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The ecological concept of disturbance and its expression at various hierarchical levels

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Current definitions of disturbance are intuitive, narrow, and only implicitly based on system structure. This is because the concepts are based on experience at particular levels of organization or on systems whose structure is well known. The definitions are thus inadequate for the development of a general theory of ecological disturbance. A universally applicable definition would 1) identify the object disturbed; 2) distinguish between change in the object that is disturbance versus change that is not; and 3) distinguish between direct and indirect consequences of disturbance. To meet these requirements, we formally link the hierarchical organization of ecological objects and the concept of disturbance. Any persistent ecological object will have a minimal structure, or system of lower level entities that permit its persistence. Disturbance is a change in the minimal structure of an object caused by a factor external to the level of interest. Using these definitions, disturbance can be unequivocally identified and associated with various specific ecological levels of organization. Because of the dependence of the concept of disturbance on recognizing the minimal structure of ecological systems, application of the concept will advance as refined models of the hierarchical structure of ecological systems are elaborated.

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Introduction

Disturbance has long been recognized as an important factor affecting community structure and dynamics (Cooper 1926, Watt 1947). More recently, emphasis has shifted from a viewpoint that disturbance is a rare and unpredictable event to treating it as a natural process that occurs at different spatial and temporal scales (e.g., White 1979, Allen and Starr 1982, Rykiel 1985, Pickett and White 1985).

The burgeoning theoretical and empirical work on disturbance focuses almost entirely on community structure as opposed to community processes or ecosystem functions (e.g., Sousa 1985, White and Pickett 1985). However, disturbance may affect each level of organization addressed by ecologists, from individual to ecosystem and landscape, and the consequences and mechanisms of disturbance are different at each hierarchical level (Rykiel 1985). Analyses of disturbance at each level and interactions among the levels are vital to understand the importance of disturbance as a natural phenomenon.

Meeting this goal will require a system of concepts for dealing with hierarchies and disturbance. Although such a system is currently unavailable, some specific elements needed for its creation have been indicated by Rykiel (1985). He argues that an ecologically meaningful characterization of disturbance requires specification of the reference conditions of the system under study. This specification depends on unambiguous and non-

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Tab. 1. Summary of the major concepts used in the conceptual system allowing discrimination of the effects of disturbance at different hierarchical levels.

Term	Definition
Entity	Any object of ecological interest. May be concrete or abstract. Synonyms include unit, and when restricted to a single hierarchical level, system.
Interaction	Any transfer of materials or information, or a connection of process between entities.
Structure	The system of lower level entities and the interactions among them. Structure exists on a particular hierarchical level.
Organization	The interaction among entities that permit them to form a persistent structure.
Minimal structure	The system of entities interacting in such a way that they persist. An organized structure.
Function	The contribution of interactions occurring on level n to the minimal structure and consequently the interactions occurring on level n + 1.

arbitrary determination of the system structure and function. Reference conditions such as averages, regimes, minimum and maximum values depend on the boundaries that are used to delimit the system. If such boundaries are arbitrary or chosen for convenience, rather than to represent actual system structure, definitions of disturbance will likewise be arbitrary. Such criteria are thus inadequate as general or widely applicable descriptors, and can lead to confusion on the nature of the system and properties under study (e.g., Ulanowicz 1978, Kolasa 1984, O'Neill et al. 1986). For example, according to one current definition (Grime 1979), the removal of biomass from a system constitutes disturbance. If some modest percentage of leaf biomass were removed from an ecosystem, the compartments and flows defining the ecosystem would still persist, although the sizes of various compartments and flows might be altered. Hierarchy theory, with its emphasis on scale of resolution and recognition of the role of observer perception (Allen and Starr 1982, O'Neill et al. 1986) might permit an equally arbitrary conversion of disturbance to non-disturbance purely by shifting the scale of observation.

In this paper we provide a framework to achieve greater generality, precision and objectivity in applying the concept of disturbance to ecological systems. We first present a concept of structure that allows unambiguous definitions of disturbance and of the object being disturbed. The core of this conceptual system is "minimal structure". Secondly, we show how this refined specification of structure also permits the effects of disturbance to be identified at particular levels or traced among hierarchical levels. Finally, we apply the concept of disturbance to ecological systems, and exemplify the different agents and effects specific to different traditionally recognized ecological levels.

The concepts of structure and organization

In order to recognize disturbance, one needs to identify an object or entity with which some action will interfere. Since all natural systems contain components that are affected by environmental agents, one cannot sensibly propose change of *any* part of an entity produced by an external agent is a disturbance. In other words, the conceptual framework should recognize a broad spectrum of effects, ranging from complete destruction of an entity at one extreme to subtle but significant changes at the other. To distinguish between non-disturbed and disturbed states, a model of the structure and function of a natural system is needed. Such a model may not always correspond to the intuitive one. Likewise, a model based on structures and

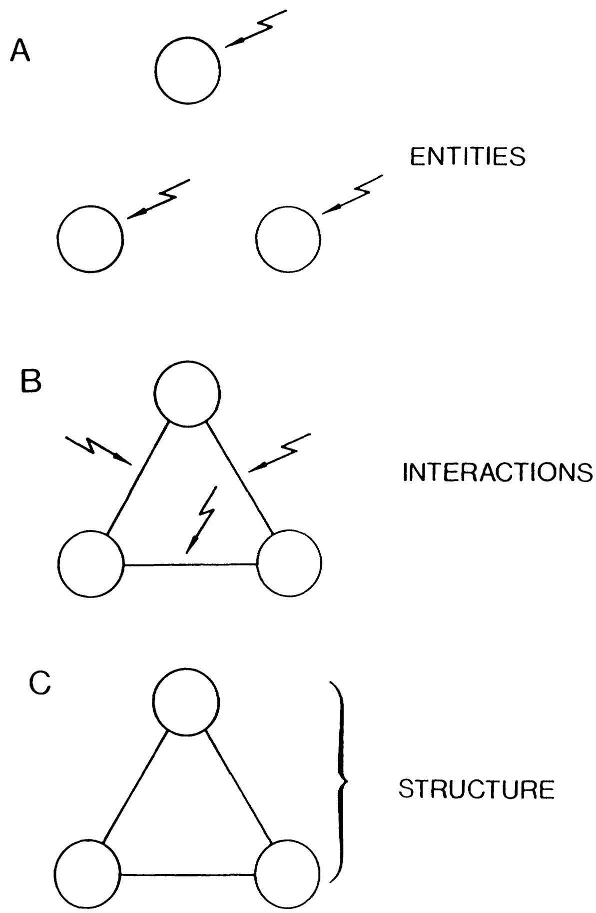

Fig. 1. Illustration of some concepts used in this paper. In each case, the arrows indicate the relevant portion of the figure. A) Physical entities. B) Interactions between physical entities. C) Structure, consisting of the physical entities and the interactions between them.

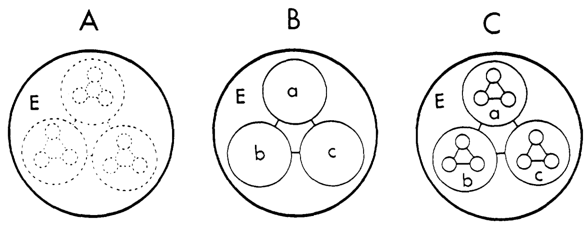

Fig. 2. Hierarchical structure of an idealized ecological system. A) Unit of interest (E); B) first-order structure of E; C) second-order structure of E, which is the first-order structure of subunits a, b and c.

functions obvious at the human size and temporal scales may differ from that determined by the scales appropriate to the ecological processes of interest (O'Neill et al. 1986), and may not adequately discriminate disturbance.

To define disturbance we must first discern an ecological entity which a certain event might disturb, and second we must determine under what conditions a disturbance affects a part of an entity without destroying that entity. A hierarchical model of the structure of an entity satisfies both criteria. The model is based on the recognition of structure as a part of a specific system of concepts aimed at advancing our understanding of disturbance (Tab. 1). Structure emerges as fundamental entities combined into more complex entities (Pattee 1973, Simon 1973). The concept of structure, however, requires an understanding of how such entities assemble. The interactions that cause the entities to combine, and which result in the persistence of the complex, constitute the *organization* of a higher level entity (Tab. 1). Organization is thus a set and configuration of interactions, and the physical complex composed of interacting fundamental entities is a structure (Fig. 1). For example, for atoms to combine into molecules, there must be a set of interactions between atoms that permit the formation and maintenance of a higher level unit, and which determine the nature of a molecule. These interactions are made possible by the characteristics of the atoms themselves and define the organization of a molecule.

Organization has several important attributes. These cannot be discussed in detail here, but we list them to indicate that organization is susceptible to operational evaluation. The characteristics of organization are 1) complementarity of the units comprising the higher order entity, 2) coordination of the interacting units, 3) regulatory functions relating the units (Pattee 1973), and 4) information flow between the units, ultimately resulting in their integration. In our conceptual framework, *structure is a system of lower level entities and the interactions that result in their organized persistence as an entity of the higher level* (Fig. 2).

Here we introduce the concept of "minimal structure", which is needed to clarify the concept of disturbance, using a hierarchical analysis. Minimal structure of an entity at a particular level is the system of interacting subunits allowing the focal entity to persist (cf. Allen et

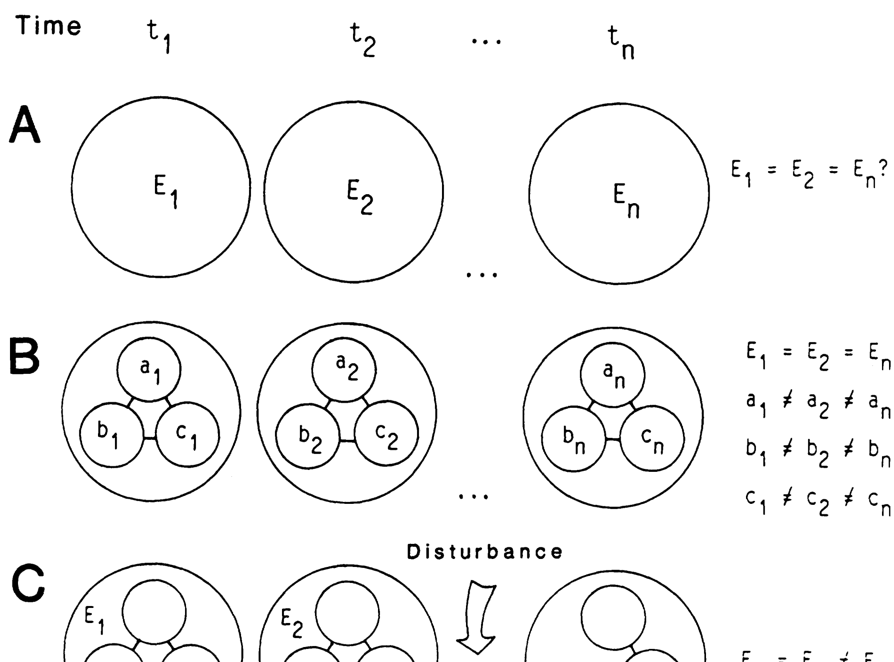

Fig. 3. Minimal and configurational structure. A) Changes in the biological entity E cannot be determined without analyzing its minimal structure. B) Configurational changes of the lower subunits a, b and c, shown by the different subscripts, do not change the minimal structure of the higher level entity over the time interval t_1–t_n. C) Disturbance that eliminates a component of the minimal structure (subunit b) changes the minimal structure of E.

al. 1984). At an even lower level, the structure of subunits appears (second order structure, and so on). *Minimal structure is defined as the structure revealed at the first lower-level when analyzing an organized entity.* The adjective "minimal" is used to emphasize that although a system may have many attributes, interactions and component entities, only some are necessary for its persistence and recognition.

The structure of any autonomous ecological (or for that matter, any physical) entity can be viewed as having a minimal structure at a particular scale of observation. For example, an individual will always have a set of systems or organs associated with living function. Likewise, to use a simple ecological system, the heterotrophic community of streams in temperate forested watersheds will have functional groups such as shredders, decomposers, predators, and filter-feeders. The lower level structure of the stream ecosystem consists of the actual species of shredders, decomposers, etc. Many configurations of the second order structure allow the persistence of the first order minimal structure. Hence, such lower level structure is called *configurational* (Tab. 1). Thus, the deeper structure (component species) of the higher level unit (functional group) can change while the structure of the higher level itself persists. The deeper (second-order) structure of subunits may be ignored in the study of properties of the highest level (first order) unit (Fig. 2).

Changes can affect either minimal structure itself, or only configurational structure. In order to discriminate between them, a hierarchical model of the multilevel system is needed. The distinction between the minimal and configurational structures helps to identify the lower level at which structural change is meaningful for the higher level (Fig. 3).

The concept of disturbance revisited

The common ecological notion that agency of disturbance is external to a system of interest can be combined with the concept of minimal structure. As minimal structure allows an unequivocal description of change in a system, disturbance can be defined in this framework without the ambiguities that result from applying the idea to arbitrarily defined systems. We can now state a precise definition of disturbance: *Disturbance is a change in the minimal structure caused by a factor external to the level of interest.* "External" refers to any action that originates outside the unit in question, including the action of the higher level unit.

The concepts of organization and minimal structure may help to reduce the degree of arbitrariness associated with the intuitive or simply convenient delimitation of boundaries. Organization and minimal structure can be operationalized and measured in ecological systems. To the extent that ecological systems in nature can be analyzed in terms of minimal structure, the unambiguous definition can be applied to real ecological systems. How this might be done is exemplified later in the paper.

Disturbance and hierarchies

The choice of the initial level of study is determined by the investigator and the scale of observation used, but the minimal structure of that level and the relationships of its structure to other levels are not arbitrary because they are determined by properties of the focal entity or process.

For example, two investigators might choose to work in a southern pine forest, but focus on different phenomena. One might choose to work on the productivity and energetics of the forest ecosystem over a certain time span. The model of minimal structure generated might include fluxes of energy as the interactions and "trophic levels" or other relatively familiar ecosystem components as entities. In contrast, a second ecologist might be struck by the phenomenon of a pine beetle outbreak. The relevant model of minimal structure of the forest might include, say, canopy characteristics and soil resources as the physical entities, and transport in the phloem as the interaction connecting the two into a persistent structure. A bark beetle population at outbreak levels would be *external* to this minimal structure, and thus disturb the system (the minimal structure). The existence of low, endemic densities of bark beetles in the forest is neither a part of the minimal structure, nor a disturbance to the minimal structure.

The example of the two ecologists studying the same forest points out three important ideas. First, the forest is, in a sense, the object of study for both ecologists. But their interests, or perhaps their funders or employers, lead them to focus on different aspects, processes or phenomena that occur in the forest ecosystem. Hence, on closer consideration, the two ecologists are studying different "things." These different things are represented by different hierarchical decompositions of the forest, and different models of minimal structure. Thus, the second point is that the various interests, each one with a clear focus, are likely to require very different hierarchical models. Third, as long as the focus remains set, there is only one model of minimal structure that will be correct and appropriate to the study. The other models of minimal structure that are implicit in the forest are appropriate for answering other questions or explaining other phenomena. Various models appear as a result of different scales of initial observation. Such models, while correct and interesting are irrelevant to the focus at hand. To summarize, the choice of an entity or process may be arbitrary, political or whatever, but once that choice is made, a single specific and objective model of minimal structure emerges as appropriate. It is not arbitrary, but is a property of the system of interest.

We must emphasize that our use of hierarchy differs somewhat from the concept advanced by O'Neill et al. (1986). In our conceptualization, systems and hierarchi-

Tab. 2. The expression of disturbance at various ecological levels of organization. No cross-level consequences are indicated although they may be possible. The concept of organization and minimal structure has not been applied to these traditionally identified levels and entities, so the terms "structure", "function", are used in their traditional senses in this table. The entries in the table are intended to convey the connotations of the disciplines represented.

Level	Components affected: Structural	Components affected: Functional	Attributes affected
Individual	Biomass	Physiology Behavior	Mortality Growth Reproduction
Population	Density Structure	Breeding biologies Social behavior	Age structure Genetic structure Evolution Extinction
Community	Vertical pattern Horizontal pattern Species composition	Resource levels Competition Mutualism	Coexistence Evenness Dominance
Ecosystem	Functional groups	Fluxes	Resistance Resilience
Landscape	Element types Configuration	Disturbance regime Fluxes of organisms	Mesh size Stability Connectedness

cal levels are not determined by scale of observation. Rather, only the first approach to the focal system is subjective and scale-dependent. Once the initial entity of interest is discerned, we propose that there is an organizational hierarchy defined by the characteristics of the entity. The organization is not arbitrary and scale-dependent, after the first entity is recognized.

The theoretical analysis of disturbance to minimal structure has a number of advantages. It alleviates level-dependence, scale-constraint, reliance on arbitrary system boundaries, and intuitive attachments to particular sites and ecosystems, which accrue to current definitions of disturbance (see Pickett and White 1985).

Disturbance and related concepts

The effects of disturbance at one level in an ecological hierarchy may propagate to higher or lower structural levels (Rykiel 1985). In other words, disturbance at a particular level may affect function at another level. We define a change in the *interaction* maintaining a minimal structure, caused directly or indirectly by an external factor, as *stress*. This contrasts with the concept of *disturbance,* which is a direct impact on physical *entities* within the minimal structure. An entity or subentity is physically destroyed by disturbance. Stress, in turn, denotes impaired interaction, without loss of minimal structure. For example, a stunted tree on a treeline maintains the minimal structure of a tree, but the rates or magnitudes of the interactions between the physical components of that tree are impaired in comparison to certain trees elsewhere. Any cause leading to this impaired state would be the agent of stress. Within a given biological entity, a disturbance at a deeper (second-order) level of structure may impair the interactions connecting the subunits and result in stress at the higher, first-order structural level. The stress induced at the first order level may be disturbance at the second order structural level. In practice, within any one system both stress and disturbance may act at the same time, at two or more levels, and be mutually interrelated (e.g., Menges and Waller 1983).

The two concepts, disturbance and stress, are also linked in the requirement that cause and effect be discriminated. The term "disturbance", is sometimes used to denote both the event and the altered structure of the system. This is well illustrated by the French term "chablis" used to refer to the creation of a treefall and the resultant complex gap in forests (Hallé et al. 1978). This combined use is not likely to cause problems in systems that ecologists are thoroughly familiar with or intuitively appreciate. However, for conducting studies in unfamiliar systems, the term disturbance must be confined to processes that disrupt minimal structure. The term *perturbation* can be used to refer to *the effects of disturbance,* and indeed of stress, on a system (Rykiel 1985). This preserves the common sense of perturbation as used in much of ecological modelling. Perturbation may be observed some time after the disturbance. There may be a time lag between the occurrence of the disturbance event and its effect on minimal structure. Thus, there is a dynamic aspect to the interpretation of disturbance.

Resilience, in our context, may be defined as the degree to which a unit or a function this unit performs can be changed without changing minimal structure. Resilience, therefore, refers to a change in configurational structure.

Application of the hierarchical concept of disturbance

The theoretical analysis must be linked to commonly recognized ecological levels of organization. This section will show how the concept of disturbance based on

Tab. 3. Three contrasting ecological hierarchies generated by consideration of different aspects of resource use and by attention to different focal levels. For each hierarchy, the levels are described, basic features of their minimal structure identified, and potential types of disturbance listed. A. Hierarchy of energy capture in plants. The focal level is the individual. B. Hierarchy of resource partitioning. The focal level is the guild. C. Hierarchy of nutrient flow. The focal level is the ecosystem. Note that different hierarchies might be generated starting with the same focal levels but considering different processes.

A. Hierarchy of energy capture in plants		
Level	Minimal structure	Example of disturbance
Stand	Interacting individuals	Fire Blowdown Dieback
Individual	Physiological integration of crowns, stems and roots	Tree fall Frost kill
Crown	Arrangement and integration of leaves and branches	Wind Ice storms
Leaf	Arrangement and integration of tissues	Herbivory
Tissues	Cellular integration	Pathogens
Cell	Metabolic integration	Membrane disruption

B. Hierarchy of resource partitioning or coexistence		
Level	Minimal structure	Example of disturbance
Community	Shared resources Coexistence of guilds	Altered resource spectrum
Guild	Use of common resources Coexistence of strategies	Loss of common resource
Individual	Resource allocation among modules/parts	Death Predation

C. Hierarchy of nutrient flow		
Level	Minimal structure	Example of disturbance
Ecosystem	Molecular exchange between compartments	Blocking of flows
Compartment	Similar modes of molecular processing	Destruction of carriers
Carriers	Metabolic or chemical processing	Altered metabolic or charge characteristics

minimal structure applies to commonly used ecological hierarchies (Tab. 2). or more specific, process-oriented hierarchies reflecting the concept of minimal structure (Tab. 3)

The consumption of plants by insects exemplifies how the fundamental definition of disturbance can be applied to any level in an ecological hierarchy. For instance, consumption of leaves by a herbivorous insect can be a disturbance to the leaves if it disrupts their physiological integrity (Tab. 3A). Herbivore damage to individual leaves may also have a significant impact on the ability of an individual plant to survive and reproduce, which can be described as stress to the plant. But such effects at the individual plant level may disappear (i.e., be "incorporated" sensu O'Neill et al. 1986) at the community level, although they may influence the population level through alteration of genetic or age structure. Whether the disturbance at the lower level disappears or not at the higher level, depends on the organization of the system, or more specifically, on the links between the levels. Once again, understanding of the interplay between the quantitative change of configurational structure and qualitative change of minimal structure appears to be crucial to consistent interpretation of disturbance and stress.

According to many authors, there is a need to employ different hierarchies in specific ecological inquiries (MacMahon et al. 1978, Allen and Starr 1982, Pickett et al. 1987). Some of the hierarchies specified in the literature may have only weak organization and poorly integrated minimal structures. The manifestations of disturbance will be distinct between and within the different hierarchies, and will have contrasting effects in those various situations. Even in cases where hierarchies are not completely decomposable (Simon 1973), or where minimal structure has not been described with certainty, clarity in the use of the concept of disturbance will result.

Scale and disturbance

An important refinement in translating the general concept of disturbance to a particular situation is to recognize the significance of scale. We assume that the minimal structure is known at least approximately in our examples. For example, we mentioned that disturbance by herbivory on an individual plant would likely have no effect on ecosystem level processes; it would be a change in the configurational structure of the ecosystem. However, *coarse-scale* defoliation by the same species of insect on many individuals of the same species of plant may have major effects on the ecosystem processes (Schowalter 1985) and would represent a disturbance of its minimal structure, where one of the component entities is a closed canopy.

Time scale will also affect how disturbance is expressed. A single fire in a community is a disturbance at the individual level, and perhaps at the population level. At the community or landscape levels of organization, individual fires no longer stand out as disturbance on the new scale of observation. Rather, to alter the structure of the higher level system (e.g., a prairie over some time), some change in the fire *regime* would be required. The parameters of interest have necessarily become the temporal and spatial distribution of various intensities of fire (Forman and Boerner 1981). Allen and Wileyto (1983) provide a clear example. Ordination of prairie vegetation based on species composition, versus ordination of cover, yield different views of the importance of fire. In essence, cover has a short time span of integration, while species composition integrates over a much longer time frame. Fires in a given year define the first principal component of the cover ordination, but the first principal component of the composition ordination is influenced by number of fires in the last five years. When focus is restricted to a single level of organization, the term *disturbance regime* is used to incorporate broader spatial and temporal scales then those appropriate to the study of single disturbance events at that level. In the context of our conceptual framework, disturbance regime affects the function of one of the complementary entities (a, b and c in Fig. 3) in the minimal structure of the higher level. Thus, as focus is shifted to higher levels of organization, disturbances may be subsumed in the normal dynamics of the higher level entity.

Conclusion

The concepts of disturbance and stress acquire clearer meaning when they are related to ecological hierarchies based on minimal structure. Furthermore, we propose that to study disturbance in a system where minimal structure is not known, an initial, or the best available approximation to minimal structure be used. The following operational program can be followed:

1) Construct a hierarchical model containing the focal system, level or phenomenon. The levels included are determined by the processes of interest at the focal level (e.g., Tab. 3).
2) Define the components and interactions within each level in the hierarchy. This will specify the boundaries of the levels. For first approximation, a hypothetical model can be constructed. Application of the model will suggest replacement or refinement.
3) Eliminate "levels" that are spurious, because they reflect our personal observational bias or simply the informal hierarchy traditionally used by ecologists (Tab. 2), rather than organized system structure. Spurious levels are those that do not link minimal structure of adjacent higher and lower levels.
4) Add the time or spatial dimension within the hierarchy to avoid confusing individual disturbances and disturbance regimes. Scale in this context applies within levels defined by minimal structure, rather than a tool for recognizing levels defined by perception (e.g., O'Neill et al. 1986).
5) Examine the ways that the proposed minimal structure of the focal level can be disrupted. This step will suggest predictions for simulation modelling or empirical test. Such evaluations may help refine the model of minimal structure as well as enhance the understanding of disturbance.
6) Examine the effect of disturbance at a particular level on adjacent levels.

The above program may have to be recycled as the subsequent hierarchical models of the system structure become more refined and in tune with the growing observational data set. This process is inevitable because first hypothetical models of the system based on minimal structure are likely to be quite crude. Without such a hierarchical model, however, statements about the nature of disturbance, its role and sources, and predictions about its consequences are not well founded. The application of the concept of disturbance that uses as a reference the hierarchical structure of ecological systems is a first step toward greater generalization and more refined predictions in the study of disturbance.

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