Disturbance, diversity and stability of ecological systems – the need for a uniform hypothesis

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One of the most consistent criticisms in ecological sciences is the continuing failure of ecologists to define concepts and to formulate general theories[1,2]. Here we compare the net effect of two fundamental hypotheses of diversity, stability and disturbance. According to the first hypothesis, i.e. the Diversity Insurance Hypothesis[3,4], which relates diversity with ecological stability, greater ecological diversity leads to greater ecosystem stability (Figure 1). According to the second hypothesis, i.e. the Intermediate Disturbance Hypothesis, intermediate disturbances enhance ecological diversity[5] (Figure 2). The lower limit of this hypothesis cautions that if disturbances are too rare, competitive dominants eliminate other species and reduce diversity as equilibrium conditions develop. The upper limit cautions that if disturbances are too frequent, most species will go locally extinct because they cannot tolerate repeated disturbances, resulting in lower diversity.

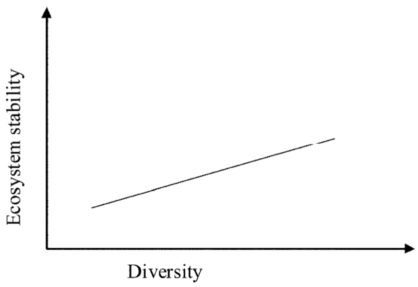

Figure 1. Diversity Insurance Hypothesis, according to which increase in diversity leads to increase in ecosystem stability.

When we derive relationships between diversity, disturbance and stability according to these hypotheses, we can see that intermediate disturbance enhances diversity and diversity enhances stability. In other words, the stability of the systems is higher at an intermediate disturbance level. But, stability is the capacity of the ecosystem to withstand a long time period, either by resisting or recovering from natural and human-induced disturbance (constancy, resilience, or persistence)[6,7]. Also, a range of experimental, theoretical and field-based studies suggest that ecosystem stability and disturbance are negatively correlated[7–10]. This relation could be linear or nonlinear and its strength depends upon the magnitude, frequency, spatial and temporal pattern, and several other aspects of the disturbance. It is also well known that the disturbance can reduce complexity, interspecific connectedness, and thereby simplify the system[11]. We believe that opposing conclusions of these two lines of thought can be largely resolved by adding a functional component to their respective hypotheses. We base our theory on the functional component or functional organization of species and its relative importance in maintaining diversity and function (e.g. production of utilizable form of energy) before and after disturbance in a hypothesized treefall gap (selective logging) in a tropical forest.

Tropical forests are one of the most structurally and functionally complex systems on earth. Utilization of sunlight to create usable forms of energy in this multilayered structure is at a maximum at all layers and, therefore, the amount of sunlight reaching the ground level is quite low. Once disturbance, for example, selective logging occurs, a gap is created and the amount of solar light reaching the ground increases, which in turn allows numerous seeds in the soil to germinate. Certainly, the number of species per unit area is higher in this disturbed habitat compared to the mature stand that previously occurred there. Though the number of species has increased, vertical stratification is absent and the species composition is a mixture of habitat specialists and generalists. Probably, the per capita energy consumption and assimilation will be lower in the generalist community than in the habitat specialist[12]. When the amount of energy that falls on a unit of space is constant irrespective of the disturbance level, the energy absorption, and thereby productivity of the system, must be lower at the disturbed level. Therefore, a restatement is required for the Intermediate Disturbance Hypothesis.

The Intermediate Disturbance Hypothesis may be rewritten as: the relationship between disturbance and mere species diversity is inverse parabolic as suggested by the original hypothesis, while the relationship between disturbance and diversity of functional guilds is negatively correlated (Figure 3). Similarly, the assumption of Diversity Insurance

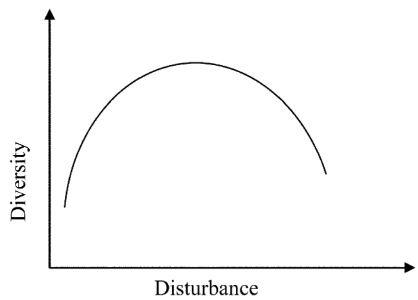

Figure 2. Intermediate Disturbance Hypothesis, according to which as the disturbance increases diversity increases up to a certain limit and then decreases.

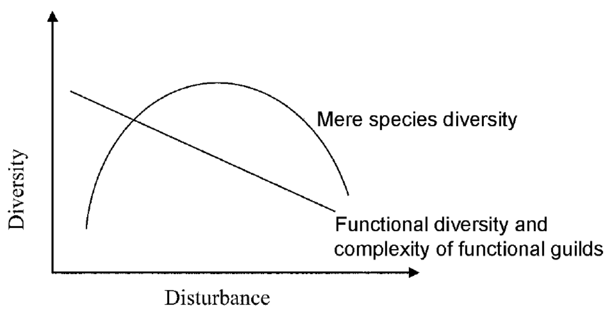

Figure 3. Modified Intermediate Disturbance Hypothesis: as the disturbance increases mere species diversity increases to a certain limit, while there is a decrease in the functional diversity and complexity of the system.

Hypothesis that species diversity and functional diversity are strongly related, may not be true under disturbance. Therefore, it could be concluded that ecological stability is a function of functional diversity and not essentially of species diversity. A well-defined, long-term experiment, both induced (theoretical) and observed (natural) at multiple scales, will also help elucidate solutions for the ambiguity of these hypotheses, maybe in the form of a uniform hypothesis.

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