individual, the temporal scale is set by the lifetime of that individual. This is the only organizational level at which a clear boundary of any type actually exists for the community concept. At the scale of an individual's community, clear spatial boundaries do not exist. Scaling up to a spatial extent or to populations indicates that clear temporal or spatial boundaries similarly are not inherent characteristics of ecological communities. Further, variation in lifespan prevents clear temporal boundaries in most circumstances. From one time period to another, spatial extent can change as the range of the mobile individuals shift. The significance of the spatial unboundedness is incorporated in a variety of ecological concepts, such as the conservation-oriented concept of corridors or in landscape connectivity. Temporal unboundedness is illustrated by the influence of historical events such that any particular contemporary community may be contingent on past events that have left no obvious evidence (Wu and Loucks 1995, Parker and Pickett 1998).

Conclusions

The core concept of interactions among individuals of different species is proposed as a basis for defining ecological communities. Linking individuals together by the diversity of possible interactions creates a complex web or network model of the ecological community. This model becomes the context for considering other, narrower models. The community of a single, focal individual uses the fewest criteria establishing the minimal domain of this core concept. Interactions with other individuals vary in frequency, duration and magnitude. Because these individuals also interact with additional individuals, linkages of interactions among individuals can influence the dynamics of other individuals indirectly. This pattern of interaction indicates a context dependency of the net impact of interactions. Because the scale of the size, lifespan, spatial range or impact of any individual can vary considerably, the dynamics of interactions within communities are variable and continuous temporally and spatially. The influence of any particular interaction generally should attenuate with the number of links between that interaction and a focal individual.

Redefining entities (e.g. as populations) result in changes to strengths or frequencies of interactions as well as changing them to probabilities for any individual in particular. Limiting the diversity of interactions (e.g. restricting definition to trophic interactions) narrows the focus of the model and may shift structural aspects of the community web. In either case, consideration must be given to the objectives of the research context when redefining either entities or interactions. For example, populations may not be the appropriate entities for exploring functional aspects of communities in the context of specific types of interactions (e.g. trophic species instead of species populations for food web research).

Web or network models have other implications concerning the structure and dynamics of communities. If focal individual communities can be conceived as the simplest organizational component of multispecies systems, one focal individual's 'community' may share nonetheless a considerable number of members with another individual's community. Because of this, focal individual communities are not completely distinct from each other and thus cannot construct distinct larger organizational components. From a basis of interactions among individuals, therefore, communities are difficult to structure into nested hierarchies without limiting the dimensionality of the system. Much of the predictive difficulty sometimes experienced in applied or experimental circumstances may arise from the contingent nature of the historical web of interactions that tie individuals together. Functional interpretations of communities require a different organizational understanding from other perspectives. Approaching communities as complex networks is challenging, because communities illustrate all the characteristics that complicate analysis; structural complexity, network evolution, connection diversity, dynamical complexity, node diversity and metacomplications (Strogatz 2001). Nonetheless, understanding the collective dynamics of ecological communities, especially functional dynamics, may require inquiry into the impact of network topology and dynamics.

Acknowledgements – The author acknowledges the help from comments on earlier drafts by S. T. A. Pickett and Janne Bengtsson. The author was supported by a grant from the USDA, NRI-99-35101-7779.

References

Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. – Am. Nat. 140: 573–600.

Allen, T. F. H. and Hoekstra, T. W. 1992. Toward a unified ecology. – Columbia Univ. Press.

Austin, M. P. 1990. Community theory and competition in vegetation. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Academic Press, pp. 215–239.

Austin, M. P. and Austin, B. O. 1980. Behaviour of experimental plant communities along a nutrient gradient. – J. Ecol. 68: 891–918.

Begon, M., Harper, J. L. and Townsend, C. R. 1996. Ecology: individuals, populations and communities, 3rd ed. – Blackwell Science.

Brand, T. and Parker, V. T. 1995. Scale and general laws of vegetation dynamics. – Oikos 73: 375–380.

Brown, J. H. 1995. Macroecology. – Univ. Chicago Press.

Brown, J. H. 1998. The desert granivory experiments at Portal. – In: Resetarits Jr., W. J. and Bernardo, J. (eds), Experimental ecology: issues and perspectives. Oxford Univ. Press, pp. 71–95.

Brown, J. H. and Davidson, D. W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. – Science 196: 880–882.

Christie, E. K. and Detling, J. K. 1982. Analysis of interference between C3 and C4 grasses in relation to temperature and soil nitrogen supply. – Ecology 63: 1277–1284.

Clements, F. E. 1916. Plant succession: an analysis of the development of vetation. Carnegie Inst. of Washington Publication 242. – Carnegie Institution.
Clements, F. E. 1936. Nature and structure of the climax. – J. Ecology 24: 252–284.
Cohen, J. 1989. Food webs and community structure. – In: Roughgarden, J., May, R. M. and Levin, S. A. (eds), Perspectives in ecological theory. Princeton Univ. Press, pp. 181–202.
Collins, S. L. and Benning, T. L. 1996. Spatial and temporal patterns in functional diversity. – In: Gaston, K. J. (ed.), Biodiversity, a biology of numbers and difference. Blackwell, pp. 253–280.
Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. – Ecology 42: 710–723.
Davis, M. B. 1981. Quaternary history and the stability of forest communities. – In: West, D. C., Shugart, H. H. and and Botkin, D. B. (eds), Forest succession. Springer-Verlag, pp. 132–153.
Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. – Am. Nat. 137: 1–26.
Dunne, J. A. and Parker, V. T. 1999. Seasonal soil water potential patterns and establishment of *Pseudotsuga menziesii* seedlings in chaparral. – Oecologia 119: 36–45.
Dunne, J. A., Williams, R. J. and Martinez, N. D. 2002a. Network structure and biodiversity loss in food webs: robustness increases with connectance. – Ecol. Lett. 5: 558–567.
Dunne, J. A., Williams, R. J. and Martinez, N. D. 2002b. Food-web structure and network theory: the role of connectance and size. – Proc. Natl Acad. Sci. USA 99: 12917–12922.
Frouz, J. and Kindlmann, P. 2001. The role of sink to source re-colonisation in the population dynamics of insects living in unstable habitats: an example of terrestrial chironomids. – Oikos 93: 50–58.
Gaston, K. J. and Blackburn, T. M. 1999. A critique for macroecology. – Oikos 84: 353–368.
Gaston, K. J. and Blackburn, T. M. 2000. Pattern and process in macroecology. – Blackwell.
Harper, J. L. 1977. Population biology of plants. – Academic Press.
Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. – Theor. Popul. Biol. 12: 197–229.
Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. – In: Ricklefs, R. and Schulter, D. (eds), Community diversity: historical and biogeographic perspective. Univ. Chicago Press, pp. 77–88.
Holt, R. D. 1997a. From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. – In: Hanski, I. and Gilpin, M. E. (eds), Metapopulation biology: ecology, genetics and evolution. Academic Press, pp. 149–164.
Holt, R. D. 1997b. On the evolutionary stability of sink populations. – Evol. Ecol. 11: 723–731.
Horton, T. R., Bruns, T. and Parker, V. T. 1999. Ectomycorrhizal fungi in *Arctostaphylos* patches contribute to the establishment of *Pseudotsuga menziesii*. – Can. J. Bot. 77: 93–102.
Kinzig, A. P., Pacala, S. and Tilman, G. D. 2002. The functional consequences of biodiversity: empirical progress and theoretical extensions. – Princeton Univ. Press.
Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.
Levine, S. H. 1976. Competitive interactions in ecosystems. – Am. Nat. 110: 903–910.
Lidicker Jr., W. Z. 1975. The role of dispersal in the demography of small mammals. – In: Golley, F.B., Petrusewiez, K. and Ryszkowshi, L. (eds), Small mammals: their productivity and population dynamics. Cambridge Univ. Press, pp. 103–128.
Looijen, R. C. and van Andel, J. 1999. Ecological communities: conceptual problems and definitions. – Persp. Plant Ecol. Evol. Syst. 2: 210–222.
Martinez, N. D. 1991. Artifacts or attributes? effects of resolution on the Little Rock Lake food web. – Ecol. Monogr. 61: 367–392.
McCann, K. S. 2000. The diversity – stability debate. – Nature 405: 228–233.
McIntosh, R. P. 1985. The background of ecology, concept and theory. – Cambridge Univ. Press.
McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. – Ecol. Monogr. 53: 291–320.
McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. – Ecol. Monogr. 55: 259–294.
Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. – Ecol. Monogr. 65: 21–74.
Morin, P. J. 1999. Community ecology. – Blackwell Science.
Nee, S., May, R. M. and Hassell, M. P. 1997. Two-species metapopulation models. – In: Hanski, I. and Gilpin, M. (eds), Metapopulation dynamics. Academic Press, pp. 123–147.
Parker, V. T. 2001. Conceptual problems and scale limitations of defining ecological communities: a critique of the CI concept (community of individuals). – Persp. Plant Ecol. Evol. Syst. 4: 80–96.
Parker, V. T. 2002. The concept of the ecological community and a clash of perspectives: a reply to Looijen and van Andel. – Persp. Plant Ecol. Evol. Syst. 5: 139–143.
Parker, V. T. and Pickett, S. T. A. 1998. Historical contingency and multiple scales of dynamics in plant communities. – In: Peterson, D. L. and Parker, V. T. (eds), Ecological scale: theory and applications. Columbia Univ. Press, pp. 171–191.
Pennings, S. C. and Callaway, R. M. 1992. Salt marsh zonation: the relative importance of competition and physical factors. – Ecology 73: 681–690.
Phillips, J. 1931. The biotic community. – J. Ecology 19: 1–24.
Phillips, J. 1935. Succession, development, the climax and the complex organism: an analysis of concepts. Part III. – J. Ecology 23: 488–508.
Pickett, S. T. A. and White, P. S. 1985. The ecology of natural disturbance and patch dynamics. – Academic Press.
Pickett, S. T. A., Collins, S. L. and Armesto, J. J. 1987. A hierarchical consideration of causes and mechanisms of succession. – Vegetatio 69: 109–114.
Pickett, S. T. A., Kolasa, J., Armesto, J. J. and Collins, S. L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. – Oikos 54: 129–136.
Pulliam, H. R. 1988. Sources, sinks and population regulation. – Am. Nat. 132: 652–661.
Pulliam, H. R. 2000. On the relationship between niche and distribution. – Ecol. Lett. 3: 349–361.
Putman, R. J. 1994. Community ecology. – Chapman & Hall.
Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. – Science 235: 167–171.
Royce, E. B. and Barbour, M. G. 2001. Mediterranean climate effects: I. Conifer water use across a Sierran Nevada ecotone. – Am. J. Bot. 88: 911–918.
Schrader-Frechette, K. S. and McCoy, E. D. 1993. Method in ecology: strategies for conservation. – Cambridge Univ. Press.
Sinclair, A. R. E., Krebs, C. J., Fryxell, J. M. et al. 2000. Testing hypothesis of trophic level interactions: a boreal forest ecosystem. – Oikos 89: 313–328.

Sousa, W. P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. – Ecol. Monogr. 49: 227–254.
Strogatz, S. H. 2001. Exploring complex networks. – Nature 410: 268–276.
Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.
Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. – Princeton Univ. Press.
Underwood, A. J. 1986. What is a community? – In: Raup, D. M. and Jablonski, D. (eds), Patterns and processes in the history of life. Springer-Verlag, pp. 351–367.
Walker, L. R. and Chapin, F. S. III. 1987. Interactions among processes controlling successional change. – Oikos 50: 131–135.
Williams, R. J., Berlow, E. L., Dunne, J. A. et al. 2002. Two degrees of separation in complex food webs. – Proc. Natl Acad. Sci. USA 99: 12913–12916.
Wooton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – Annu. Rev. Ecol. Syst. 25: 443–466.
Wu, J. and Loucks, O. L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. – Q. Rev. Biol. 70: 439–466.