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Towards a definition of ecological disturbance

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Abstract

The terms disturbance, perturbation, and stress have been used in various ecological contexts, often synonymously, inconsistently and ambiguously. Consequently, the meaning of these terms lack any ecological rigor upon which to construct a coherent theory of ecosystem response to disturbance. Herein are some of the semantic and conceptual problems involved in defining disturbance, perturbation and stress, and proposals of working definitions as a basis for further discussion.

Introduction

The terms disturbance, perturbation, and stress have been applied in various ecological contexts, often synonymously, inconsistently, and ambiguously. The term disturbance has been used for many years in ecology and, consequently, has an historical context that perturbation and stress lack. However, few attempts have been made to define the ecological meaning of disturbance (Spurr & Barnes 1980; Bormann & Likens 1979; Grime 1979; Weaver & Clements 1938). Ecologists generally recognize the traditional meaning of disturbance as an event that is massively destructive and rare. This view of disturbance is now being revised (e.g. White 1979). Although many ecologists consider disturbances to be normal events in the course of ecosystem dynamics, a definition incorporating this viewpoint has not been developed. The difficulty of constructing a satisfactory definition of disturbance is related both to the generality and ambiguity of the term; generality because 'disturbance' is applied to a wide range of phenomena and ambiguity because the specific circumstances surrounding the occurrence of a disturbance are often implicit, and, therefore, dependent on the subjective context in which the term is used. Some of the semantic and conceptual problems involved are outlined here and working definitions are proposed as a basis for further discussion.

Semantic and conceptual problems

Inadequacy of ordinary language

The meanings of disturbance, perturbation, and stress are readily interpreted both from their dictionary definitions and the context in which they are used. Disturbance and perturbation are, in fact, synonyms. Rendered freely from their root languages, disturbance suggests disorderly 'stirring' or disruption as in stirring up trouble; perturbation implies excessive stirring or turning, which is to say, stirring beyond a normal level. Stress indicates tension or emphasis, as in placing weight upon something. The ordinary meanings of these terms are not adequate to convey ecological concepts. Efforts to avoid development of an ecological language (jargon) by reliance on vernacular meanings are often self-defeating and indicative of a body of knowledge relatively poor in concepts. In astronomy, mathematics, and engineering, for example, perturbation has specific meanings (which have essentially no ecological content) as required by conceptual development of those disciplines.

Cause and effect

Another problem arises because all three terms may refer to either a cause or an effect (e.g. Franz 1981). For example, disturbance may refer to a cause such as a hurricane, or to an effect such as the disruption caused by a hurricane. Ordinarily, the generality and ambiguity of these terms is ameliorated by reference to the context in which they are used. The semantic difficulty that may occur when cause and effect cannot be separated in these terms is illustrated by Odum *et al.* (1979). They defined perturbation as a deviation or displacement from the nominal state in structure or function at any level of organization. This definition describes an effect. They then describe perturbation as an ecosystem input, which is a cause, and refer to perturbations that cause deviations (i.e. perturbations cause perturbation). Ecological systems have sometimes been described as circular causal systems (e.g. Patten *et al.* 1976), suggesting the difficulty of assigning cause-effect relationships. Any system containing feedback loops could be characterized as circularly causal. The presence of feedback does not in principle prevent the tracing of cause-effect pathways (or it would be impossible to repair any complicated equipment). However, a semantic problem appears whenever an effect becomes the cause of another effect. The challenge is to define terms that distinguish between cause and effect in so far as possible.

Reference state or condition

All three terms (disturbance, perturbation and stress) require that a reference condition be defined. In ordinary circumstances, a reference point is usually implicit in the context of a given situation. In ecology, it seems necessary to state the reference condition explicitly. The significance of stress, perturbation, and disturbance is determined by comparison with a reference state which includes some measure of biological and ecological impact. Unless a reference state is defined, the occurrence of a stress, perturbation, or disturbance cannot even be detected let alone measured. Two possible ways of identifying the reference state are (1) to define a steady state expected to occur under optimal conditions (i.e. a potential state), or (2) simply to accept a pre-existing state (i.e. an actual state), regardless of its dynamic status, as a reference point. The steady state reference may be an idealization that does not exist in reality, while acceptance of a pre-existing state may fail to encompass the ecologically realistic range of possible behaviour. To interpret the meaning of disturbance, both a system and a reference state must be defined, although neither need be static.

Propagation of effects: Hierarchical organization and level of resolution

The nature and impact of disturbance are related to both the hierarchical organization of ecological systems ranging from individuals to ecosystems and the level of resolution (or scale) used to characterize these structures (Allen & Starr 1982). Bormann and Likens (1979), for example, define disturbance as disruption of the pattern of the ecosystem, principally by external physical forces. Aside from the problem of defining the meaning of pattern, this definition limits the concept of disturbance to one organizational level and a low level of resolution. At the ecosystem level of organization, disturbances which affect individuals (for example, treefall caused by wind) may appear to have no effect. That is, no perturbation is induced in ecosystem variables or properties. However, a disturbance to an individual has certainly occurred and caused a perturbation. The effect of a disturbance depends on the organizational level used as a frame of reference, the scale at which the system is observed, and the ecological processes which can propagate the disturbance across levels at the specified scale. A disturbance at one level does not necessarily induce perturbations in all levels.

In a hierarchically structured system, a disturbance at any level can be 'absorbed' by moving up the hierarchy, in effect, placing the disturbance within a new and larger system. The disturbance thereby appears to become endogenous. This larger system has properties that differ from the former system and the original disturbance now appears to be a part of the internal workings of the system rather than a disturbance to the system. For example, a forest fire is clearly a disturbance to the forest defined on one scale. But if the scale of observation is changed to much longer time spans that include the generation and destruction of many forests on a given site, then fire is absorbed into a new and larger system, and becomes an apparently internal component. Nevertheless, a forest fire is still a disturbance to a forest.

Gradients

Trophic structure, energy flow, and nutrient cycling indicate that ecological systems are open, dissipative systems. The requirement for continuous input to maintain system viability and organization means that living components and systems always exist in a non-equilibrium state responding continuously to environmental gradients (e.g. rainfall, temperature) and ecological interactions (e.g. competition, predation). Disturbances are abnormal only in the sense that they are not continuous inputs (although they may recur regularly on an appropriate time scale). A complication occurs, however, because otherwise normal ecological stimuli and processes, which constitute a continuum, become disturbances when nominal bounds are exceeded. Distinguishing the normal range of ecological stimuli from extremes involves establishing criteria to determine when a normal stimulus becomes a disturbance.

Resource availability

Ecological disturbances are generally perceived as negative events because an element of damage or destruction is often imputed. The ecosystem then 'recovers' from disturbance. However, disturbance may also free resources that have become unavailable in the existing system (Bazzaz 1983). The intermediate disturbance hypothesis (Connell 1978), for example, hinges on two factors: (1) disturbances of a certain frequency and intensity prevent monopolization of resources by one or a few species, and (2) disturbances are not so biologically destructive that only a few species can exploit the resources made available. In addition, disturbances with particular characteristics may stabilize ecosystem behaviour by determining the pattern of resource availability in space and time. In this sense, disturbance may be a necessary condition for maintenance of a stable community. Suppression of a disturbance to which the community is adapted results in change to a different stable community.

Generic disturbance

Ecologists and ecological modellers often treat disturbance as a generic event lacking specific ecological characteristics, while professing that system response depends on properties of both the system and the disturbance (e.g. Pimm 1984). Usually, model variables or structures are altered as if by disturbance. In essence, the hope is that a single disturbance characteristic, such as destruction of biomass or species removal, is of over-riding importance. It may be that relatively few disturbance characteristics are needed to evaluate the responses of a variety of ecological systems, but very little work has been devoted to this subject. The scale at which the system is defined and observed would appear to be a most important factor determining the level of detail required in characterizing disturbances.

Stability

The concept of ecological stability has provided the basis for much theoretical discussion of the impact of generic disturbance. Almost lost in these discussions, however, is the fact that stability has no intrinsic meaning without reference to a disturbance, even if the nature of the disturbance is only implicit (as in, a 'displacement' from steady state, or a stable point). The question of stability in real ecological systems arises precisely because they are subject to disturbances and can potentially be permanently altered or destroyed by a disturbance (or disturbance regime) with the appropriate characteristics. On the other hand, disturbance cannot be made into a non-disturbance simply because it is necessary to maintain a particular long-term ecological steady state. Conceptually, ecological stability is always associated with, and relative stability depends upon, the nature and characteristics of disturbance.

Working definitions

With these problems in mind, the following definitions for the terms perturbation, stress and disturbance are proposed (Table 1). In general, disturbance is defined as a cause (which may be a system input) that results in a perturbation, which is an effect (or, change in

TABLE 1. Summary of concepts and working definitions of perturbation, stress, and disturbance

A. Perturbation	An effect; the response of an ecological component or system to disturbance or other ecological process as indicated by deviations in the values describing the properties of the component or system; relative to a specified reference condition; characterized by direction, magnitude, and persistence. (See also, Lewontin 1969; Odum *et al.* 1979.)
1. Transient	Temporary deviation which becomes zero over time with return to approximate original steady state.
2. Permanent	Deviation which becomes fixed in magnitude over time leading to steady state different from the original.
B. Stress	An effect; a physiological or functional effect; the physiological response of an individual, or the functional response of a system caused by disturbance or other ecological process; relative to a specified reference condition; characterized by direction, magnitude, and persistence; a type of perturbation. (See also, Barrett & Rosenberg 1981; Grime 1979.)
1. Survival trauma	Stress-induced loss of biomass which results in preservation of perennating tissue; e.g. drought-deciduous shrubs.
2. Lethal trauma	Stress-induced individual death; e.g. over-grazing.
C. Disturbance	A cause; a physical force, agent, or process, either abiotic or biotic, causing a perturbation (which includes stress) in an ecological component or system; relative to a specified reference state and system; defined by specific characteristics. (See also, Vitousek & White 1981; Bazzaz 1983.)
(a) destruction	Existing biomass is reduced in quantity. (See also, Grime 1979.)
(b) discomposition	Particular populations are selectively eliminated, reduced, added, or expanded.
(c) interference	Matter/energy/information exchange processes are inhibited.
(d) suppression	Prevention of natural disturbance.

system state). Stress is also an effect (or state change) and is a specific type of perturbation which has particular biological meaning. Disturbance is categorized and quantified in terms of characteristics such as type, frequency, and intensity, whereas perturbation and stress are measured in terms of deviations in steady state variables. Occurrence of disturbance (cause) presupposes the existence of a detectable perturbation (effect). Disturbance is propagated within a system by ecological components and processes that are amplified by the perturbations induced. The perturbed component or process, not the perturbation, becomes the agent of propagation.

Four categories of disturbance are distinguished to include situations where destruction of existing biomass is the predominant effect, but also situations where biomass loss may be relatively small and other effects more important. The category of interference represents in part the situation of disturbance-induced stress.

The working definitions proposed address some, but not all, of the semantic and conceptual problems associated with the use of these terms. Particularly in the context of developing disturbance theory in ecology, these or similar definitions are needed to clarify concepts and guide future developments. The difficulty remains that we seek to define in static terms relativistic concepts that change with our frame of reference.

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