

Biotal evolution: a manifesto¹

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ABSTRACT: Evolution occurs in more than lineages, in more than the component traits of an organism. Biotas also evolve, and this has diverse ramifications. There are many kinds of biotas. Biotas have structure and dynamics, and they are evolutionarily natural units if looked at appropriately. Different evolutionary processes have different foci, and our studies should reflect this. Energy flow is central to biotal evolution. Integration of systems ecology with evolution would benefit both. Biotas, like organisms, evolve at many spatiotemporal scales and with equilibrial and nonequilibrial processes. Some biotal evolution is adaptive for biotas, from direct and indirect causes. Taking biotal evolution seriously requires us to broaden our concept of natural selection.

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Kinds of evolution

We have been conditioned to think of evolution as something which happens within lineages, or at most within clades. And of course it does occur there. However, we thereby ignore another sort of evolution, or at most relegate it to a peripheral background to serve variously as a context or a vague summary. Even the community ecologist Hutchinson (1965) did so in his famous metaphor of the evolutionary play *in* an ecological theater.

We commonly divide evolution into phyletic evolution and lineage branching, and think that this exhausts the subject. It does nearly exhaust the domain of population genetics, although other subjects also live here in part. Merger of lineages should be added too, as hybridogenic plant species, integrated endosymbionts, lichens, and other examples testify, and we now also need the partial reticulation provided by horizontal transfer. All these can be called **lineage evolution**, where the focus is on what happens to lineages. A somewhat broader view leads to **clade evolution** or **taxon evolution**, where the focus is on what happens to clades or taxa at any level. Lineage, clade, and taxon evolution overlap broadly but are each partly disjoint from the others: e.g., we may want to focus on a natural paraphyletic taxon like the Charophyta, or on the history of the human lineage back to protists. We can group lineage, clade, and taxon evolution together as **organismal evolution**.

Orthogonal to organismal evolution is what can be called **trait evolution**. Here the focus is on particular traits or components or functions of organisms, wherever they occur. Molecular evolution is a major aspect of trait evolution, and evolutionarily comparative studies of any aspect of organisms are studies of trait evolution. Trait evolution and organismal evolution partition nearly the same set of phenomena in

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different ways, and one can of course study both together, as with the evolution of flowers or of frog calls. Population genetics has, more or less, its counterpart in trait evolution as quantitative genetics. Some understanding of trait evolution is necessary for estimating phylogenies, the foundation of much of organismal evolution, and the converse relationship also holds. The study of organismal and trait evolution are mutually reinforcing, a helix of knowledge rather than a circle.

What we are missing in all this is the evolution of biotas themselves. Such **biotal evolution** contrasts with organismal and trait evolution in that its units are ecological groups of one sort or another. It isn't something really separate from organismal-trait evolution; evolution is a single overall phenomenon and ecology, via natural selection, drives all adaptive evolution (including internal coadaptation) directly or indirectly. (I use "biotal" rather than "biotic" to avoid confusion with the biotic adaptation which Williams discussed in 1966; biotal adaptation, discussed below, is not the same.)

Communities are biotas, and they occupy probably the most familiar scale. I don't want to define a community, or specify what its scale is; obviously, if one thinks about it, the scale of communities differs for bacteria and trees. (OK, a community represents the scale at which populations interact. But what's a population, Mommy?) Much community evolution of bacteria can take place on one tree during the lifetime of the tree. On the other hand, a tree community has bacteria too. The scale of biotas extends below as well as above that of communities. A patch, where individuals interact ecologically, is probably the lowest level causally distinguishable. A guild represents a different focus. Above communities there are at least two quasi-hierarchies which have partly separate causal processes. One is ecological, with levels such as biome or all caves, while the other is geographic, with levels such as water mass or island. Of course the quasi-hierarchies interact and the levels of each intergrade, but the use of distinguishing them is that different processes, and different scales of the same processes, predominate at different points. Thus dispersal is a geographic process, although it is affected by ecological processes, and climatic adaptation is an ecological process, although it is affected geographically. The two quasi-hierarchies converge with each other and with the taxonomic hierarchy at the level of the whole Earth's biota.

Evolution occurs throughout these scales, and it is worthwhile to have each part of each scale, and of their interactions, as a potential conceptual focus. What we see then is not at all what we see when we look at organismal evolution. I don't want to belabor the point, so I merely list some diverse aspects of biotal evolution: extinction patterns, rates of speciation and patterns of morphological and adaptive innovations, succession, overall evolution of complexity, patterns of historical vicariance and dispersal, ecological vicariance, arms races, the mid-Mesozoic reorganization of the marine benthos, physiognomy of vegetation, niche diversification, diversity and its changes at all scales, distributions (spatiotemporal, intensity, and other) of competition and other factors, patch selection, food webs, distribution of body sizes, influence of body size on diverse aspects of biotal evolution (and vice versa), maintenance and evolution of energy and nutrient flows, diffuse coevolution, relative importance within and among biotas of different processes regulating density and energy flow of populations and metapopulations, transition from water to land, flight, the sulfide biota, reef evolution, guilds, adaptations to deserts or the spaces among sand grains on the shore, sharpness or fuzziness of biotal transitions in space or time.

These aren't peripheral aspects of organismal-trait evolution; they represent a different and equally important focus. There is perhaps an echo of the man in Molière's *Bourgeois Gentilhomme* who suddenly realized he had been speaking prose for more

than forty years without knowing it. Studies like the ones listed aren't new, but we have been relegating biotal evolution to ecology and thereby thinking it dismissed from evolution, or studying it as merely an adjunct to organismal-trait evolution. It isn't.

The usual view, as expressed by May (1978), is that, "strictly speaking, ecological systems as such do not evolve." This view is based on a prior assumption, that evolution centers around genetics. And, yes, ecological systems as such don't have much genetics. If evolutionary biologists take real ecology seriously, this assumption of a genetical center for evolution begins to unravel and may quite evaporate. Strictly speaking, ecological systems as such do evolve. That they don't evolve in the same way as organisms is important and has relevance to organismal evolution itself. May's paper is still perhaps the best introduction to biotal evolution, despite its need for supplementation.

It is common for botanists to distinguish the flora of a region from the vegetation of the region. The flora is the set of species present, while the vegetation is the total plant cover, how individual plants are arrayed together. Both of these are subjects of biotal evolution, but a vegetation is richer in structure than is a flora. There are no existing terms for the distinction at the level of the whole biota; "biota" may be used for both aspects, with adjectives like "organismal" or "taxonomic" or "systemic" or "holistic" making the distinction when necessary.

Biotal evolution is not an epiphenomenon of organismal-trait evolution: the causal processes of each sort of evolution affect the other sort of evolution mostly indirectly, via their evolutionary results. Thus biotal evolution causes organismal-trait evolution too, as the list of examples should make obvious. The bibliography contains a somewhat nonrandom sampling of papers and books on biotal evolution.

Note that very different time scales are involved in different aspects of biotal evolution. Succession normally occurs on a time scale which we don't even think of as evolutionary except when there happens to be organismal evolution involved in a prominent way, as with industrial melanism or adaptation to mine spoils or pesticides. Succession *is* low-level biotal evolution, though, however often it cycles, and it is only our conditioning which makes us think that this perspective is odd. Evolution doesn't require irreversibility. Think of Dobzhansky's restrictive maxim that evolution is change in gene frequencies: the increase in one environment of the allele for sickle-cell anemia (for hemoglobin S, if you prefer), and its later decline in another environment over a few generations, are conventionally regarded as evolutionary. The maxim doesn't specify time scales.

Foci and focal lengths in evolutionary biology

I have been making distinctions based on our "focus." That is because we can't study or understand everything together in one swell foop. Our focus has no necessary counterpart in real processes, although of course we try to make them correspond. Any particular focus has the risk of ignoring what is thereby out of focus, whence the desirability of looking both as widely as possible and at different focal lengths. There may well be other conceptual frameworks as different from those I have mentioned as they are from each other. (Can truly comparative physiology provide one?) In the study of human history the identification of such new approaches, at various levels, has a distinguished record and has contributed much to the subject's vigor. (Examples are social class, culturally basic presuppositions, religion, family, disease, housing, energy, musical style, rise and decline of civilizations.) It would be to our advantage to obtain and retain a similar diversity of foci and focal lengths.

Natural processes also have different foci and focal lengths. Obviously desiccation by wind isn't one of the problems faced by the biota of submarine vents, and species (or their avatars: Damuth, 1985) can interact directly only where they overlap spatiotemporally. It is less obvious to many of us that a single process can operate on quite different scales. Dispersal may be within a patch or to another continent, with different frequencies and perhaps different time scales but often by the same mechanism. What is nonequilibrium at one spatiotemporal scale may be equilibrium at a larger scale, and vice versa. And natural selection itself ramifies in several dimensions, as I discuss later.

The structure and reality of biotas

Communities and other biotas are now usually regarded as artificial constructs which we impose on the world in order to comprehend it. This view is a generalization of Gleason's denunciation of the superorganism approach to communities, Gleason's approach having later been consolidated by Whittaker and others. And I suppose it's true, in a myopic sort of way. The distribution and abundance of species depend on what affects each particular species, not on properties of the community as a whole. Species go their own way, and their presence and abundance reflect mostly pre-existing properties rather than locally adaptive evolution. (No, I'm not denying local adaptation or even its near ubiquity; I'm rather conceding that its importance at the community level usually seems to be minor. But this is subjective; there is no comparative survey.)

Communities and other biotas usually lack even approximately sharp boundaries in both space and time. An island is distinct from the sea, the vertical zonation of the littoral may be obvious to a child, treeline is a small proportion of either the taiga or the tundra even if not a line, a lava flow destroys one community and the ensuing succession starts with another, and so on. Such quasisharp boundaries do seem a bit unusual, though. (Again, there is no objective survey.) So what? Most things and classes in the world, especially the natural world, have fuzzy boundaries or even no natural boundaries at all. This doesn't prevent them from being and acting different from their neighbors. My wife and I differ on where to separate green from blue. Maybe some seagoing cultures have bluegreen as a primary color. A genetical example of such arbitrarily bounded or overlapping classes is Wright's isolation by distance, and biotas often do the same if more complexly.

The usual conclusion is that communities are epiphenomena of our own making because they aren't superorganisms. So skeletonized, the fallacy is obvious: maybe they are something else. And they are. Systems ecology has been isolated from the rest of biology, perhaps mostly because its concepts seem to have no obvious interfingerings with other areas. (Again, the reasons for this isolation, and its extent, deserve empirical study.) Perhaps the field was founded mostly by Elton and Hutchinson, both very broadminded people, but even to them it was apparently a world of its own. This need not have been the case. For instance, the famous paper by Hairston, Smith, and Slobodkin (1960), which purported to be about the regulation of populations, is actually not about that at all: its argument is valid (given its premises) only for the regulation of trophic levels *per se* by energy and therefore falls into systems ecology. Even people like Hutchinson or Lamotte, most of whose work has been outside systems ecology and has had a strong evolutionary focus, have simply accepted its isolation. (Whittaker and Woodwell, 1972, is an interesting exception.) Community ecology has dealt with topics like the structure of food webs or abundance of species without incorporating the quantitative energetic relations

involved. Some of this is changing a little, and systems ecology is therefore less completely isolated than it has been. It should not be isolated at all.

An organizing principle

Communities, patches, biomes, guilds, and whatever are real parts of the world, if fuzzily bounded or even broadly overlapping, because they have causal processes of their own which structure them and make the dynamics of any one partly distinct from that of an adjacent biota. (A symptom of the nonevolutionary thinking of most systems ecologists is the common use of the word "function" to refer to ecosystem dynamics. Implicit and sometimes even explicit in this usage is the view that the dynamics is adaptive at the ecosystem level. Maybe some of it is -- I discuss this heretical view later -- but it is as naive to assume so without evidence as it would be to assume that, say, the dynamics of the atmosphere or of plate tectonics is adaptive for itself. Even homeostasis doesn't imply adaptation, as the dynamics of a valley's geomorphological evolution or of the Sun testifies.)

The processes which integrate a biota are those studied by systems ecology and community ecology and, to some extent, by ecological biogeography. Although the latter emphasizes species-level phenomena, these are ordinarily correlated among species because of environmental structure. And dispersal is a prerequisite for integration at more than a very local level. Predation, parasitism, and herbivory (which I have lumped together under the term "phagy": Van Valen, 1989b) are integrative, as are specific and diffuse symbiosis and competition and coevolution. What systems ecology brings to this is a different focus, sacrificing taxonomic precision for knowledge of what and how much is being transferred along different paths.

The center of systems ecology is energy flow. Free energy is what powers life, and most of the content of physiology and biochemistry consists of the manifold effects and control of the flow of this energy through single individuals. Similarly in ecology. We all realize, I hope, that a biota or a population or a species or whatever exists only to the extent that it can obtain and process free energy. It may be less obvious that this energy has a primary role in the integration of biotas, but it does. The amount available is determined by the amount of photosynthesis (or rarely chemosynthesis) and import, and the amount used is this amount minus what is lost by fire, irrevocable burial, and export. It is this amount used, the free energy actually available, which determines the scope of the biota. (I simplify a bit; e.g., "use" is the total oxidation of the carbon reduced in photosynthesis, and the amount of photosynthesis itself has internal and external controls.)

How this available energy is partitioned then determines the nature of the biota, in any perspective from which one wishes to view the biota. Thus one can partition the biota by trophic level (more or less), by guild, by body size, by taxon, by clade, by longevity, by successional stage, by seasonal phenology, by metabolic rate, by microhabitat, or whatever focus one has. I don't mean that the total causation is energetic, but energy is causal rather than a bookkeeping convention. Any organism uses as much energy productively as it can in the circumstances where it finds itself. (Try to think of any which doesn't. A desert shrub, e.g., uses as much solar energy as it can with the water it can get; that's why it gets the water.) This quite universal imperative for evolutionary survival and expansion creates mutually conflicting pressures in every direction because of the largely unresponsive constraint given by the amount of available energy. I have elsewhere (Van Valen, 1976, 1989a) argued that energy provides a secure foundation for

fitness in all respects and removes all the peripheral anomalies which come out of the purely genetical approach.

Some partitions and foci correspond more closely to causal processes than do others. One goal in the study of biotal evolution should be clarification of these still mostly vague processes of partition and regulation of energy flow. What is causally relevant from the viewpoint of the organisms themselves and their interactions? It is important not to abstract away central causes, or impose our preconceived order (which we fallaciously accept if it is not statistically rejected), and it is easy to do so. We think it an accomplishment to demonstrate a case of competition, or discover what regulates a population or a metapopulation. And commonly it is, so much so that a strictly bottom-up approach to biotal-level questions seems unpromising. Broader questions aren't necessarily harder to answer, but they may require a different perspective.

Extension in time

All biotas change over time, and they change at many time scales. It is artificial to separate changes which are short-term to us from those which are longer. It is probably not artificial to distinguish, at first order, repeatable from nonrepeatable changes. Gross aspects of seasonal plankton cycles are often repeated yearly. Different species of tree may each preferentially replace another to give a larger-scale stability. A landslide or a treefall or a fire or a plague commonly give predictable results which may, indeed, be scattered in space as well as in time. Such repeatability requires regulation, that there be a stable attractor or potential well in the appropriate phase space. (We now know that the converse is false, and even that there can be different attractors depending on where the process starts or is perturbed to. The attractor's cause can be internal to the biota or external, forcing the cycle.) For stability, though, as distinct from a random walk with quasiregular perturbations, there must of course be regulation of the biology itself.

Such equilibrical cycles, however, grade into directional changes. At least part of the Kenya plateau seems to have a major dry-wet cycle with a wavelength of a century or so (S. Altmann, personal communication). Other climatic changes are longer, and some of them, such as glaciations, are also cyclic. The longest probable cycle relevant to biotal evolution is that of plate tectonics, with pangaeas forming and breaking up every few hundred million years. At such a wavelength it doesn't seem useful to speak of equilibria at all. At shorter wavelengths, and with noncyclic perturbations, some processes may be equilibrical while others are directional. An obvious example is the chestnut blight, where a formerly dominant tree is effectively extinct in its region of dominance (even the resprouting is getting sparse) but the overall vegetation has no evident change. A less obvious class of examples involves those introduced species which have no apparent effect on the pre-existing biota. That this apparent free lunch is usually an illusion is shown by considering energy flow: there is commonly no overall change here, as inferred from causes rather than from direct measurement. Thus the invader is detrimental to some set of species, even if none of this set is at all similar to the invader itself and even if none can be directly identified.

Evolution without adaptation -- or is it?

If biotal evolution occurs entirely as a result of changes at the species level and below, then any adaptation at the level of a biota is an accidental byproduct. At least, accidental in part. It is not automatically excluded that lower-level processes tend to

produce equilibria or repeatable structure at levels where biotas exist, in a way analogous to the invisible hand of Adam Smith's economics. And we know that such equilibria and structure occur -- they constitute much of the subject matter of community and systems ecology, and even aspects of paleobiology. That they occur doesn't mean, though, that they are adaptive for the biota. For Adam Smith, adaptation did reappear at the level of the ensemble, and this is what makes his result astonishing: in his system adaptation appears at one level wholly by selection at another. (The criteria for adaptation, the properties maximized, weren't quite the same for the two levels, though.)

In ecology the term "balance of nature" refers vaguely to a similar hypothesis, that biotas are structured in a manner which is both adaptive for the biota and equilibrational, i.e. resistant to small enough perturbations. It's a slippery hypothesis in that if one aspect doesn't conform it retreats to another. Use of the term by Panglossian followers of Rousseau or Paley doesn't help. Nevertheless, it is an interesting and important question whether there are any aspects of biotas which satisfy the hypothesis as just stated.

I think there are, and that they fall into three partly separable and mutually compatible classes: aspects where biotal adaptations correspond to lower-level adaptations, aspects where biotal adaptations result from indirect effects analogous to the invisible hand, and aspects which are selected directly at the level of the biota. (I reject the occasional restriction of the term "adaptation" to adaptations which originated for the same function(s) which they now have. Change in function is a common aspect of the process of adaptation.)

An example of the first class, of adaptations which span levels, is extinction resistance. This is a somewhat complex subject, one which I plan to pursue elsewhere, but I hope it is obvious that extinction resistance can be selected for at the species level or below and that it helps to maintain the integrity of biotas. An example of the second class of biotal adaptations, indirect byproducts of lower-level adaptations, is Elton's pyramids of body sizes and trophic levels, a phenomenon which had been noted by Wallace as an aside in his 1858 publication with Darwin. There are progressively fewer individuals and species toward larger body size and higher trophic level. Again there are ramifications, but again I hope the nature of the biotal adaptation and stabilization tendency are clear.

The third class, of adaptations directly selected at the level of biotas, is more heretical. I don't want to advocate selection among communities (Dunbar, 1960, 1972), although there may just possibly be scope for it in situations of repeated local extinctions in metapopulations of largely co-occurring species, as in early succession (including the soil biota), or in repeated bloom-crash cycles, as in the plankton. There may also be a process of selection among sets of isolated biotas with some similar properties, like island biotas, which are conventionally regarded (on inadequate evidence: Van Valen, 1988c) as usually inferior. A more generally applicable mechanism and one at a lower scale, but unfortunately also hard to study, is David Wilson's trait-group selection, which I have called patch selection because the unit of selection is the set of inhabitants of a spatial patch. As Wilson (1980) has shown, this mechanism is fully adequate to bring even phenomena such as aspects of biogeochemical cycling under the scope of adaptation. The importance of this mechanism needs further study, perhaps best by investigation of the degree of generality of its assumptions, but clearly any result of patch selection is an adaptation at the level of the patch on the time scale of the selection. Beyond this scale there is correlation, not causation.

(Unless there is a malignant pattern of environmental autocorrelation, easy to model but almost never realized, natural selection always, and necessarily, produces adaptation at the level and time scale at which it occurs. We usually try to infer the

production of adaptation beyond this, but more exceptions occur the farther away we go, and these exceptions are then used to deny the adaptiveness of the selection itself. Meiotic drive need not produce adaptation for individuals, although it is adaptive for the favored allele. [Exercise for the reader: just how is this adaptive?] Reproductive selection, including sexual selection, may interfere with adaptation for viability, and vice versa. Short-term adaptation may set the stage for later extinction, and selective extinction may truncate short-term adaptation. And so on.)

Imperfect correlation with an adaptive process gives less adaptation than at the level or spatiotemporal scale of the process itself. For instance, environmental autocorrelation in both space and time is usually a decreasing function of distance from the spatiotemporal place of selection. Selection then gives progressively less expected adaptation at greater spatiotemporal distances. And there can be negative correlation: what is adaptive on one level or scale may actually be inadapative on another. Such conflicts are too well known to need further discussion. Their existence means, though, that one can't assume that biotal evolution of any kind is adaptive on the whole despite the existence of mechanisms promoting such adaptation. So is it? We don't know. Even just what adaptation means for a very fuzzily bounded unit like a biota hasn't been studied seriously.

Natural selection

In biotal evolution we can't avoid broadening the usual view of natural selection. Consider a biota which greatly expands its distribution as a result of climatic change or of removal of a barrier to a region inhabited mostly by competitively inferior organisms. (An apparent example of the latter is the nearly complete replacement of the indigenous Cretaceous mammalian fauna of South America in the early Paleocene by a broad invasion from the north: Bonaparte and Kielan-Jaworowska, 1987; Van Valen, 1988b. The better-known Pliocene exchange was much evenner until the megafaunal extinction a few thousand years ago.) In each case the biota has expanded as a result of its properties, and another biota has diminished or even become extinct. We want to say that the first biota was, at that time, fitter than the second, but this raises several difficulties.

If the biota's expansion was entirely the result of adaptations of its constituent species, as was probably true to a first approximation, is it still useful, as an aspect of the historical-narrative explanation, to say that the biota itself was more fit? It is, partly because the association of invading and declining species is nonrandom: the organization is lost by focusing only on species. Another reason is that the greater fitness of the species and individuals evolved as part of the biota, not randomly over the total area later occupied. It is directly relevant which biota a species and its included individuals evolved in, what their physical and biotic environment was. When causes overlap different levels of evolution, as these do, it distorts reality to try to restrict them to a single level.

Secondly, not all species of the expanding biota are likely to move, and not all of the contracting one are likely to make way for them. We see a problem here only because we try to make mutually exclusive categories for our own convenience. By shifting one's perspective, one can compare the histories of the biotas which inhabit two regions at time t , those which inhabit these regions at time $t + \Delta t$, those which inhabit a different partition of the area involved, and so on. Most possible sequences like this will not correspond to actual processes, but the format includes those which do. In our case most of the energy flow in the invaded region now passes through invaders, while the indigenes are as a group less successful. This is an evolutionarily significant fact.

Furthermore, there is no increase in the number of biotas, although one of them may have effectively vanished. How then can we say that the expanding biota has increased its fitness? Well, maybe it is now less subject to future disruptions, maybe it can send off propagules more often, and so on. These are pretty tenuous hooks to hang a theoretical hat on. The obvious change is the expansion itself, but this isn't a category conventionally recognized as a component of fitness. It isn't important in individual selection, where our concepts are still centered. For biotal evolution we need to consider the possibility of such nonstandard extensions of received theory. Our concepts should reflect the causal processes involved, not tradition. I have argued elsewhere (Van Valen, 1976, 1989a) that expansion is causally central in much group selection. This is equally the case for biotas.

If energy flow is causally central in the dynamics of biotas, it is natural to give our concepts and notation for biotal dynamics a foundation in energy flow. The fitness of a biota over some time interval is then its expected (in the statistical sense) energy flow at the end of that interval. Because biotas themselves change, this change must be allowed for also, and of course any useful notion of fitness makes fitness vary with environment, broadly conceived.

In addition to following the course of the descendants of an existing biota, it is causally and conceptually relevant to consider the change in the biota inhabiting a particular region. Here the region, not the biota itself, is our focus. Similarly, we can consider the ecologically based hierarchy. For instance, does the epigeal biota replenish the cave, and similar subterranean, biota more than the reverse? If so, as conventional wisdom holds (I suppose correctly), there is long-term selection against the cavernicolous biota and a selective equilibrium between invasion and extinction like that I once found for body size in the two groups I looked at (Van Valen, 1975).

It may seem that some aspects of biotal evolution are random. I think that this will usually prove to be a matter of mistaken focus, of not looking at where the real causes are, although sampling error at one extreme and quasirandom perturbations at the other do provide entries. Unpredictability itself commonly (not always) occurs within a statistical distribution which can itself be adapted to, as with plasticity in trait evolution. Thus organisms which can resist a stress are selected for in stressed habitats, thereby making the biota as a whole more resistant, although this biotal adaptation decays until the next stress if the stress is discontinuous. Even deterministic chaos is attenuated by complex interactions of semi-independent units as in a biota. To think of an aspect of biotal evolution which is not in some way selectively caused requires a bit of imagination. This is one of a number of general patterns (to be discussed elsewhere) which argue for an overwhelmingly predominant role of adaptation in all varieties of supramolecular evolution.

It is commonly believed that many communities and other biotas lack organization, and Rosenzweig (1987) has borrowed the term "anomic" for them from sociology. Whether there are any such biotas at all is doubtful. Some aspects of some biotas, like species composition of flies on carrion, are more variable than others and subject to sampling error. The energy flow from a corpse is less sensitive to what flies are present (although the absence of any insects lets mummies form), and even the species composition is presumably regulated at the level of the regional (meta)population of corpses, as shown by its persistence. Causes of organization can be sporadic and yet effective. Giller and Gee (1987) and Van Valen (1988a) discuss the general problem, with similar conclusions.

Prospect

The ecological interactions among organisms evolve even though not entirely in the same manner as the organisms themselves. Which of these sorts of evolution is primary is a matter of our perspective, not of the biological processes. Some properties of biotas are just the conjunction of properties of their constituents, while others are emergent. (The same is true for properties of species, and of higher taxa.) Whether emergent or not they are valid properties at the biotal level because they are parts of the structure of the biota.

The biotic world is, among other things (but basically), a system of energy flow. Biotas have diverse manifestations; a natural group from one causal perspective may be unnatural from another. For any biota, though, we can consider the energy flow itself. We can ask such questions as how the flow is partitioned, what causes and regulates the flow and its partitions, how these change over time at various scales, and what processes cause these changes. One doesn't need to be a systems ecologist in order to appreciate and study such questions. However, in this way the focus of systems ecology can be incorporated into the study of evolution in a central position and in a causally natural way.

Biotas aren't superorganisms, but they are organized and have diverse sorts of processes and regularities. The phenomena are real, and they deserve real attention from evolutionary biologists.

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