
Species Redundancy and Ecosystem Reliability

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Abstract: *The concept of species redundancy in ecosystem processes is troublesome because it appears to contradict the traditional emphasis in ecology on species singularity. When species richness is high, however, ecosystem processes seem clearly insensitive to considerable variation in biodiversity. Some elementary principles from reliability engineering, where engineered redundancy is a valued part of systems design, suggest that we should rethink our stance on species redundancy. For example, a central tenet of reliability engineering is that reliability always increases as redundant components are added to a system, a principle that directly supports redundant species as guarantors of reliable ecosystem functioning. I argue that we should embrace species redundancy and perceive redundancy as a critical feature of ecosystems which must be preserved if ecosystems are to function reliably and provide us with goods and services. My argument is derived from basic principles of reliability engineering which demonstrate that the probability of reliable system performance is closely tied to the level of engineered redundancy in its design. Empirical demonstrations of the value of species redundancy in ecosystem reliability would provide new insights into the ecology of communities and the value of species conservation.*

Redundancia de Especies y Confiabilidad del Ecosistema

Resumen: *El concepto de redundancia de especies en procesos ecológicos es problemático puesto que aparentemente contradice el énfasis tradicional en ecología sobre la singularidad de las especies. Sin embargo, cuando la riqueza de especies es alta, los procesos del ecosistema parecen claramente insensibles a variaciones considerables de la biodiversidad. Principios elementales de confiabilidad en ingeniería, donde la redundancia es evaluada como parte del diseño de sistemas, sugiere que deberíamos repensar nuestra postura sobre la redundancia de especies. Por ejemplo, un principio central de confiabilidad ingenieril es que la confiabilidad siempre incrementa cuando componentes redundantes son agregados al sistema, un sistema que directamente soporta especies redundantes como garante del funcionamiento del ecosistema. Yo argumento que deberíamos abarcar la redundancia de especies y percibir redundancia como una característica crítica del ecosistema que debe ser conservada si los ecosistemas funcionarían confiablemente y nos provean de bienes y servicios. Demostraciones empíricas de el valor de la redundancia de especies en confiabilidad de ecosistemas provee nuevas intuiciones dentro de la ecología de comunidades y el valor de la conservación de las especies.*

Introduction

A variety of simple hypothetical relationships between variation in biotic diversity and variation in ecosystem functioning have been postulated (Vitousek & Hooper 1993; Mooney et al. 1996) (Fig. 1). Although these hy-

potheses are too simple to capture the true complexity of the relationships, they serve to facilitate discourse among ecologists (Schulze & Mooney 1993; United Nations Environment Programme [UNEP] 1996) and to motivate empirical evaluations of these relationships (Naeem et al. 1994; Tilman & Downing 1994; Tilman et al. 1996). Here, ecosystem functioning refers to the biogeochemical activities of an ecosystem or the flow of materials (nutrients, water, atmospheric gasses) and processing of energy. Because ecosystem functions include the regula-

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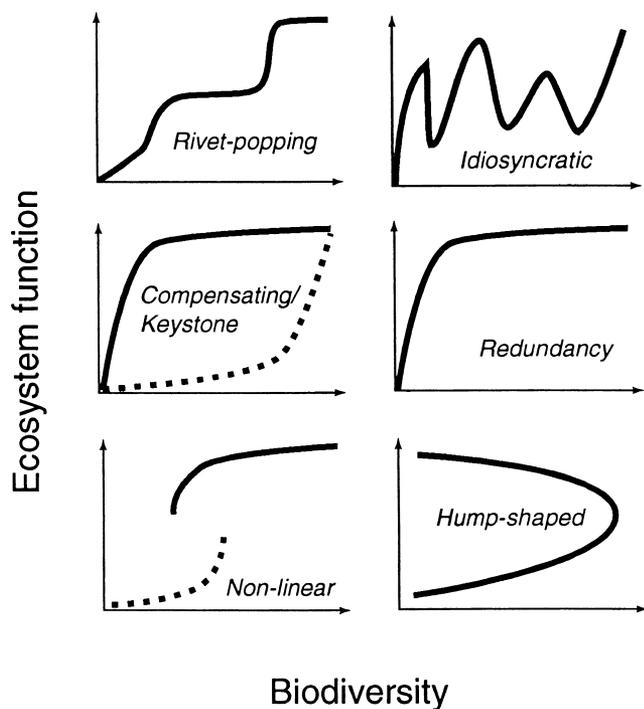


Figure 1. Examples of several proposed hypothetical associations between biotic diversity and ecosystem function. Function refers to biogeochemical processes of ecosystems. Authors for the hypotheses are as follows: rivet-popping, Ehrlich and Ehrlich (1981); non-linear, Carpenter (1996); redundancy, Walker (1992) and Lawton and Brown (1993); idiosyncratic, Naeem et al. (1995); humped-shaped, Rosenzweig and Abramsky (1994); and compensating/keystone, Sala et al. (1996).

tion of atmospheric composition, water availability and quality, nutrient retention, and other processes important to human welfare (Ehrlich & Wilson 1991; Vitousek 1994), the term ecosystem services has sometimes been substituted for ecosystem processes. Similarly, the production of game, forest products, fish, and other biological resources provided by ecosystems and important to humans may be referred to as ecosystem goods. Note that *function* does not imply purpose or design, only activity.

Species redundancy (Walker 1992) is currently part of several hypothesized relationships between biodiversity and ecosystem functioning, including the redundancy, compensatory/keystone, rivet-popping, and nonlinear hypotheses (wherever slope ≈ 0 in Fig. 1), and it has increasingly become an important concept in understanding the ecological values of biodiversity (di Castri & Younes 1990; Walker 1992; 1995; Franklin 1993; Lawton & Brown 1993; Vitousek & Hooper 1993; Gitay et al. 1996).

The word *redundancy* in its literal sense, means superfluous or unnecessary; as such, it is repugnant to defenders of biodiversity and has led to the informal sug-

gestion that it be struck from the lexicon of ecology (Walker 1995). Walker introduced the concept for the purposes of assessing conservation priorities (Walker 1992, 1995), arguing that conservation efforts should focus first on species that are singular in their contribution to ecosystem functioning. Objection to the term *redundancy* arises from the concern that redundancy implies that conservation of redundant species is unnecessary, the unintended corollary of Walker's hypothesis (Walker 1995; Gitay et al. 1996). That is, although Walker (1995) recognized the value of species redundancy, the term itself did not convey this effectively.

I introduce a novel way of considering the relationship between biotic diversity and ecosystem functioning that is based on simple concepts from reliability engineering (Billinton & Allan 1983; Dhillon 1983; Lewis 1987). In so doing, I hope to provoke ecologists to rethink and reevaluate the ecosystem redundancy of species, to discard current negative connotations of redundancy, and to adopt the perspective that species redundancy is necessary and valuable.

Preliminary Concepts

Functional Groups

Functional groups are variously defined in ecology (Barbault et al. 1991; Körner 1993; Gitay et al. 1996). Grouping species by ecological equivalency—such as guilds (Root 1967), trophic levels (Hairston et al. 1960), and functional groups (Raunkier 1934)—is a useful device for understanding complexity in ecological systems (Körner 1993; Gitay et al. 1996). Within the context of ecosystem functioning, functional groups may be defined as groups of species that share common biogeochemical attributes. For example, photoautotrophs store light energy as carbon products and decomposers move nutrients between dead organic matter and inorganic nutrient pools.

A common structure, consisting of biotic and abiotic compartments, can be defined for most ecosystems. Autotrophs and decomposers are common to most ecosystems and represent core biotic compartments (Harte & Kinzig 1993). Pools of organic nutrients (e.g., dead organic matter) and inorganic nutrients are also common to most ecosystems and represent core abiotic compartments (Harte & Kinzig 1993). Peripheral compartments, or nondecomposer heterotrophs, consist of chains or webs of autotrophically- or decomposer-derived consumer species grouped by trophic function. Six main flows link these core compartments (Fig. 2). These are (1) the acquisition of energy by autotrophs (e.g., photosynthesis or chemosynthesis); (2) mineralization, or the return of nutrients to inorganic pools by heterotrophs; (3) decomposition, or the transfer of material from dead

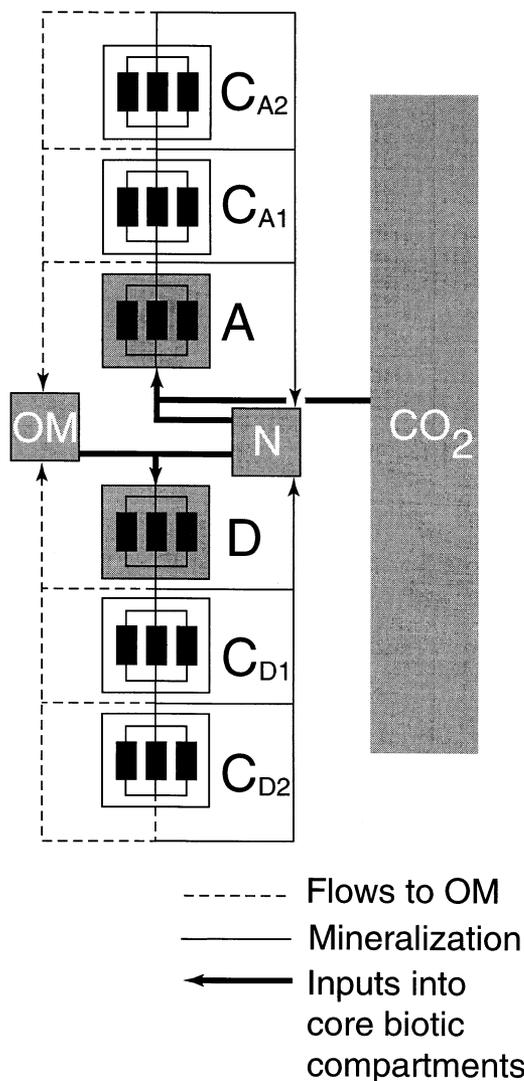


Figure 2. Engineering diagram of a generic ecosystem. Compartments are shown as boxes containing three species (solid rectangles) linked in a parallel redundancy configuration. The core biotic compartments are autotrophs (A) and decomposers (D). The core abiotic compartments are nutrients in either organic material (OM) or inorganic material (N). Peripheral compartments are autotrophically derived (CA) or decomposer-derived (CD), occupying different trophic levels (numerical subscripts). For simplicity, omnivores that consume from different compartments are not shown.

organic matter to decomposer biomass; (4) immobilization, or the acquisition by decomposers of nutrients from inorganic pools; (5) death, or the accumulation of organic nutrients into organic nutrient pools; and (6) assimilation, or the acquisition of inorganic nutrients by autotrophs. Peripheral compartments are linked trophically—by herbivory, predation, detritivory, or omnivory—

to core biotic compartments. Ecosystems have structures much more complex than that portrayed in Fig. 2, but at the root of most ecosystems is this basic structure (Harte & Kinzig 1993). This basic structure can be used to identify the compartments and the links among them which form the basis for qualitatively and quantitatively assessing redundancy and functioning in ecosystems.

Local Extinction and Ecosystem Complexity

Within an ecosystem, each species is represented by a population and each population has a finite probability of local extinction. The probability of local extinction is likely different for each species. Local extinction for some species may be due to unstable relationships with predators or pathogens; others might go extinct because of a drought, fire, a severe frost, or simply by chance because their population size is small. For the purposes of this discussion, local extinction of species within a functional group will be considered a stochastic process.

ECOSYSTEM COMPLEXITY

Complexity, like functional groups, is variously defined in ecology. I use *complexity* to refer to the number of functional groups in an ecosystem. This usage is quite different from the more common use of complexity to describe community complexity or the per-species number of biotic linkages to other species (May 1973; Goodman 1975; Pimm & Lawton 1977; Pimm 1984; Haydon 1994). For the purposes of this paper, it is important to not conflate ecosystem complexity with community complexity.

ECOSYSTEM FAILURE

From an engineering perspective, *failure* refers to failure of a system to provide services or goods upon demand. If a machine has an on and off switch, for example, at each demand (switch on) the machine either provides the services or produces the desired goods (success) or it does not (failure). Reliability of a machine is the probability that the machine will function upon demand. Demand is often continuous, which is equivalent to repeated demands over small units of time (Δt). That is, if p is the probability of failure upon demand and r is the probability of success, or $1 - p$, then reliability after n demands is

$$R_n = r^n,$$

and reliability after n units of Δt , or $t = n\Delta t$, is

$$R(t) \cong e^{-\lambda t},$$

where $\lambda = p/\Delta t$ and Δt is a small increment in time (Lewis 1987). Thus, reliability of a system in continuous operation without repair declines with age.

Failure is seldom total. For example, failure of a cathode ray tube within a television does not mean that all components of the television have failed but that the machine as a whole has effectively failed because it no longer provides the service demanded of it. From an ecosystem perspective, an ecosystem fails when it ceases to provide the services or goods demanded of it. As with machines, the ecosystem does not have to collapse. For example, if a pond shifts from a desirable state as a net carbon sink to an undesirable state as a net carbon source (say, upon entering an anoxic state after eutrophication), the pond is still a functioning ecosystem, but it has failed in the sense that it no longer provides the original service desired of it.

COMPLEXITY AND SYSTEM FAILURE

If each component in a system has an independent, finite probability of failure, and all components are mutually dependent upon one another for the functioning of a machine, then the more complex a machine—the more components it has—the more likely it will be to fail or the less reliable it will be. This idea is formally equivalent to

$$R_T = \prod_{i=1}^M R_i, \quad (1)$$

where R_T is the reliability of the machine and R_i is the reliability of the i^{th} component and reliability varies from 0 to 1.

This formula shows that the more mutually dependent components in a system there are, the lower its overall reliability will be. For an ecosystem, the same is true. The more functional groups required for an ecosystem to provide goods and services at particular levels, the less reliable it becomes. This statement echoes the continuing complexity-stability debate in ecology, but it is important not to confuse the two. Whereas a complex community can be dynamically more stable than a simple community (Haydon 1994), a more complex ecosystem, as defined in equation 1, is always less reliable than a less complex system (Futuyma 1973).

SINGULARITY VERSUS REDUNDANCY

By definition, species are phylogenetically singular, and by inference species are likely to be autecologically singular. From an ecosystem perspective, however, species are rarely singular. For example, all photoautotrophs sequester carbon, and all decomposers acquire energy and nutrients from dead organic matter. Species vary in their characteristic rates or efficiencies of contributing to ecosystem processes, but there may be no clear association between the characteristics of a species and its net contributions to ecosystem processes. For example, one plant

species may photosynthesize more than others in an ecosystem but contribute less to net ecosystem sequestration of carbon than other species if its density is maintained at low levels due to intra- or interspecific interactions.

Variation in species richness within an ecosystem can lead to variation in both the number of functional groups and the number of species within and among functional groups. Lawton and Brown (1993) suggest that the apparent redundancy of species is due to the fact that most small changes in species composition are likely to involve species within functional groups rather than entire functional groups. Ecosystem functioning is likely to show significant changes in response to variation in species composition when such changes involve the loss or addition of entire functional groups (Lawton & Brown 1993). This principle is the same used by Walker (1992, 1995) who argues that ecosystems are likely to show greatest sensitivity to variation in species composition when species within functional groups are represented by one or a few species. Thus, one can formally define ecosystem redundancy as follows: let $N_j(S_j)$ equal the amount of material or energy processed by the j^{th} functional group over t as a function of S_j , the number of species in the j^{th} functional group. Then if

$$N_j(S_j) = N_j(S_j - 1) + \varepsilon = N_j(S_j - 2) + \varepsilon = \dots N_j(1) + \varepsilon,$$

where ε is an error term associated with stochastic deviation from the mean ecosystem function expected at that species richness, then the species within the functional group are redundant. That is, N_j is independent of S_j . Net ecosystem flows will show a significant relationship with increasing species richness until each functional group is represented, at which point an asymptote is soon reached as more species are added, a formulation consistent with Lawton and Brown's (1993) definition of species redundancy (see Fig. 1).

This definition of species redundancy is similar to "congeneric homotaxis" as defined by Hill and Wiegert (1980), a form of parallel redundancy of species which theoretically contributes to regulatory control of ecosystems and is sensitive to ecosystem stress (Odum 1985). Walker (1995) similarly predicts that species redundancy enhances ecosystem resilience. As defined here, however, redundancy of species does not necessarily guarantee resiliency of ecosystem processes.

Mechanistically, species redundancy in ecosystem functioning is consistent with current ecological knowledge. Species redundancy stems from the compensatory abilities of species within functional groups. Local extinction of species within functional groups is often followed by compensatory growth of others, which effectively leads to a replacement of the contributions of lost species to overall group functioning (e.g., compare the redundancy and compensatory curves in Fig. 1). Drought recovery in prairies (Tilman & Downing 1994; Tilman 1996), drought and fire recovery in fynbos (Cowling et al. 1994a,

1994b; Linder & Midgley 1994), pollination by hummingbirds in the West Indies (Feinsinger et al. 1982), and the compensatory activities of soil biota (Beare et al. 1995) are some examples. Such redundancy is known in engineering as *parallel redundancy* (Billinton & Allan 1983; Dhillon 1983; Lewis 1987) and is schematized in Fig. 2 as three species per functional group, each set of three linked in parallel to the flows of materials or energy through the group. Parallel redundancy increases the reliability of an ecosystem; singularity decreases it.

Species Singularity, Redundancy, and Ecosystem Reliability

Using the terms as I have defined, the following considerations lead to a formal definition of the role of species in ecosystem functioning. Assume a population of the i^{th} species within the j^{th} functional group has a finite probability of local extinction, p_{ij} , and the probability of the species being present over a unit time is equal to $(1 - p_{ij})$. That is, over some small increment in time, t , following the derivation for reliability as above (Lewis 1987),

$$P_{ij}(t) = e^{-\lambda t},$$

where $\lambda = p_{ij}/\Delta t$ and P_{ij} is the probability that the i^{th} species in the j^{th} functional group is present after t . Rescue from local extinction occurs when recolonization occurs. If the probability of recolonization of the i^{th} species in the j^{th} functional group equals q_{ij} , then the probability of not being colonized is $(1 - q_{ij})$ and, following the derivation for reliability as above,

$$C_{ij}(t) = 1 - e^{-vt},$$

where C_{ij} is the probability that the i^{th} species in the j^{th} functional group colonizes the system after t , and $v = q_{ij}/\Delta t$. As habitats become more fragmented $v \rightarrow 0$.

Probability theory says that where R_{ij} is the probability that the i^{th} species in the j^{th} functional group is present by time t , $R_{ij}(t)$ is equal to the probability that extinction, colonization, or both occur ($P\{P \cup C\}$), or,

$$R_{ij}(t) = P_{ij}(t) + C_{ij}(t) - P_{ij}(t) C_{ij}(t). \quad (2)$$

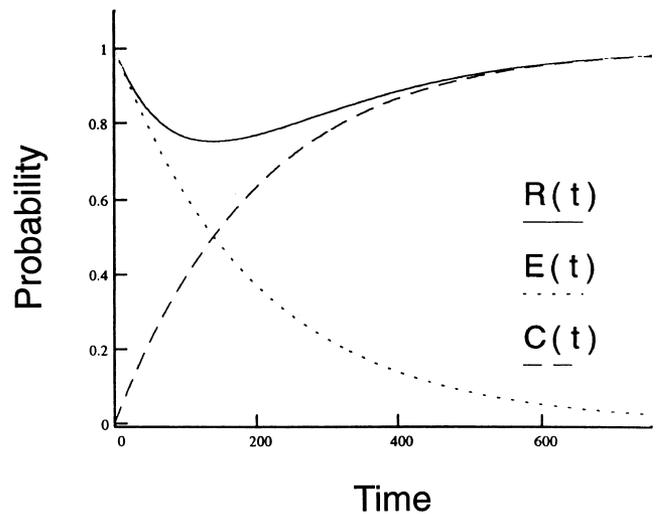


Figure 3. The probability that a species is present in an ecosystem (R) as a function of the probability of local extinction (E) and colonization (C) over time ($v = 0.005$ and $\lambda = 0.005$).

Figure 3 shows this relationship for $v > 0$ and if $\lambda > 0$. Note that as long as $v > 0$ over a long time, a species has a probability of more than 0 of being present at least some of the time, even if $\lambda \ll 1$.

Operation of a functional group depends on the number of species within the group. If each species can compensate for the loss of another by parallel redundancy, then the probability that a functional group will provide its service to the ecosystem is

$$F_j(t) = 1 - \prod_{i=1}^{S_j} [1 - R_{ij}(t)]. \quad (3)$$

The probability that an ecosystem provides service H over time t if it contains M functional groups is

$$H(t) = \prod_{j=1}^M F_j(t). \quad (4)$$

It is apparent from these simple formulas (2-4) that increasing species redundancy within ecosystems in-

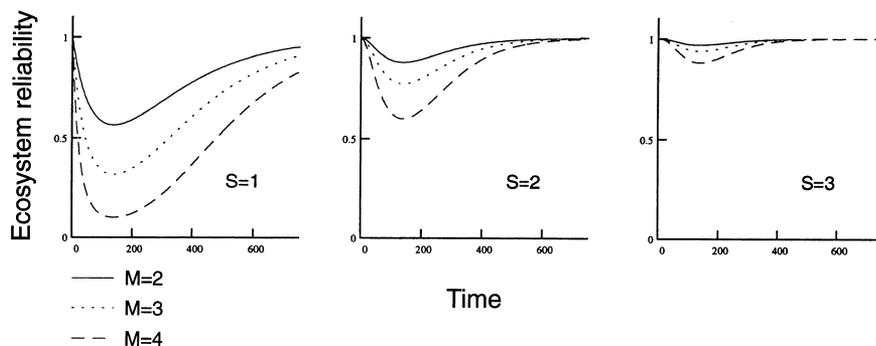


Figure 4. The relationship between ecosystem reliability $H(t)$, the number of functional groups (M), and the number of species per functional group (S). Parameter values are $\lambda = 0.005$ and $v = 0.005$.

creases the reliability of complex ecosystems (Fig. 4). That is, increasingly complex ecosystems (higher values of M) are less reliable over short periods of time, but increasing species redundancy (higher values of S) can compensate for reduction in reliability (Fig. 4). As long as $v > 0$, then recolonization is likely over long periods of time. Thus, an ecosystem is likely to provide services or goods over long periods as long as species are not globally extinct and recolonization is possible. If $v = 0$, then all curves in Fig. 4 would approach zero asymptotically.

These models assume constancy and independence of species extinction and colonization probabilities. In nature neither extinction nor colonization rates are constant (e.g., colonization may be seasonal) or independent (e.g., during drought all drought-sensitive plants face greater probabilities of extinction). Relaxing these assumptions and developing further models is a straightforward process (e.g., load-sharing and Markov reliability models in Dhillon [1983], Billinton & Allan [1983], and Lewis [1987] for systems in which probability of component failure is neither independent or constant). But such an exercise is beyond the scope of this paper and would not change the qualitative conclusions from these models.

Value of Species Redundancy

Petroski (1994) notes that distraction by new paradigms in engineering often results in engineering disasters. One example is the collapse of the 24-story Ronan Point apartment building. Demand by its occupants was continuous. Failure, in this case collapse of the entire corner of the building after an accidental explosion on the 18th floor, resulted in loss of service and of human life. The Ronan Point building lacked structural redundancy, a well known means of guarding against failure in buildings but overlooked during a period of uncritical adoption of modularization as a new paradigm in engineering (Petroski 1994). The chance explosion that knocked out the corner wall of one of the modules led to the failure of that module, and lack of redundancy meant that the modules mutually dependent on one another for structural integrity also failed.

The lesson learned from the Ronan Point disaster can be applied to the natural world. Natural ecosystems, as outlined in Fig. 2, often contain many species per functional group. Local extinction of species within functional groups is inevitable and frequent, but reservoirs of species from adjacent ecosystems generally ensure that functional group or ecosystem failure, if it occurs, is likely to be transient. But increased rates of global extinction mean that functional group diversity is irrevocably reduced, and increasing habitat fragmentation means that recolonization is likely to play a decreasing role in

our equations for ecosystem functioning. Furthermore, the replacement of species-rich, species-redundant ecosystems with modular ecosystems such as managed forests, fisheries, agroecosystems, and other simple systems is leading to landscape-level decreases in biodiversity. With respect to ecosystem functioning, declining biodiversity means loss of species redundancy in ecosystems.

To my knowledge, empirical demonstrations of ecological redundancy are few and rarely couched in such terms. More attention has been directed to the complexity-stability debate in ecology. Empirical demonstrations of dynamic stability and resilience are difficult (Lawler & Morin 1993; Tilman & Downing 1994), and little consensus exists on the issue of whether or not more diversity begets more complexity which in turn begets more stability. Demonstrating the compensatory abilities of species as the basis for species redundancy should be a less formidable challenge, however, and would go a long way toward supporting the value of biodiversity as an element of ecosystem reliability, even if it is uncertain that species-rich systems are dynamically more stable.

From the arguments presented here, it seems almost inescapable that species richness within functional groups provides redundancy in ecosystem functioning, a potentially critical feature affecting ecosystem reliability. In the absence of sudden, dramatic changes in the physical conditions of our planet, it is possible that ecosystems will forever continue to function at long-term averages conducive to human interests, but the reliability of their functioning will be contingent on the richness of their biota and the redundancy this richness bestows upon ecosystems.

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