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BIOLOGICAL COMMUNITIES AS FUNCTIONALLY ORGANIZED UNITS

David Sloan Wilson

Department of Biological Sciences, Binghamton University, State University of New York,
Binghamton, New York 13902-6000

Abstract. Multilevel selection theory, which has been used to explain the functional organization of individuals and single-species social groups, can be extended to explain the functional organization of multispecies communities. Adaptation at lower levels of the biological hierarchy, such as the individual, does not automatically lead to adaptation at higher levels. Community-level functional organization therefore requires a process of natural selection among local communities that vary in their species and/or genetic composition. Community-level selection has been demonstrated in the laboratory and is plausible for many natural communities. Mutualisms, strong ecological effects, and complex systems dynamics do not by themselves produce functional organization and therefore should be studied in conjunction with multilevel selection theory.

Key words: complex dynamics; ecosystem ecology; functional organization; group selection; multilevel selection; mutualism; superorganism.

The concept of biological communities as functionally organized units has a long and troubled history. The naturalists that preceded Darwin envisioned all of nature as part of a grand design. Darwin realized that his theory justified only a limited form of functionalism. Natural selection can cause individuals to become well designed to survive and reproduce, but adaptation at the level of individuals does not necessarily lead to adaptation at the level of groups, much less multispecies communities. Darwin's image of nature as a multitude of inwardly pointed wedges being driven against each other seems the very opposite of Paley's image of nature as an exquisitely crafted watch. Nevertheless, grandiose functionalism did not disappear after Darwin, but persisted and even flourished by being reformulated in superficially Darwinian terms. Communities and ecosystems were compared to single individuals in their functional organization. Ecosystem-level properties such as productivity, complexity, or ''information'' were said to be maximized by evolution in the same way that natural selection maximizes the relative fitness of individuals. The possibility that lower level adaptation does not lead to higher level adaptation was either ignored or assumed to be resolved in favor of the higher levels. These ideas were scrutinized by evolutionary biologists in the 1960s and were easy to dismiss (e.g., Williams 1966). As a result, most community ecologists with an evolutionary background regard the concept of community ''superorganisms'' as unlikely, bordering on the heretical. Nevertheless, this did not prevent Lovelock (1979) from proposing his Gaia hypothesis, in which earth's entire biota supposedly acts like a great big organism to regulate its atmosphere. Even more recently, complex systems dynamics has been claimed to produce community-level functional organization as an emergent property (e.g., Depew and Weber 1995).

Against this background, it may sound surprising that there *is* a viable theory of community-level functional organization. The theory has emerged, not from the fields of ecosystem ecology or complex systems dynamics, but from evolutionary biology. It does not justify the grandiose view that all of nature is functionally organized, but it does show how smaller multispecies assemblages can acquire the properties that are usually associated with single organisms. The purpose of this paper is to outline the elements of the theory and its implications for the study of biological communities. I will also attempt to distinguish the theory from other major themes in community ecology, including mutualisms, strong ecological and evolutionary effects, and complex systems dynamics.

Multilevel selection theory

In his classic book entitled *Adaptation and Natural Selection,* Williams (1966) argued (along with Darwin) that higher level adaptation does not arise automatically from lower level adaptation. Natural selection within a single population maximizes the *relative* fitness of individuals and is insensitive to the fitness of the population per se. A trait that decreases the fitness of the entire population will be favored if it gives the individual a bigger slice of the smaller pie. Similarly, a trait that benefits the entire population but involves

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a cost for the individual will be selected against. Thus, a group of well-adapted individuals (in the sense of maximizing relative fitness) does not equal a well-adapted group. A well-adapted group might regulate its population size to avoid overexploiting its resources, or cooperate to defend itself against predators, or improve its common physical environment, but none of these traits are likely to evolve when natural selection is insensitive to the welfare of the group per se. Williams claimed that functional organization at any level of the biological hierarchy requires a corresponding process of natural selection *at that level.* Groups can become well designed only by a process of between-group selection and ecosystems can become well designed only by a process of between-ecosystem selection.

Although Williams (1966) stressed that higher level functional organization is possible in principle, he also felt that it was unlikely to evolve in practice, because natural selection at higher levels was invariably weak compared to natural selection at lower levels. His assessment became the majority view during the 1960s and 1970s, leading to an individualistic perspective in evolutionary biology. More recently, however, the issue has been revived and even Williams has emphasized the importance of group selection for the evolution of some traits. For example, here is Williams and Nesse's (1991:8) description of multilevel selection in disease organisms:

> *Bacterial pathogens may complete a million cycles of fission within the lifetime of one human host, and there may be more pathogens in one individual than the earth's human population. Even in one host, a pathogen can be expected to produce highly improbable mutations many times and to evolve significantly in response to even minute selection forces. . . . It has been realized for many years that some bacteria rapidly acquire high levels of antibiotic resistance . . . and that resistant strains can locally replace susceptible ones in a few weeks. A less commonly appreciated phenomenon, the evolution of virulence, will be emphasized here. . . . As an extreme example of within-host selection of virulence, imagine two pathogen clones competing within a host. One uses optimal exploitation, which results in the maximum number of propagules dispersed during the lifetime of the host. The other uses maximal (lethal) exploitation, which converts host resources to propagules at the maximum possible rate. The host will disperse more of the lethal type than its restrained competitor. The cost of the host's death is borne equally by the two competitors, whereas only the more virulent benefits from a greater rate of transmission. . . . In highly virulent cases of cholera and shigillosis propagules may be dispersed at more than a hundred times the rate in less virulent cases. The host's final output of both strains, of course, may be less than the long-term output from the less virulent type when it is the sole exploiter. The evolutionary outcome will depend on relative strengths of within-host and between-host competition in pathogen evolution. This is a clear example of group vs. individual (clone) selection for altruism, for which many formal models have been proposed.*

It is interesting to compare this description with Williams' (1966) earlier treatment of group selection. In both cases, it is clear that evolution within a single population (favoring virulence) does *not* increase the fitness of the population as a whole. It is also clear that a process of group selection is required to evolve the group-level adaptation (reduced virulence). The only difference is that group selection is seen as a potentially significant force that is not invariably weak compared to individual selection. In short, Williams has not changed his basic framework for thinking about the subject, but merely his assessment of the balance between levels of selection. This reassessment is warranted not only for the evolution of virulence but also for many other traits. Thus, the same conceptual framework that made higher level functional organization appear unlikely during the 1960s and 1970s makes it appear likely today, for at least some traits. It all depends on the balance between levels of selection, which in turn depends on the details of population structure; the existence of groups, the partitioning of variation and selection within and among groups, how old groups contribute to the formation of new groups, and so on.

Applying multilevel selection theory to multispecies communities

The recent developments in multilevel selection theory have focused largely on the evolution of social behavior within single species and therefore are not well known to community ecologists. Nevertheless, the theory is as relevant to interactions among species as among conspecifics. Just as single species are often subdivided into local populations that can serve as units of selection, communities are often subdivided into local patches that vary in their species and genetic composition. We can begin to understand the implications of community-level selection by comparing the classic group selection experiments of Wade (1976, 1977) with more recent community-level selection experiments by Goodnight (1990*a*, *b*). Wade formed groups of $N = 16$ flour beetles (*Tribolium castaneum*) and treated population size after 37 d as a group-level phenotypic character in an artificial selection experiment that would have been mundane if it had been conducted at the individual level. In one treatment, the most productive groups were the ''parents'' from which a new generation of groups were formed. In a second treatment, the least productive groups were the ''parents.'' In a third treatment, groups contributed to the next generation in proportion to their productivity. Finally, in a fourth treatment each group contributed an equal number of progeny to the next generation regardless of its productivity. Within-group selection operated in all treatments and was the only evolutionary force in the fourth treatment because the differential fitness of groups was suppressed. Within-group selection favored cannibalism, decreasing group size and demonstrating once again that evolution within groups does not automatically increase the fitness of the group. Group selection operated in the other three treatments because gene frequency change was influenced by the differential fitness *of* groups in addition to differential fitness *within* groups. Wade's experiments showed that group selection could have a strong effect despite the fact that the group members were not closely related to each other genetically. In a series of follow-up experiments, Wade and his colleagues showed that variation in the phenotypic character ''group size after 37 days'' was not caused directly by variation in the fecundity of individuals. Rather, it was caused by a complex interaction of traits involving cannibalism, synchrony of development, and response to crowding (Wade 1979, McCauley and Wade 1980). Just as a phenotypic response to selection at the individual level can have a complex genetic and physiological basis, so also can phenotypic response to selection at the group level have a complex genetic, physiological and *social* basis.

Goodnight's experiments were similar to Wade's except that his groups were composed of two species of flour beetles (*T. castaneum* and *T. confusum*) and therefore were miniature communities. Goodnight treated the density of *one* of the species as a community-level phenotypic character in an artificial selection experiment. In other words, whether a community was used as a ''parent'' to found the next generation of communities depended upon the number of *T. confusum,* regardless of the number of *T. castaneum.* In other treatments, the density of *T. castaneum* and emigration rates rather than density were used as community-level phenotypic characters. Goodnight's communities responded to higher level selection, but when he investigated the mechanistic basis of the response, he discovered that it had an interspecific ecological basis in addition to an intraspecific social basis. Because selection operated on the entire community as a unit, genes in *either* of the two species that caused an increase in the phenotypic character (density of one of the species) were selected. In fact, the experiment had selected a particular *interaction* between the genes in the two species because when the selected populations of each species were raised in isolation or with members of the other species from the original laboratory stock, the response to selection disappeared. In short, the community responded to selection as a single interactive system because the entire community was selected as a unit. The fact that the genes existed in separate gene pools from the standpoint of reproduction was unimportant.

These laboratory experiments illustrate a concept of *shared fate* that is central to multilevel selection theory (Wilson and Sober 1989, 1994). The activities of an organism can affect its abundance relative to other conspecifics and species in the local community, but they can also affect the abundance of *all* organisms in the local community as a unit. By definition, the shared effect has no impact on the local species composition or genetic composition within species. However, when many local communities exist that vary in their species and genetic composition, those that function well as a unit contribute differentially to the next generation of local communities. Traits can therefore spread, not by virtue of their advantage within local communities, but by virtue of the advantage that they bestow on their local community, relative to other local communities. If the process of between-community selection is sufficiently strong, then local communities become functionally organized to maximize their contribution to future local communities. Of course, all of this requires an appropriate population structure. If there is only one local community, then the shared effect becomes irrelevant. If many groups are present but community-level selection is weak, then the activities that would turn the community into a functional unit will largely succumb to activities that succeed within the local community.

Natural communities frequently consist of a mosaic of semi-isolated patches, similar to the local communities of Goodnight's (1990*a*, *b*) laboratory experiments. In addition, many activities of organisms have a shared component, resulting in a process of natural selection at the community level that closely parallels the process of artificial selection described above. The following examples will make the process of community-level selection intuitive.

Single organisms as multispecies communities.—It is becoming increasingly certain that single organisms are themselves highly integrated multispecies communities whose members previously led a more independent existence. The history of life on earth has been marked by a number of these coalescing events; molecular reactions into ''hypercycles,'' genes into chromosomes, prokaryotic cells into eukaryotic cells, and so on (Michod 1983, May 1991, Maynard Smith and Szathmary 1995). The fact that organisms are communities shows that the concept of communities as organisms is no mere metaphor. The same evolutionary forces that produced the extreme functional integration that we call organisms may have produced more moderate functional integration in other multispecies assemblages that currently is not recognized at all. Thinking of organisms as communities leads to two insights that are relevant to the more general subject of community ecology. First, population structure is not just a feature of the external environment, but can itself evolve. In modern-day organisms, the differential fitness of elements *within* the organism is highly suppressed by genetic mechanisms, such as the rules of meiosis, and developmental mechanisms, such as the division of cells into a germ line and a somatic line (Buss 1987). These mechanisms cause the individual to be the unit of shared fate with respect to most traits, concentrating natural selection, and therefore functional integration, at the level of the individual. In the terminology of Dawkins (1982*a*, *b*), the individual is the vehicle of selection. These mechanisms are not just a happy coincidence, however, but are themselves the product of evolution. We might, therefore, expect other multispecies assemblages not only to be functionally organized, but also to include features similar to the genetic rules of meiosis that regulate within-community processes, concentrating natural selection at the between-community level.

Second, the mechanisms that regulate evolution within organisms are largely, but not completely successful. As a result, some genetic and cellular elements *do* spread at the expense of other elements within the same organism. As expected from the rule ''adaptation at level x does not automatically lead to adaptation at level $x + 1$,'' these ''selfish'' elements tend to subvert individual-level functional organization and are often classified as diseases, even though they are as much a part of the organism as genetic elements that contribute to functional design. It is more appropriate to think of these elements as asexual species that are increasing at the expense of other species within their local community. In other words, the conventional image of biological communities needs to be applied to organisms, just as the conventional image of organisms needs to be applied to biological communities.

Discrete symbiotic associations.—Virtually every metazoan organism serves as a host to a local multispecies community of bacteria, viruses, protozoa, nematodes, and other small species. The population structure of symbiotic associations closely resembles the artificial selection experiments described above. For example, insects that reproduce on patchy ephemeral resources such as carrion, dung, and wood often carry a diverse community of wingless species who disembark and pursue a free-living existence along with their host (the use of one species for transport by another is termed phoresy). Phoretic communities can potentially have a positive or negative effect on the carrier species. Because the phoretic community requires the insect carrier for dispersal, those with a positive effect on their carrier will differentially contribute to future resource patches, as surely as the flour beetle communities artificially selected by Goodnight. However, phoretic associates that benefit the carrier species do not necessarily increase their relative abundance within the local community. Between-community selection has caused some phoretic associations to evolve into functionally organized ''teams'' of species that both feed and protect their insect carrier (e.g., Batra 1979). Other phoretic associations appear to have a more neutral effect on their host, but when removed they are soon replaced by species from the surrounding environment that have a negative effect (Wilson and Knollenberg 1987). In other words, commensalism is not an absence of interactions but an evolved set of interactions that eliminates negative effects on the host that might otherwise easily occur. The same phoretic associates that do not harm their own hosts act as competitors and predators to other insect species that they do not depend upon for transport (reviewed by Wilson 1980:119–126). Some phoretic associations are commensalistic rather than mutualistic, in part because their hosts live in a benign environment that is not easily improved by the activities of the phoretic associates (Wilson and Knollenberg 1987). Removing their own negative effect is the best that they can do.

Even if a symbiotic community can potentially benefit its host, it may not evolve to do so if the population structure favors within-community processes over between-community processes. Some host species have evolved to manipulate the population structure of their symbionts, playing the role of the experimenter in an artificial selection experiment. For example, horizontal modes of symbiont transmission can be suppressed and the number of symbionts colonizing offspring can be reduced to a low number, increasing variation among local communities. Frank (1996*b*) has suggested that some hosts even divide their symbionts into a germ line that is transmitted to their offspring and a somatic line that benefits the host, so that the products of within-community selection during the lifetime of the host are not passed to the next generation. Frank's research (1994*a*, *b*, 1995, 1996*a*, 1996*b*, *c*) provides an excellent example of how multilevel selection theory can explain both intragenomic and interspecific processes within a single conceptual framework.

Nutrient cycling in open water.—At first glance, the open-water ecosystems of lakes and oceans might seem like the last place to find a population of isolated local communities. However, it appears that much of the photosynthesis and nutrient cycling that takes place in the open water is on the surface of tiny aggregates of organic matter that serve as a substrate for phytoplankton, bacteria, flagellates, and ciliates (Goldman 1984; discussed by Stone and Weisburd 1992). These may act as micro-ecosystems in the capture, retention, and flow of nutrients that keep algae growing at near-maximal growth rates even in highly nutrient-poor environments. The open water consists of billions of these micro-ecosystems, some of which must surely function better than others, based on their species and genetic composition. If the most productive micro-ecosystems contribute differentially to the colonization of new micro-ecosystems, then it is possible to envision the selection of micro-ecosystems in which nutrient cycles and energy flows among species become functionally organized, much as Odum (1969) and others have speculated for ecosystems in general. Thus, adaptive ecosystem processes are a genuine possibility, but they require a mechanism. The problem with earlier theories of ecosystem function is not that they are necessarily wrong, but that they were proposed as if they applied to all ecosystems without any attention to mechanism.

Localized interactions in spatially continuous communities.—So far, all of my provisional examples of community-level selection have involved local communities with discrete boundaries. However, discrete boundaries are not required for community-level selection. Localized interactions are required, such that shared effects remain in the vicinity of the assemblage that causes them. Localized interactions can occur in spatially continuous communities as easily as communities that are broken into discrete patches. For example, the soil community under each plant is likely to have a large effect on the plant, which will in turn have a shared effect on the soil community under the plant but not 1 or 2 m away. The fact that the plant is adjacent to other plants and the soil community under one melds with the soil community under another does not prevent spatial variation in the composition of local communities and the localization of shared effects.

Leigh (1991, 1994) has recently interpreted the structure of tropical forest communities in terms of multilevel selection theory. He suggests that certain plant dispersal regimes favor within-community processes, resulting in ‘‘spiteful’’ species that degrade their environment in the process of capturing a large slice of the pie. Other dispersal regimes favor between-community processes, resulting in species that are ‘‘good neighbors,’’ improving their local environment even when it does not increase their relative abundance within the local environment. As one example from Leigh (1994:679), ‘‘Some trees form root grafts with neighbours of the same, or different species. . . . On the wet, windward slopes of Puerto Rico, the dominant canopy tree, *Dacryodes excelsa* (Burseraceae) forms root grafts with conspecific neighbors. During the destructive hurricane Hugo, root grafts saved their possessors from being uprooted (Basnet et al. 1993).’’ Leigh's speculations do not constitute a rigorous test of multilevel selection, but they do illustrate how novel and interesting hypotheses can be generated by the theory.

Distinguishing multilevel selection theory from related subjects in community ecology

Community-level functional organization often involves mutualisms, strong ecological interactions, and complex systems dynamics. However, these subjects by themselves do not provide the vital ingredient for community-level functional organization, which is a process of natural selection at the community level. When these subjects are studied apart from multilevel selection theory, they often contribute little or nothing to our understanding of community-level functional organization. It is, therefore, important to show why they are insufficient by themselves and how they can be studied more profitably.

Mutualism.—It has become a truism to say that mutualism is a neglected subject in community ecology. Recent models and empirical studies have shown that mutualisms are common, in part because they arise inevitably from indirect species interactions. For example, even if all species in a community compete directly with each other, a large fraction of the relationships are indirectly mutualistic because the species suppress other competitors more than they suppress each other (e.g., Stone and Roberts 1992). Similarly, almost any modification of the habitat or alteration of nutrient cycles and energy flows will benefit some species, even as they harm others (e.g., Jones et al. 1994).

These studies are interesting and important in their own right, but their very success makes them nearly irrelevant to the subject of community-level functional organization. Since mutualisms are an inevitable by-product of indirect effects, they will exist even in highly dysfunctional communities. Mutualisms must certainly play a role in community-level functional organization, and may be more common in functional than dysfunctional communities, but knowing the proportion of interactions in a community that are mutualistic says very little about its functional organization. Furthermore, community-level functional organization can involve antagonistic processes, such as competition and predation, in addition to mutualism. Even the process of individual development involves interactions that would look like competition and predation if the cells were regarded as a multispecies ecological community. Community-level functional organization must be studied in the same way as individual-level functional organization, by investigating the properties that contribute to functional design. The question of whether these properties are created by mutualistic or antagonistic interactions among members of the community is a secondary issue.

Strong ecological interactions.—The Gaia hypothesis (Lovelock 1979), which portrays the earth's entire biota as one big organism, is one of the most recent expressions of grandiose functionalism. The fact that it could be proposed and taken seriously at all reveals a discouraging lack of communication among evolutionary biology and some subdisciplines of ecology. Discussions of the Gaia hypothesis often confuse higher level functional organization with strong ecological effects and dynamic equilibria. For example, it is entirely possible that biotic processes could have a strong influence on the earth's atmosphere. It is also plausible that biotic processes could be included in dynamic equilibria, returning the concentrations of gases to a set point when they are perturbed. However, strong effects and dynamic equilibria are properties of many chemical, physical, and biological systems and do not imply functional organization. A consumer population can have a carrying capacity, regardless of whether it manages or overexploits its resources. Even the most dysfunctional communities can be stable, responding in ways that resist perturbation. Indeed, the best example of life's influence on the earth's atmosphere involves the slow accumulation of a toxin (oxygen) that only later became a resource. By analogy, we might imagine humans generating vast landfills of waste products and later utilizing them as a resource after they have degraded the rest of their environment. This is interesting and important, but it is a far cry from imagining the human population as one big organism that regulates its environment for its own benefit. In general, the fact that organisms have strong effects on each other and their environment, often resulting in dynamic equilibria, should not be confused with higher level functional organization.

Complex systems dynamics.—The ''emerging sciences of complexity'' (Kauffman 1993) have many important implications for ecology and evolution. Sometimes it is claimed that complex system dynamics can produce higher level functional organization in the absence of natural selection. For example, consider the following passage from Depew and Weber (1995:474):

> *Ecosystems favor species that, in funneling energy to their own production and reproduction, also increase the total energy flow through the system. The effect is to increase the dissipation of energy as entropy production to the surroundings. This greater entropy production produces autocatalytic energy and matter flow cycles that not only become sinks in themselves but also facilitate greater flow of energy through the system as a whole. This process results in a decrease in the intensity of energy flow as the biomass increases, after an initial ''charging'' period when the intensity of energy flow is increased. Individual nodes become more efficient.*

Embedded in the thermodynamics talk is the naive assumption that adaptation at level x (''in funneling energy to their own production and reproduction . . . '') automatically leads to adaptation at level $x + 1$ ('' . . . also increase the total energy flow through the system''). Williams (1966) examined and rejected this assumption 30 yr ago, and many examples of adaptations at level x that *disrupt* functional organization at level $x + 1$ have accumulated since then. Williams' analysis had such an impact on evolutionary biologists that it is now a struggle to convince them that higher level functional organization exists at all. It is, therefore, discouraging that ''the emerging sciences of complexity'' are so isolated from evolutionary biology that the mistakes of the 1940s and 1950s are being repeated.

It is certainly true that complex systems dynamics can produce striking *patterns* in the absence of natural selection, similar to the colorful computer art that can be generated by complex systems of equations. However, *pattern* is not the same as *functional organization.* An object that is designed to do something well, be it a machine, an organism, or an ecosystem, must be structured in a highly specified way. Complex systems dynamics are no more likely than simple systems dynamics to produce just the right combination of properties in the absence of natural selection.

It is also true that complex systems dynamics can be highly relevant to community-level functional organization when studied in *conjunction* with multilevel selection theory. As an example, Wilson (1992) built a simulation model in which local communities are colonized from a global pool of species. The species in each local community interact for a period of time and then disperse back into the global pool. Sampling error during the colonization process causes local communities to vary in their initial composition. When species interactions are simple, the initial variation is of little consequence because each local community converges on one or a few stable equilibria. However, when species interactions are complex, sensitive dependence on initial conditions magnifies the initially random variation among local communities rather than shrinking it. Natural selection at any level requires variation among units, and complex interactions provide an important source of variation at the level of local communities. In the simulations, communities governed by complex interactions responded to community-level selection, whereas communities governed by simple interactions did not. In general, complex interactions may play a critical role in the evolution of community-level functional organization, but we will never know until we study complex systems dynamics in conjunction with multilevel selection theory.

Despite its long history, the concept of biological communities as functionally organized units has never become a productive research program. Multilevel selection theory provides a theoretical framework that will allow the concept to be rigorously studied for the first time. The first insights to emerge from this framework are encouraging. Anyone who studies communities knows that they tend to vary at a local scale. Anyone who has tried to perform a replicated experiment in community ecology knows that the replicates within a treatment have a perverse way of becoming different from each other, even when every effort is made to keep them identical. Phenotypic variation at the community level has been shown to be heritable in the only experiment that addresses this issue (Goodnight 1990*a*, *b*). It is often plausible from the natural history standpoint to expect multispecies communities to be units of shared fate. Mutualistic symbiotic associations have been known for decades, but in retrospect it is likely that they provide evidence for community-level selection in nature.

Some implications of multilevel selection theory are so new that they are almost disorienting. Biological communities are conventionally viewed as collections of species that evolve as separate entities. The evolution of a species can be influenced by other species in the community, but it remains a separate entity with its own strategy of survival and reproduction. When natural selection operates at the community level, all of the species in a local community become part of a single interacting system that produces a common phenotype, more like genes than species as we usually think of them, and the local community acquires the properties of adaptation that we usually associate with individuals. The novelty of this perspective is perhaps best illustrated by the fact that Goodnight (1990*a*, *b*) is evidently the first person in the history of biology to treat multispecies communities as evolvable units whose properties can be shaped by standard artificial selection procedures. We do not know how often natural selection operates at the community level, but there is every reason to find out.

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LITERATURE CITED

Basnet, K., F. N. Scatena, G. E. Likens, and A. E. Lugo. 1993. Ecological consequences of root grafting in Tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. Biotropica **25**:28–35.

Batra, L. R. 1979. Insect–fungus symbiosis: nutrition, mutualism, and commensalism. John Wiley, New York, New York, USA.

Buss, L. 1987. The evolution of individuality. Princeton University Press, Princeton, New Jersey, USA.

Dawkins, R. 1982*a*. The extended phenotype. Oxford University Press, Oxford, England

———. 1982*b*. Replicators and vehicles. Pages 45–64 *in* K. C. S. Group, editor. Current problems in sociobiology. Cambridge University Press, Cambridge, England.

Depew, D. J., and B. H. Weber. 1995. Darwinism evolving. MIT Press, Cambridge, Massachusetts, USA.

Frank, S. A. 1994*a*. Genetics of mutualism: the evolution of altruism between species. Journal of Theoretical Biology **170**:393–400.

———. 1994*b*. Kin selection and virulence in the evolution of protocells and parasites. Proceedings of the Royal Society of London B, **258**:153–161.

———. 1995. The origin of synergistic symbiosis. Journal of Theoretical Biology **176**:403–410.

———. 1996*a*. Models of parasite virulence. Quarterly Review of Biology **71**:37–78.

———. 1996*b*. Host control of symbiont transmission: the separation of symbionts into germ and soma. American Naturalist **148**:1113–1124.

———. 1996*c*. Host-symbiont conflict over the mixing of symbiotic lineages. Proceedings of the Royal Society of London B, **263**:339–344.

Goldman, J. C. 1984. Conceptual role for microaggregates in pelagic waters. Bulletin of Marine Science **35**:462–476.

Goodnight, C. J. 1990*a*. Experimental studies of community evolution. I. The response to selection at the community level. Evolution **44**:1614–1624.

———. 1990*b*. Experimental studies of community evolution. II. The ecological basis of the response to community selection. Evolution **44**:1625–1636.

Jones, C. G., J. H. Lawton, and M. Shachak, 1994. Organisms as ecosystem engineers. Oikos **69**:373–386.

Kauffman, S. A. 1993. The origins of order. Oxford University Press, Oxford, England.

Leigh, E. G. J. 1991. Genes, bees and ecosystems: the evolution of common interest among individuals. Trends in Ecology and Evolution **6**:257–262.

———. 1994. Do insect pests promote mutualism among tropical trees? Journal of Ecology **82**:677–680.

Lovelock, J. E. 1979. Gaia: a new look at life on earth. Oxford University Press, Oxford, England.

May, R. M. 1991. Hypercycles spring to life. Nature **353**: 607–608.

Maynard Smith, J., and E. Szathmary. 1995. The major transitions of life. W. H. Freeman, New York, New York, USA.

McCauley, D. E., and M. J. Wade. 1980. Group selection: the genotypic and demographic basis for the phenotypic differentiation of small populations of *Tribolium castaneum.* Evolution **34**:813–821.

Michod, R. E. 1983. Population biology of the first replicators: on the origin of the genotype, phenotype and organism. American Zoologist **23**:5–14.

Odum, E. P. 1969. The strategy of ecosystem development. Science **164**:262–270.

Stone, L., and A. Roberts. 1992. Can there be a war of all against all? Journal of Social and Evolutionary Systems **15**:315–318.

Stone, L., and R. S. J. Weisburd. 1992. Positive feedback in aquatic ecosystems. Trends in Ecology and Evolution **7**: 263–267.

Wade, M. J. 1976. Group selection among laboratory populations of Tribolium. Proceedings of the National Academy of Sciences (USA) **73**:4604–4607.

———. 1977. An experimental study of group selection. Evolution **31**:134–153.

———. 1979. The primary characteristics of *Tribolium* populations group selected for increased and decreased population size. Evolution **33**:749–764.

Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton New Jersey, USA.

Williams, G. C., and R. M. Nesse. 1991. The dawn of Darwinian medicine. Quarterly Review of Biology **66**:1–22.

Wilson, D. S. 1980. The natural selection of populations and communities. Benjamin Cummings, Menlo Park, California, USA.

———. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology **73**:1984–2000.

Wilson, D. S., and W. G. Knollenberg. 1987. Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites. Evolutionary Ecology **1**:139–159.

Wilson, D. S., and E. Sober. 1989. Reviving the superorganism. Journal of Theoretical Biology **136**:337–356.

Wilson, D. S., and E. Sober. 1994. Re-introducing group selection to the human behavioral sciences. Behavioral and Brain Sciences **17**:585–654.