

# Trophic-dynamic considerations in relating species diversity to ecosystem resilience

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## ABSTRACT

Complexity in the networks of interactions among and between the living and abiotic components forming ecosystems confounds the ability of ecologists to predict the economic consequences of perturbations such as species deletions in nature. Such uncertainty hampers prudent decision making about where and when to invest most intensively in species conservation programmes. Demystifying ecosystem responses to biodiversity alterations may be best achieved through the study of the interactions allowing biotic communities to compensate internally for population changes in terms of contributing to ecosystem function, or their intrinsic functional redundancy. Because individual organisms are the biologically discrete working components of ecosystems and because environmental changes are perceived at the scale of the individual, a mechanistic understanding of functional redundancy will hinge upon understanding how individuals' behaviours influence population dynamics in the complex community setting. Here, I use analytical and graphical modelling to construct a conceptual framework for predicting the conditions under which varying degrees of interspecific functional redundancy can be found in dynamic ecosystems. The framework is founded on principles related to food web successional theory, which provides some evolutionary insights for mechanistically linking functional roles of discrete, interacting organisms with the dynamics of ecosystems because energy is the currency both for ecological fitness and for food web commerce. Net productivity is considered the most contextually relevant ecosystem process variable because of its socioeconomic significance and because it ultimately subsumes all biological processes and interactions. Redundancy relative to productivity is suggested to manifest most directly as compensatory niche shifts among adaptive foragers in exploitation ecosystems, facilitating coexistence and enhancing ecosystem recovery after disturbances which alter species' relative abundances, such as extinctions. The framework further explicates how resource scarcity and environmental stochasticity may constitute 'ecosystem legacies' influencing the emergence of redundancy by shaping the background conditions for foraging behaviour evolution and, consequently, the prevalence of compensatory interactions. Because it generates experimentally testable predictions for *a priori* hypothesis testing about when and where varying degrees of functional redundancy are likely to be found in food webs, the framework may be useful for advancing toward the reliable knowledge of biodiversity and ecosystem function relations necessary for prudent prioritization of conservation programmes. The theory presented here introduces explanation of how increasing diversity can have a negative influence on ecosystem sustainability by altering the environment for biotic interactions – and thereby changing functional compensability among biota – under particular conditions.

*Key words:* competition, density dependence *versus* density independence, ecological complexity, functional groups, generalism *versus* specialization, generalist *versus* specialist life-history evolution, interpopulation compensation, opportunism, phenotypic plasticity, trophic niche dynamics.

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## I. INTRODUCTION

In his 1942 monograph on ecological dynamics, Raymond Lindeman integrated perspectives from the ecological subdisciplines of autecology, population ecology, and synecology by linking successional theory with trophic interactions. Lindeman (1942) discussed the flow of energy in an ecosystem from exogenous inputs through the hierarchy of productivity in a food web, along a gradient of successional time. His essay addressed several theoretical concepts, including the evolution of generalist foraging strategies as a consequence of resource limitation and environmental stochasticity, how foraging strategies facilitate coexistence of species, and how multiple states for ecosystem productivity develop. Lindeman’s (1942) ‘trophic–dynamic’ synthesis helped formalize the ecosystem concept in ecology by reducing a complex and changing system to tangible interacting components.

While ecological research today engages increasingly in discovering how the sustainable functioning of ecosystems is influenced by biodiversity, much about the responses of ecosystems to diversity alterations remains unpredictable. Here, I abstract Lindeman’s (1942) trophic–dynamic aspect of ecology to a mechanistic, hypothetical framework for modelling functional redundancy, and thus resilience to disturbances, in ecosystems.

## II. CONSERVATION AND TROPHIC DYNAMICS

### (1) Trophic dynamics and ecosystem sustainability

Increases in species extinction rates associated with elevated use of natural resources by humans have naturally raised concerns that the sustainable functioning of the Earth’s ecosystems is being threatened (Elton, 1958; Chapin *et al.*, 1997). The perception that the functioning of ecosystems may relate directly to the number of species present in them has inspired research to determine the extent to which species contribute uniquely to ecosystem function (Lawton, 1994; Johnson *et al.*, 1996; Huston, 1997). Productivity is an ecosystem function of particular interest to economists because of its direct importance to the sustenance of human populations (Kohen, Santus & Hirschberg, 1996; Chapin *et al.*, 1997) and to ecological modellers because it encapsulates net energy exchanges throughout an ecosystem (Lindeman, 1942; Ulanowicz, 1995*b*; Johnson *et al.*, 1996). Consequently, productivity typically serves as the primary ecosystem-level measurement variable in studies relating biodiversity to ecosystem function (e.g. Margalef, 1969; McNaughton, 1993; Chapin *et al.*, 1997; Tilman, Lehman & Thomson, 1997*b*; Doak *et al.*, 1998; Hector, 1998; Lundberg & Frodin, 1998;

Loreau, 1998 *a, b*; Yachi & Loreau, 1999). Utilizing productivity for human sustenance implies some form of extraction of biomass or energy, which is the most fundamental definition of disturbance (Grime, 1979, p. 39). Sustainability of productivity under exploitation depends on the ability of the system to recover to normal levels after such disturbance. Therefore, this paper focuses on the resilience (*sensu* Holling, 1973 and Webster, Waide & Patten, 1974) of productivity as influenced by species composition.

The functional importance of species diversity is most directly examined in the context of ecosystem responses to diversity manipulations, controlling for other variables (e.g. Naeem *et al.*, 1994). An induced species deletion can be considered a true disturbance to an ecosystem, conforming to Grime's (1979) definition in that a finite loss of biomass, however small, from an ecosystem compartment occurs at the time of extinction. Not all manipulations of diversity need include complete removal or addition of a species; altering relative abundances can also be taken to be a form of diversity manipulation. The discussion in this paper will be directed primarily toward changes in species richness because species additions/deletions offer the clearest treatments for investigating diversity–ecosystem function relations, but the concepts will extend to all types of diversity alterations. In the context here, ‘resistance’ of the ecosystem to a disturbance equates to the biomass change caused directly by the disturbance (Holling, 1973; Webster *et al.*, 1974; Smedes & Hurd, 1981). In the case of a species removal, resistance is simply the biomass removed from the system. Resistance is therefore simply a measure of the perturbation intensity. (Note that this definition refers to local resistance, rather than to overall resistance of a system to being displaced functionally into an entirely new domain of attraction, which, as discussed below, depends on resilience.) ‘Resilience’ of the system is defined as the rate and extent of recovery of ecosystem function after the disturbance, and is the more compelling modelling problem. Whether an extinction is the direct result of or time-lags behind a primary disturbance, resilience to extinction will be the most relevant consideration concerning the diversity–sustainability question. Thus, elucidating the impacts of anthropogenic species extinctions on ecosystems’ collective ability to sustain human populations largely condenses to the issue of determining the degree to which species richness drives ecosystem resilience. Species’ contributions to the resilience of ecosystem productivity will depend on trophic dynamics because it is the

combination of all such energy exchanges in a system which determine its productivity.

On the surface, it may seem intuitive that ecosystem productivity and stability will depend on the diversity of species present because organisms are the actively working components of any ecosystem. The greater the number of species in the system, the greater the number of tasks and their inter-relatedness is expected to be, increasing the efficiency and robustness to disturbance of ecosystem function. MacArthur presented a version of this idea formally in 1955, followed soon after by Elton (1958). Now called the diversity-stability hypothesis, it was tested in field experiments throughout the 1960s and into the 1970s (Margalef, 1969; Hurd *et al.*, 1971; Hurd & Wolf, 1974; Mellinger & McNaughton, 1975; see also McNaughton, 1977). Approaches and quality control varied between field experiments, but their collective results surprisingly showed that diversity does not always improve the productivity and stability of ecosystems in nature (Johnson *et al.*, 1996). Results were often contradictory and difficult to interpret (McNaughton, 1977, 1993) and the idea of species redundancy had not yet been popularized.

Within the last decade, increasing public and scientific awareness of rapidly growing species extinction rates stimulated a strong resurgence in biodiversity–ecosystem function research. Many pivotal papers advanced the perspective that losses of species could be expected to affect ecosystem functioning (e.g. Naeem *et al.*, 1994), and even that they should predictably cause declines in ecosystem functioning and sustainability (e.g. Frank & McNaughton, 1991; Kareiva, 1994; Tilman & Downing, 1994; Navarette & Menge, 1996; Power *et al.*, 1996; Tilman, 1996; Wedin & Tilman, 1996; Tilman *et al.*, 1997 *b*; Daily, 1997, preface; McGrady Steed, Harris & Morin, 1997). However, a good deal of literature already containing clear evidence that species diversity – whether measured as species richness or as community equitability – could be unrelated or even negatively related to rates of ecosystem processes (including productivity) and to functional stability had yet to be reviewed. In their 1996 review, Johnson *et al.* evaluated such long-standing evidence in relation to the newly resurgent paradigm that the sustainable functioning of the Earth's ecosystems depends positively and directly on species diversity. Johnson *et al.* (1996) demonstrated that species diversity *per se* had variable relationships to ecosystem processes and that better experimental designs and a mechanistic focus on modelling functional niche dynamics, especially in

terms of evaluating relative redundancy, should prove to be the key to improving biodiversity–ecosystem function research (see especially p. 375). Subsequently, new evaluations from other scientists (e.g. Hooper and Vitousek, 1997, 1998; Naeem and Li, 1997, 1998; Tilman *et al.*, 1997*a, b*; Hooper 1998; Naeem, 1998; Tilman, Lehman & Bristow, 1998; Covich, Palmer & Crowl, 1999) emerged in the prominent literature also suggesting that ‘functional diversity’ or ‘functional group diversity’ rather than species diversity *per se* was the principal determinant of ecosystem productivity and stability. This repositioning away from the former paradigm that diversity itself consistently benefits the functioning of ecosystems (e.g. especially Tilman & Downing, 1994; Power *et al.*, 1996; Tilman, 1996; Wedin & Tilman, 1996; Tilman *et al.*, 1997*b*; Daily, 1997, preface; McGrady *et al.*, 1997) in favour of declarations that ‘functional diversity’, ‘species composition’, and ‘species identity’, rather than species diversity *per se*, determine biodiversity–ecosystem function relations, continues today.

Although this more recent literature has taken the direction of modelling niche differentiation as suggested by Johnson *et al.* (1996, pp. 375–377), there remains much to be desired in quantitative modelling of functional niche dynamics and of overall system dynamics in realistic, many-species ecosystems. Specifically, two shortcomings remain with the utility even of a ‘species composition’ perspective for modelling biodiversity–ecosystem function relations. First, species composition alone is logically only a partial determinant of the nature of the biotic interactions and hence the functional niche dynamics determining ecosystem functioning because interactions likely to influence biodiversity–ecosystem function relations, such as resource competition, depend largely on the environmental background conditions shaping those interactions. That is, interactions can change (and thus biodiversity–ecosystem function relations can change) with, for example, changes in the abundances of resources such as light, nutrients, and water (e.g. see Johnson *et al.*, 1996; Cottingham & Carpenter, 1998; Cottingham, Carpenter & Stammer, 1998). This probably can happen independently of changes in species composition (Johnson *et al.*, 1996). Aspects of the physical environment (such as relative nutrient scarcity) shaping the types and strengths of interactions typically have not simultaneously been acknowledged as co-determinants of biodiversity–ecosystem function relations in the most recent literature (e.g. Hooper and Vitousek, 1997, 1998;

McGrady Steed *et al.*, 1997; Naeem and Li, 1997, 1998; Tilman *et al.*, 1997*a, b*, 1998; Hooper, 1998; Naeem, 1998; Covich *et al.*, 1999; but see Loreau, 1998*a*). So, the newly revised dominant paradigm that attributes of species composition *per se* (including ‘functional diversity’) determine biodiversity–ecosystem function relations arguably remains naive in continuing to emphasize species themselves apart from their interaction environment as the determinants of ecosystem function. That is, species composition remains the focus of biodiversity–ecosystem function research at the expense of a direct, mechanistic focus on modelling functional niche dynamics – especially compensatory dynamics – which itself requires modelling the feedbacks between the abiotic environment (background conditions shaping interactions and evolutionary trajectories) and functional, life-history attributes of organisms; this is the objective of the present paper.

The second principal shortcoming of the new paradigm that ‘species composition’/‘functional diversity’ *per se* determines ecosystem functioning as stated in the most recent literature is that it offers no mechanism accommodating the potential for additional species to lower productivity or decrease functional stability. This is an important limitation because much evidence has been compiled demonstrating that increases in species richness sometimes result in decreases in productivity and stability (Johnson *et al.*, 1996). This should not seem counterintuitive to those familiar with pathological biological invasions. It seems likely that a truly effective mechanistic biodiversity–ecosystem function modelling approach will provide insight about various expected results of diversity alterations, including the potential for ‘negative’ implications of higher diversity. An unbiased, more rigorous approach should be based objectively on modelling functional niche dynamics themselves as the determinants of biodiversity–ecosystem function relations, especially compensability. Modelling niche dynamics requires modelling in multiple dimensions of biotic interactions among and between individuals and populations, and the way that those interactions change through time as a result of environmental influences on the interaction environment. A genuine trophic–dynamic treatment of biodiversity–ecosystem function relations will link the functioning of individuals to the functional and evolutionary trajectories of populations at the temporal scales both of ecological (real) time and evolutionary time, as they change through succession and with overall system productivity. This may sound impossibly



difficult, and indeed has not been accomplished by the literature to date. But, much of the conceptual groundwork is already in place. By following Lindeman's (1942) lead in unifying the ecological study of individuals, their trophic interactions, and the ways that attributes of individuals change with one another and through succession on the evolutionary playing field, we should find it possible to synthesize some important generalizations about trophic dynamics over time in evolving systems into a useful framework for modelling biodiversity–ecosystem function relationships. Toward this end, a brief review of some important early studies providing clues for linking food web interactions to biodiversity–ecosystem function relations, and which continue to be neglected by the current literature, is worthwhile.

Some of the earliest designed experiments investigating diversity and ecosystem function relations were conducted in old fields and involved perturbation of real food webs with pulses of N-P-K fertilizer (Hurd *et al.*, 1971; Hurd & Wolf, 1974; Mellinger & McNaughton, 1975). The experimental approach generally was not to manipulate diversity *per se*, but the results offer some interesting insights about the relationship of trophic dynamics and functional redundancy not yet addressed in current literature. Among trophic guilds, primary producers responded most rapidly and recovered quickest to ground state after fertilization, while the effects of the perturbation took increasingly more time to appear with progression up the food web (Hurd *et al.*, 1971; Hurd & Wolf, 1974; Mellinger & McNaughton, 1975). One of the more profound conclusions from these studies was that diversity–stability relations (including resilience – Hurd & Wolf, 1974) varied among trophic guilds, decaying as trophic position increased. In other words, the relationship between diversity and stability in these studies decreased from the bottom of the trophic pyramid to the top. These results remain interesting and somewhat mysterious today (McNaughton, 1993; Johnson *et al.*, 1996), especially in light of recent biodiversity and ecosystem function research (e.g. Naeem *et al.*, 1994; Hooper and Vitousek, 1997, 1998; McGrady Steed *et al.*, 1997; Naeem and Li, 1997, 1998; Tilman *et al.*, 1997*a, b*; Hooper, 1998; Naeem, 1998), which has not resolved or addressed these phenomena. Searching for potential mechanisms behind such patterns within and between food webs introduces opportunity for new integration of a genuinely trophic–dynamic perspective into biodiversity–ecosystem function

science. In this paper, I suggest that the study of functional redundancy in trophic dynamics (i.e. trophic compensability) may provide new insights about biodiversity–ecosystem function phenomena and enhance our understanding of ecological dynamics in general.

From the outset, it should be noted that the implications from the trophic–dynamic viewpoint developed here differ in many important respects from previously published perspectives. Unlike other modelling viewpoints, the trophic–dynamic approach is based on rigorous stability analysis and considers how biodiversity–ecosystem function relations might change over time as the life histories shaping biotic interactions evolve in response to environmental conditions. The approach focuses on mechanistic modelling of particular interactions hypothesized to have specific influences on ecosystem function (*sensu* Johnson *et al.*, 1996). By contrast, other approaches have been aimed up front at rationalizing presumed non-negative (in fact, almost always positive) relationships between biodiversity and ecosystem function (e.g. Tilman, 1996; Tilman *et al.*, 1997*b*; Doak *et al.*, 1998; Loreau, 1998*a*; Naeem, 1998; Yachi & Loreau, 1999) in support of observations from controversial analyses of results from experiments with documented design limitations (e.g. Naeem *et al.*, 1994; Tilman & Downing, 1994; Tilman, 1996; for examples of critical reviews, see Johnson *et al.*, 1996; Aarssen, 1997; Huston, 1997; Hodgson *et al.*, 1998). In some cases, simulation models have been programmed *a priori* such that their results demonstrate a positive dependence of ecosystem function on biodiversity. In an important example of the latter, Tilman *et al.* (1997*b*) modelled nutrient retention and productivity in relation to species richness in a mathematical analysis examining three different simulated systems characterized according to the types of interspecific interactions intentionally programmed into the model. In all of their scenarios, species were programmed to exhibit competitive interactions and to share some nutritional resources. The intensity of the competitive interactions varied between scenarios. They concluded that biodiversity appears consistently to enhance productivity and to stabilize nutrient retention because new species added to their model systems were always characterized by unique contributions to nutrient processing (Tilman *et al.*, 1997*b*). This conclusion, however, is of a circular nature because the omnipresence of interspecific competition and sharing of consumable resources programmed into their models in all cases

makes such results virtually inevitable. The models were not set up to accommodate other, potentially confounding interactions (such as regulation of competition by predators) likely to occur in nature (Hairston & Hairston, 1993) and therefore may have limited utility as an effective theory. Furthermore, although the authors state that their analysis demonstrates that ‘compensation’ between populations stabilizes community dynamics (Tilman *et al.*, 1997*b*), their approach does not satisfy criteria for rigorous stability analysis required actually to demonstrate compensation; this analytical shortcoming is common among recent papers on the topic (e.g. Naeem and Li, 1997, 1998; Naeem, 1998) and will be discussed in further detail below (Sections IV.2 and VI). The new, trophic–dynamic theory developed here indeed recognizes compensability itself as the mechanism determining ecological stability as suggested by Johnson *et al.* (1996, pp. 373–376), but, uniquely, it does not assume that the interspecific competitive interactions stemming from niche overlap – hence compensability – should increase as species are added to a system. That is, it does not treat compensability as a necessarily or even probable emergent property of biodiversity, unlike other studies. This trophic–dynamic approach is therefore the first mechanistic theory to address how biodiversity and interspecific compensability can vary independently or even inversely to one another.

The trophic–dynamic approach accommodates possibilities for any of an array of different relationships along an interaction continuum to develop – including scenarios where adding one or more species can reduce ecosystem productivity, resilience, or both – depending on particular environmental conditions. Because the approach integrates many ecological concepts and has not previously been brought in this form to the study of biodiversity and ecosystem function relations, I include considerable review of the concepts of biotic interactions, trophic dynamics, and stability analysis in presenting these ideas. I specify some refinements to popular definitions of terms important to the topic of biodiversity–ecosystem function relations, especially functional redundancy, disturbance, and ecosystem resilience, and integrate these concepts into defensible analytical and graphical models which should help stimulate and refine further research. The new concepts will be discussed in detail in relation to both earlier and current research in this field.

## (2) The case for redundancy

Functional redundancy among species was discussed

some time ago by Rutledge, Basore & Mulholland (1976) and Ulanowicz (1980, 1986), who considered redundancy in resource processing as an emergent property of trophic dynamics among populations in nonequilibrium systems. Their analyses complement May’s (1974) mathematical arguments that diversity probably does not stabilize the population structures of natural communities as a general rule. Ehrlich & Ehrlich (1981) and Walker (1992, 1995) began to bring the idea that species redundancy was a parameter defining diversity–stability relations into mainstream discussions on conservation, perhaps independently of Rutledge *et al.* (1976) and Ulanowicz (1980, 1986). The idea that some redundancy may exist among coexisting species under certain conditions deserves further consideration as a compelling explanation of why alterations of community composition have varying system-level effects between and within particular ecosystems.

The concept that varying degrees of functional redundancy can exist among components of working systems has long been accepted as elementary by molecular biologists, physical scientists, and engineers (e.g. see discussions by Clark, Masreliez & Burrows, 1976; Clark & Setzer, 1980; Assal, Berman & Gupta, 1981; Kiss, Amin & Pearlman, 1981; Brand, Micklem & Nasmyth, 1987; Harr, 1987; Lewis, 1987; Zarkower & Wickens, 1988; Catuneanu & Mihalache, 1989; Wallace, 1989; Birolini, 1994; Hoyland & Rausand, 1994). The proposition of functional redundancy has been comparatively controversial in ecology, perhaps because it has been perceived as a threat to species-oriented conservation advocacy. Ecologists recently challenging the notion of species redundancy have defined it as being synonymous with weak sources of direct interactions (e.g. Navarrette & Menge, 1996; Power *et al.*, 1996) or as implying that a species has no potential to contribute significantly to ecosystem function (e.g. Tilman & Downing, 1994; Gitay, Wilson & Lee, 1996; Power *et al.*, 1996; Ghilarov, 1998; see also Foote, 1995). Accordingly, they have presented evidence that species characterized by predominantly weak direct interactions or low relative abundance can nonetheless be important to ecosystem functioning as evidence against the concept of redundancy (Navarrette & Menge, 1996; Power *et al.*, 1996; see also McCann, Hastings & Huxel, 1998 for an examination of weak direct interactions). Some ecologists may now be starting to re-value the concept, (e.g. McGrady Steed *et al.*, 1997; Naeem & Li, 1997; Naeem, 1998), but

prohibitive inconsistencies in how redundancy is defined and interpreted persist. The most useful interpretation of the original concept of functional redundancy, however, may be as the degree to which coexisting species compensate for one another at the population level in terms of contributing to ecosystem function following disturbance (Johnson *et al.*, 1996; see also Ehrlich & Ehrlich, 1981; Walker, 1992, 1995; and Frost *et al.*, 1995), probably through indirect interactions (Johnson *et al.*, 1996). The present paper advocates and develops this definition. Ecologists should consider functional redundancy to be relative and not so much an absolute (i.e. discrete) pattern to be confirmed or refuted, but a real, measurable attribute of natural systems which varies across a continuum of environmental conditions as they shape food web interactions, and which determines ecosystem sensitivity to perturbations. As such, functional redundancy may be a useful modelling parameter to consider in demystifying ecosystem responses to disturbances such as species deletions. Toward this end, it will be helpful to study how redundancy according to this definition arises and where and to what degree it may manifest in different systems. A redirected study of trophic dynamics may offer the most useful clues to help us generalize about when and where various amounts of functional redundancy (i.e. functional compensability) may be found in nature because resource-acquisition strategies are subject to natural selection and determine the functional roles of organisms in ecosystem energetics.

### (3) What can we predict? Some legitimate generalizations about trophic dynamics

A half-century of food web ecology has elucidated some widely accepted principals of trophic interaction. The assimilation of energy from a resource base by consumers is not perfectly efficient because energy is used in finding and handling prey and in the consumers' own metabolism and maintenance (Lindeman, 1942; Belovsky, 1978; Hairston & Hairston, 1993). This inevitable loss of energy between trophic tiers forces consumer populations to be smaller in terms of caloric content than those of their resource bases, and becomes increasingly evident as prey items become increasingly evasive. The progression toward smaller caloric populations with increasing trophic scale has been graphically portrayed using Elton's (1927) familiar trophic pyramid (Lindeman, 1942). Theoretically, this progressive, hierarchical diffusion of energy avail-

able from resource bases for sustaining consumer populations ultimately limits the collective abundance of consumer guilds, number of trophic tiers in a community, and foraging strategies of individuals (Holt, 1995; but see also Pimm, 1991, pp. 224–225).

It can also be shown that food-limited populations can persist in the face of fluctuating resource abundances by opportunistically exploiting a variety of resources (MacArthur, 1955; Levins & MacArthur, 1969; Belovsky, 1978; Jarman & Sinclair, 1979; Grant & Grant, 1993). Without such opportunistic resource acquisition, a consumer population will be relatively vulnerable to fluctuations in abundance of a particular resource (Dall & Cuthill, 1997). Pronounced decrease in a prey population will cause severe decline in abundance of a food-limited predator specializing on that prey. As a supportive anecdote, consider the fates of two species of predators of prairie dogs (*Cynomys* spp.) in North America. Prairie dog populations have declined dramatically as civilization advanced across the native prairies. Black-footed ferrets (*Mustela nigripes*) prey exclusively on prairie dogs and have declined towards extinction with decreasing prairie dog abundance (Reading & Miller, 1994). Meanwhile, populations of the badger (*Taxidea taxus*) – an often food-limited consumer generalist (Minta, 1993) capable of opportunistically exploiting a variety of alternative forages – have fared much better. In this light, generalist foraging can be viewed as a mechanism facilitating sustained existence of a predator population in a stochastic, food-limited system: as one species of prey becomes relatively rare, opportunities for its acquisition by consumers may decrease, and exploitation of another resource may increase. Flexibility in foraging behaviour is a form of phenotypic plasticity (Stearns, 1989; Pigliucci & Schlichting, 1995; Dall & Cuthill, 1997; see also Crick & Koch, 1990 and Windholz & Grimsley, 1992), and can be expected to increase in evolutionarily selective advantage as variability in abundance of limiting food supplies increases (Sultan, 1987; Coleman, McConaughay & Ackerly, 1994; Via *et al.*, 1995). In situations where sensitivity of populations to resource abundance fluctuations increases with food chain position (Lindeman, 1942; Pimm, 1991, p. 224), the selective advantage of generalism should likewise increase with trophic level; indeed, Ulanowicz (1995*a, b*) has reported a general decrease in trophic efficiency with increasing trophic position arguably congruent with such a pattern of progressive sensitivity for Florida's Crystal River (see also May, 1974, pp. 6–7). The above

contextually constrained rules of trophic dynamics are presented as simplistic generalizations to help focus our expectations of which foraging behaviour will be the evolutionarily stable strategy (ESS; Maynard Smith, 1982) under particular conditions. These ideas are traceable to Lindeman's (1942) trophic–dynamic perspective and remain compelling (Ulanowicz, 1995*a, b*), arguably because they make Darwinian sense.

The same environmental conditions giving rise to trophic generalism set the stage for resource (i.e. exploitative) competition by fostering broad, overlapping niches between sympatric consumers. Evolutionary theory (MacArthur & Levins, 1967; Turkington & Merhoff, 1990) – and now quantitative empirical evidence (Grant & Grant, 1993; Martin, 1996) – holds that fitness is maximized when competition is avoided, other factors remaining constant. Given sufficient biological time for chance mutations to occur which give rise to phenotypes on which natural selection can act, coexisting competitors can be expected to specialize into divergent niches. Partitioning of food resources is one example of such functional specialization. Specialization through competition-induced niche divergence is an equilibrium process (Sultan, 1987; Grant & Grant, 1993; Cowling *et al.*, 1994). In relatively stochastic environments, generalists are not likely to give way to specialists (Klopfer & MacArthur, 1960; MacArthur & Levins, 1967; Sultan, 1987). These idealized patterns of tendency toward particular resource acquisition strategies for individuals occur at the population level in evolutionary time. Grant & Grant (1993), through observation of several generations of finches in the Galapagos Islands, have documented these disturbance-mediated evolutionary trends attributable to food competition.

Generalism in the context of functional role means flexibility in resource use, not just that a variety of resources is exploited (polyphagy). In developing a conceptual, trophic–dynamic framework for modelling functional redundancy, this distinction between diet and diet flexibility is important. For example, a plant that requires a particular ratio of several nutrients will be a specialist for the kind of microsite providing that nutrient combination. A generalist would exhibit a much less exclusive microsite affinity, being able to prosper over a range of conditions. If that generalism is adaptive, the organism will be able to increase its uptake of resources as they become increasingly available. To resurrect the black-footed ferret example, the ferret is not a specialist simply by virtue of its ability to

survive on prairie dogs alone, but because it can survive on nothing else (i.e. it is obligatorily monophagous). With this contextual refinement of generalism and specialization in energy acquisition (i.e. functional role) in place, the system-wide consequences of foraging behaviour as a life-history attribute influencing interspecific redundancy can be explored.

### III. MECHANICS OF FUNCTIONAL REDUNDANCY

#### (1) **Scaling: from individuals to ecosystems**

Behavioural and population-level dynamics related to resource acquisition have direct ramifications for the collective dynamics of trophic guilds in response to disturbance. Disturbance here refers to an extrinsic event that directly alters the size of a population, *sensu* Grime (1979). If food is the primary limitation on abundances, the reduction of a consumer population should free up resources for another population to exploit. If a consumer guild is characterized by generalist foragers, the likelihood of another species being able partially, if not with complete effectiveness, to take over the function of a declining population by expanding its own functional niche will be greater than if guild members were obligate specialists (see Pimm, 1991, pp. 59–62). The interspecific compensatory response defining redundancy necessitates an ability of one species to acquire and process the same nutrients as another species upon reduction of the latter population (Frost *et al.*, 1995; Johnson *et al.*, 1996); to be in accordance with biological first principles, this response must occur first at the scale of the discrete individual because this is where resource consumption is actually perceived. It is precisely this scenario which is described by exploitative competition. Under exploitative competition, coexisting species are limited by shared food resources. Reduction in abundance of a superior competitor for a shared resource facilitates niche expansion, and therefore population increase, of the inferior competitor (Klopfer & MacArthur, 1960; Schoener, 1974; Connell, 1990; Chase & Belovsky, 1994). Generalist competitors implicitly have greater potential to adjust their realized niches – both at the scale of individuals and of their aggregation into populations – in the face of varying competition intensity than do strict specialists (Johnson *et al.*, 1996). Consequently, the relationship between ecosystem resilience and species diversity can be hypothesized to depend on



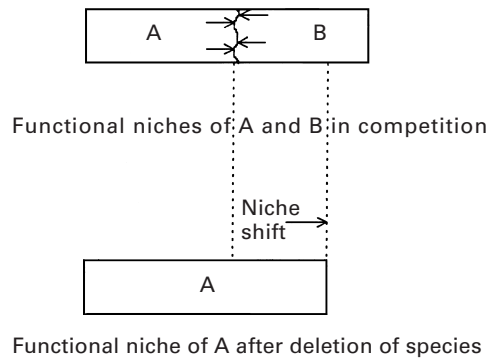


Fig. 1. Fundamental *versus* realized niches of coexisting competitors. Fundamental niches compress to smaller, realized niches as a result of competition (top). This compression can be observed at the scale of the individual, the aggregate of individuals comprising a population, or both. In terms of acquiring and processing nutrients and energy, the potential for redundancy will be synonymous with diet overlap. Actual functional redundancy will depend on the extent to which organism A (or species A) expands its niche to compensate for a reduction in B's niche. The compensatory niche shift is the measure of actual redundancy of A with respect to B, and all such shifts in the community constitute the system-wide redundancy with respect to B. For productivity and related processes, redundancy will manifest most clearly as a release from exploitative (i.e. resource) competition. Note that if a predator (not shown) regulates at least one population sufficiently to override any competition effects, the potential for interpopulation compensation (i.e. redundancy) will be reduced or eliminated, regardless of diet overlap, as discussed in Section III.2. There are various ways to express this idea analytically, but it is simple enough to convey here without mathematics beyond that provided in Section IV. The precise, refined definition of redundancy used here is unique in relation to definitions used previously by others (e.g. Walker, 1992, 1995; Ehrlich & Walker, 1998; Naeem, 1998).

the amount of trophic generalism among coexisting species as that generalism determines the potential for community-wide interpopulation compensation (*sensu* Walker, 1992; Frost *et al.*, 1995; Johnson *et al.*, 1996).

## (2) Competition and keystones

Recently, some ecologists have put forth the notion that diet overlap alone is synonymous with redundancy (Gitay *et al.*, 1996; Jaksic, Feinsinger & Jimenez, 1996; Power *et al.*, 1996); however, this concept of redundancy is somewhat limiting in that diet similarity itself may not indicate compensatory ability. Power *et al.* (1996) state that the chance for interpopulation compensation after removal of a

particular species will be directly proportional to the degree to which species in the community are 'trophically similar' to the deleted species. One situation where diet overlap may not indicate interpopulation compensability is in the case of abject predator-mediated competition, originally described as keystone predation by Paine (1966, 1969). In the case of classical keystone predation, coexistence of species which would otherwise compete for space to the point of exclusion is achieved through regulation of the superior competitor by predators. If regulation by the predator of the superior would-be competitor is sufficient to preclude it from taking up newly available resources or space, and if no important direct or indirect interactions occur between the predator and the weaker competitor, removal of the weaker competitor will prove benign to the superior competitor's population dynamics. In this case, removing the weaker potential competitor would result in negligible interpopulation compensation by the stronger competitor, even if they consume the same resources. Only the potential for functional compensation in terms of acquiring and processing a consumable resource is given by diet overlap between community members (Fig. 1). The degree to which this potential is realized is entirely dependent on the strength of the interpopulation compensatory response (i.e. competition/density dependence). Compensation is a density-dependent response and can result from release from various forms of competition such as direct interference (Paine 1966, 1969) or indirect forms such as exploitation (Schoener, 1971), lottery (Chesson & Warner, 1981), or apparent (Holt, 1977) competition. Actual interpopulation compensation can therefore be inferred from diet overlap only through simultaneous consideration of competition intensity; the relationship will be most direct in the case of purely exploitative competition. Keystone effects in the form of mediation of competition can therefore reduce the ability of species to contribute to ecosystem resilience, making the system less robust to disturbance.

Competition for non-consumable resources such as space, light, mates, physical structures, etc. constitutes direct, interference (Lotka-Volterra) competition when the competition effect is through physical contact. With any form of competition, reduction in one species will result in a corresponding increase in the competitor's population. This numerical population effect of density dependence corresponds to the competition coefficient  $\alpha$  in Lotka-Volterra (L-V) models (see May, 1975 and

Yodzis, 1978, 1989 for details of L-V equations). In its classic application,  $\alpha$  does not explicitly address the foraging niche, and there is no guarantee that the same nutrient/energy processing function will be retained to any degree by species involved in direct competition. In so far as we are interested in the cycling of a particular nutrient(s) as the ecosystem-level process variable, some ability of a species to replace trophically its competitor must exist for any amount of functional redundancy to occur, and this is explicit only in exploitative competition. Schoener (1974; see source for equations and discussion) denoted the numeric exploitation effect of one species on another as  $\beta$  but this term, too, is phenomenological and does not explicate the consumer's role in processing any particular resource(s) as a contribution to ecosystem function. Neither these nor the resource-ratio approach (e.g. Tilman, 1985) to modelling competition and coexistence address multiple consumer levels or accommodate changes in resource-acquisition capability among and between species which stem from the appearance and fixation of new traits in evolutionary time. Addressing the evolution of resource-acquisition strategies will be essential to the development of a predictive theory of functional redundancy in dynamical systems because such evolution comprises the feedback loop linking the trophic behaviours of individuals with the dynamics of their interacting populations and the ecosystem. An analytical approach is needed which will incorporate adaptation of individual species' resource-acquisition strategies into a framework for modelling ecosystem resilience.

#### IV. ANALYSIS OF TROPHIC-DYNAMIC ORIGINS OF REDUNDANCY

##### (1) Resource acquisition and interpopulation compensation

In so far as some ecosystem attribute (e.g. biomass)  $A$  is a composite of contributions from  $j$  species, their respective contributions  $\nu_j$  can be represented as

$$A = \sum_j \nu_j. \quad (1)$$

$\nu_j$  then represents the contribution of species  $j$ . Ecosystem function (e.g. net ecosystem productivity,  $NEP$ ) is conventionally a rate relative to time  $t$ , and as far as it depends on biota, it is made up of functional contributions from each species ( $F_j$ ) with

$$dA/dt = \sum_j (d\nu_j/dt) = \sum_j F_j. \quad (2)$$

At a given time after a disturbance, the contribution of species  $j$  to the overall attribute may be different than before disturbance. The new relationship can be denoted

$$A' = \sum_j \nu'_j, \quad (3)$$

where  $\nu_j$  is the contribution of species  $j$  to the overall ecosystem attribute before disturbance (time  $t$ ) and  $\nu'_j$  is its contribution at time  $t+1$  after disturbance. The niche shift  $s$  after disturbance can be expressed as

$$s_j = \nu'_j - \nu_j. \quad (4)$$

Equilibrium values for species  $j$  contributions to  $A$  indicate the realized niche,  $\nu_j^*$ . In the context of trophic dynamics (i.e. when the relevant ecosystem function is productivity), equilibrium values for post-disturbance contribution,  $\nu'_j^*$ , describe  $j$ 's fundamental niche when there is no diet overlap with other species and if  $d\nu'_j/dt$ —as a measure of population change—is totally resource dependent. This latter condition is met in isolation from interspecific competition and regulation by consumers of  $j$ . Satisfying these criteria makes

$$s_j = |\nu_j^* - \nu'_j^*| \quad (5)$$

a measure of the difference between the fundamental and realized niches as portrayed in Fig. 1.  $s$  is useful thus as a measure of niche plasticity (albeit *post-hoc*), with overlap between  $\nu_j^*$  and  $\nu'_{j+n}$  determining potential interspecific redundancy.

The integration of contributions by community members into the cumulative performance of the system over a given time interval  $t$ ,  $t+n$  can be expressed as

$$\int_t^{t+n} dA = \sum_j \int_t^{t+n} d\nu_j. \quad (6)$$

Any amount of ecosystem recovery after disturbance necessarily reflects some change in a functioning population. In the case of an extinction, this compensation must come entirely from other remaining species. Any such interpopulation compensation equates to redundancy. The relaxation response  $\Gamma$  (a continuous function not detailed further analytically here) of the perturbed ecosystem trajectory across the interval of time  $t$ ,  $t+n$  is a measure of resilience, and will be determined by the combination of niche shifts

$$\Gamma = \sum_j \int_t^{t+n} s_j, \quad (7)$$

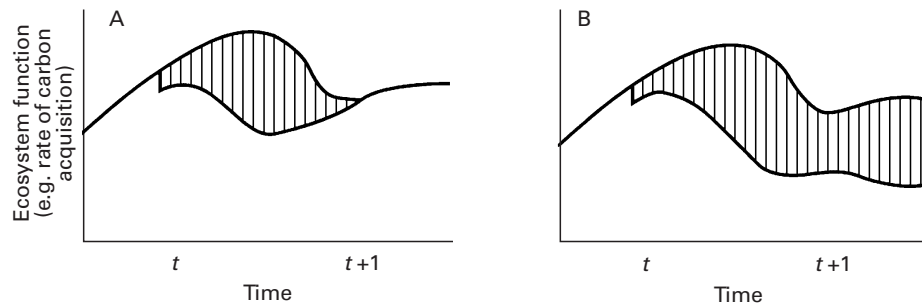


Fig. 2. Cost of disturbance (e.g. an extinction event) to a dynamic system. Two cases are illustrated. In A, the system has recovered from a perturbation which occurred at time  $t$  to its normal functional trajectory (net ecosystem productivity *NEP* or change in biomass) by time  $t+1$ . The interval between  $t$  and  $t+1$  is the 'relaxation time' for the ecosystem after perturbation. Cost (area of the shaded region) is determined by the function describing the pattern of relaxation, which itself depends on the cumulative compensatory responses throughout the community. In B, the system features insufficient redundancy to be resilient to the event, and the cost perpetuates through time.

as shown in Fig. 2. Thus, the cumulative functioning of and niche adjustment within dynamic systems are tangible and can be observed, regardless of the number and complexity of interaction networks. Quantification of interspecific redundancy and its influence on ecosystem function is therefore theoretically plausible for a given perturbation of a system, meaning that the capability exists for quantitatively testing *a priori* hypotheses about relative redundancy in ecosystems.

## (2) A cost of extinction

Prudent conservation requires gaining the most reliable knowledge (*sensu* Romesburg, 1981) possible about the likely impacts of hypothesized or impending events. For the purpose of modelling the risk posed to an ecosystem by a change in the abundance of a species (including an extinction), some measure of impact or 'cost' of the event is useful. Mathematically analyzing the long-term change in the functional trajectory of a dynamic ecosystem caused by a perturbation in relation to the system's resilience will help clarify how the net effects of compensatory interactions can be considered to be deterministic and tangible, ecological complexity (i.e. indeterminacy of the Jacobian matrix imparted by indirect interactions, *sensu* Yodzis, 1989, 1995; Abrams *et al.*, 1995; see also McCann *et al.*, 1998) notwithstanding. Derivation of a working, general mathematical expression for this purpose has not been presented in other papers, largely because modelling ecosystem dynamics in relation to diversity has only been approached from other perspectives. Often, species richness or species composition itself, rather than the compensatory interactions constituting redundancy

as defined here, has been evaluated as the variable determining ecosystem function (e.g. Tilman & Downing, 1994; Tilman, 1996; Naeem and Li, 1997, 1998; Tilman *et al.*, 1997b; Doak *et al.*, 1998; Tilman *et al.*, 1998). Ecologists who have tried to analyze ecological redundancy have not distinguished between changes in the functioning of ecosystems in response to perturbation (where compensatory interactions are potentially observable) *versus* temporal changes in the functioning of unperturbed systems (which are considered here to equate to changes in background conditions for biotic interactions, rather than deviations from ground state) (Walker, 1992, 1995; Lawton & Brown, 1993; Lawton, 1994; Naeem, 1998). This is true even for ecologists proposing to discuss redundancy in the context of ecosystem resilience (Walker, 1992, 1995; Ehrlich and Walker, 1998; Naeem, 1998). For example, although Walker (1992, p. 20) originally suggested that ecosystems with relatively high redundancy should be more resilient to disturbance, he specified that: 'Resilience in this context is taken to be the capacity of the ecosystem to maintain its characteristic patterns and rates of processes (such as primary productivity, allocation of photosynthate, surface hydrology, energy exchange, nutrient cycling, herbivory, *etc.*) in response to variability in its climatic regime' (*italics added*).

This definition differs from the more rigorous definition used by Holling (1973), Webster *et al.* (1974), and Smedes & Hurd (1981) in the context of actual perturbation-induced deflection from ground state. Holling (1973) and Webster *et al.* (1974) define resilience of an ecosystem as the rate of recovery to ground state following disturbance. The other, more contemporary treatments of resilience (Walker,

1992, 1995; Tilman & Downing, 1994; Ehrlich and Walker, 1998; Covich *et al.*, 1999) potentially dilute the rigour of stability analysis by confusing the concepts of temporal variability of dynamic systems with *bona fide* perturbation from ground state (Johnson *et al.*, 1996). Failing to distinguish between these two forms of variation precludes using ground state as a reference for measuring ecosystem stability because ecosystems are inherently variable to begin with. So, no tenable measurement standard will exist with which to determine resilience. This may be one reason why more progress has not been made in evaluating redundancy as a driver of ecosystem resilience in spite of increased research into biodiversity and ecosystem function. Walker (1992, 1995) and others may have glimpsed the importance of redundancy for modelling ecosystem sustainability, but have not discussed ecosystem resilience in the proper context of rigorous stability analysis as initially brought from the discipline of particle physics into the field of ecosystem ecology (e.g. Holling, 1973; Webster *et al.*, 1974; see also Smedes & Hurd, 1981). This potentially confuses the study of ecosystem stability in general and weakens the specificity of the concept of resilience. Furthermore, ecologists have defined redundancy either as a simple, qualitative, system-wide, curvilinear pattern showing a saturating effect of species number on ecosystem function (Lawton, 1994; McGrady Steed *et al.*, 1997), or as an all-or-none, absolute state of functional equivalence among species in which removal of a species has no significant effect on system functioning (Lawton & Brown, 1993; Tilman & Downing, 1994; Gitay *et al.*, 1996; Navarette & Menge, 1996; Ghilarov, 1998; Covich *et al.*, 1999). Naeem (1998, pp. 41–42) simultaneously perpetuated both of these contradictory viewpoints. All previous treatments of redundancy have also considered it to be a static property, rather than one that responds to changes in alterations of the environment shaping biotic interactions (e.g. Tilman & Downing, 1994; Naeem & Li, 1997, 1998; Naeem, 1998; Ehrlich & Walker, 1998). While these other, recent discussions have stimulated constructive debate (see especially Johnson *et al.*, 1996; Huston, 1997; Hodgson *et al.*, 1998; Loreau, 1998*a, b*; and Lawton *et al.*, 1998), the various interpretations of resilience and redundancy have thus limited the effectiveness of modelling biodiversity–ecosystem function relations. (These limitations will be examined further in Section VI.) Indeed, Ghilarov (1998) declared that no observations or modelling strategies published to date offer any successful means truly to

quantify functional redundancy *versus* functional diversity, adding that redundancy itself should therefore be considered a dead-end topic for ecological modellers. My explicit, mechanistic focus here on genuine compensatory niche adjustments as the definition of redundancy and which, in aggregate, determine a perturbed ecosystem's ability to recover to baseline functional trajectory (resilience *sensu* Holling, 1973; Webster *et al.*, 1974) establishes the uniquely effective context for successfully defining a precise expression for a cost of perturbing a dynamic system.

The result of a change in ecosystem function caused by a perturbation, denoted 'C', can be quantified as the difference between the trajectories of ecosystem function along the interval  $t, t+n$  after disturbance:

$$C = \int_t^{t+n} dA' - \int_t^{t+n} dA, \quad (8)$$

as illustrated in Fig. 2.  $C$  is a measure of the cumulative difference in  $NEP$  in units of biomass or calories between perturbed and ground-state trajectories of ecosystem function. The graphical examples (Fig. 2) illustrate the importance of differentiating relative redundancy. The long-term change in ecosystem function will be greatest where the system is characterized by relatively low redundancy, making it the least resilient to the disturbance event. Note that  $C$  need not be negative, as a perturbation could result in an increase in ecosystem function under certain circumstances, discussed later (Section V.4).  $C$  can be multiplied by a monetary constant representing the per unit market value of the commodity so as to gauge the financial impact of the perturbation in real numerical units for straightforward communication to economists. Thus, the cost of perturbing a functioning, dynamic system can be modelled and empirically measured as a deterministic result of cumulative, compensatory niche shifts, which themselves can be observed. That is, ecosystem resilience is a deterministic result sensitive to the initial condition of functional niche overlap among biota. The functional niche overlap programming compensatory niche shifts, in turn, is determined simultaneously by diet overlap and competition intensity (see also Johnson *et al.*, 1996). This potentially is a considerable step forward in demystifying the functional dynamics of ecosystems. Anticipating when, where, and to what relative degrees such niche shifts can be expected is the next step toward improved modelling of biodiversity–ecosystem function relations.



### (3) Gaining predictability

The analysis so far has provided a treatment of species' functional niches and interspecific functional compensation showing how functional redundancy arises from diet overlap among competitors, and how redundancy determines ecosystem resilience to disturbances which alter relative species composition. Continuing on towards a predictive theory of functional redundancy calls for formalizing expectations about when and where diet overlap among competitors will show up in trophic dynamics.

Ulanowicz (1980, 1995*a, b*), building on the work of Rutledge *et al.* (1976), has formulated a modern analytical articulation of Lindeman's (1942) trophic-dynamic synthesis based on network analysis. Network analysis provides a framework for modelling exchanges of currency throughout a producer-consumer hierarchy. Energy is the currency of exchange in the commerce of trophic systems. And, since energy also generally functions as a currency of ecological fitness (Schoener, 1971), efficiencies of energetic acquisition lend evolutionary significance to food web commerce. Ulanowicz's (1980, 1995*a, b*) analyses help to formalize expectations about the evolution of trophic generalism and specialization, *ala* Lindeman (1942). Trophic generalism is the means by which species make adaptive niche shifts in the community setting, so the conditions giving rise to the evolution of generalism among coexisting species implicitly will be those that spawn redundancy. Here, I adapt the network-analysis framework in developing a probabilistic model of when and where functional redundancy should arise in ecosystems. Specifically, I present modifications to make trophic network analysis explicit to *NEP* and its resilience, and conceptually reevaluate the previously phenomenological analysis in more mechanistic terms of the co-evolution of species' functional niches and density dependence in dynamic ecosystems. I have conserved the original notation where it does not conflict with that of other equations above and the reader is encouraged to review the sources referenced.

Consider a transfer of currency between donor  $i$  and consumer  $j$ , denoted  $T_{ij}$ . In the context of trophic dynamics, this represents a transfer of energy between resource  $i$  and consumer  $j$ .  $T_{ij}$  is therefore a special case of  $v_j$  where the relevant ecosystem attribute to which  $j$  contributes explicitly involves the acquisition and processing of energetic currency. Resource acquisition by community component  $j$  increases its biomass, at least instantaneously (*vis-à-*

*vis* Ulanowicz 1995*b*); the energy transfer may or may not notably increase  $j$ 's metabolism, as well. Thus, change in biomass can be used as an indicator of energy exchange. Import of energy from sources conventionally considered exogenous, such as sunlight, is denoted  $T_{0j}$ , and system export is  $T_{i0}$ . The summary of all such energy transfers is the cumulative network exchange  $T$ , where

$$T = \sum_i \sum_j T_{ij} \quad (9)$$

(Ulanowicz, 1995*b*). If energy transfer is quantified, such as by scaling  $T$  to caloric content,  $T$  will relate directly to community biomass, and  $dT/dt$  indicates net ecosystem productivity. Ulanowicz (1995*b*) has asserted that  $T$  and consequently *NEP* can increase with no instantaneous changes in biomass at intermediate consumer levels when top consumers increase their rates of consumption in response to population growth of the intermediate consumers. However, such an interpretation violates biological first principles and the stringent assumption of network flow analysis (Rutledge *et al.*, 1976) that transfer of energy between consumer level occurs in discrete steps. (Where this assumption is violated, the quantitative probabilities ascribed to resource transfers between particular trophic agents – discussed below – may not be attributed directly to generalist-*versus*-specialist life-history differences between consumers. They may, for instance, reflect differences in 'how hungry' individuals are at any instant, and may depend partly on random chance in sampling.) The contention that there is no relevant time lag for the functional responses of top consumers (Ulanowicz, 1995*b*) is rather dubious, and supportive observations are probably artefacts of too infrequent or imprecise sampling to satisfy thoroughly the scaling assumptions underlying the application of network analysis to trophic flow. The energy must go somewhere in order for  $T$  to change. Long-term *NEP* can be presented as the cumulative sequential throughput over  $z$  periods,

$$NEP_z = \sum_z T. \quad (10)$$

The functional contribution of  $j$  ( $F_j$ ) to overall ecosystem functioning through time relates to  $T_{ij}$  such that

$$NEP_z = \sum_z T = \sum_i \sum_j (T_{ij}) = \sum_j F_j. \quad (11)$$

By equation (11),  $F_j$  is now a representation of  $j$ 's functional role in the energetics of the ecosystem which explicitly addresses consumption of each of  $i$

resources. That is,  $F_j$  now relates to the realized foraging niche as depicted in Fig. 1. Recall that  $F_j$  alone will not provide information about the functional uniqueness of  $j$  because it does not explicate the potential for interpopulation compensation (that is, it does not address overlap with other niches and the intensity of competition). The shifting of  $j$ 's functional niche within a dynamic system is shown by recasting equation (5):

$$s_j = |F_j - F'_j|. \quad (12)$$

Actual interpopulation compensation will depend on the intensity of response to a change in a sympatric population and will terminate at equilibrium. The functional compensation response will be most straightforward in the case of pure exploitative competition, with the rate of compensation  $dF'_j/dt$  determined by the strength of resource limitation (density dependence) on the responding population.

The degree to which exploitation interactions characterize a system will depend on the abilities of different consumers to sequester the same resources, in addition to resource limitation. The conditional probability that a quantum of energy ( $Q$ ) will enter consumer  $j$  from resource  $i$  is given as

$$Q_{ij} = T_{ij} / \sum_k T_{kj}, \quad (13)$$

for all resources,  $k$  (Ulanowicz, 1995b). The aggregation of all  $k$  probabilities that particular resources will be consumed by respective particular species of a total of  $l$  consumers (i.e. specialist foraging),  $I$ , is a standard measure of information

$$I = \sum_i \sum_j (T_{ij}/T) \log (T_{ij}T / \sum_k T_{kj} \sum_l T_{il}). \quad (14)$$

There is a general pattern apparent in the ways that specificity in resource use and community-wide energetics change together through succession. The developmental stage of the system ( $D$ ) in terms both of specificity in consumption vectors ( $I$ ) and in total energetic throughput ( $T$ ) is given by the equality

$$D = I \times T. \quad (15)$$

$D$  is expected to increase as the links between consumers and resources become increasingly specific (increasing  $I$ ), improving total energetic efficiency in the food web (increasing  $T$ ), throughout succession. Ulanowicz (1980, 1989, 1995b) suggestively calls this 'system ascendancy' in ref-

erence to a presumed general tendency toward self-organization in ecosystems after disturbance. The successional pattern toward increasing  $D$ , particularly in donor-controlled systems, is congruent with the theories of Odum (1969, 1985), Odum, Flinn & Franz (1979) and Grime (1974, 1979) on ecosystem development and is supported by a body of observation (e.g. Grant & Grant, 1993, Prach, Pysek & Smilauer, 1997; see also MacGillivray & Grime, 1995 and Dall & Cuthill, 1997). This hypothesized pattern makes evolutionary sense in so far as specialization at any scale is a deterministic process. Where donor control is weak or unimportant, different system-wide patterns of trophic specialization may result, depending on how trophic niche evolution tracks selection for other life-history aspects such as habitat affinity or mate choice.

Obviously, the potential for growth in ecosystems is finite, and resources may even be leached from a system as background conditions for energetic commerce change. For a given set of conditions,  $D$  will be limited by the upper bounds on  $I$  and  $T$ , where

$$I_{\max} = - \sum_i \sum_j (T_{ij}/T) \log (T_{ij}/T), \quad (16)$$

and where inputs and physiological constraints limit  $T$  (Ulanowicz, 1995b). Respiration losses ( $S$ ) throughout the system are expressed as the quantity

$$S = - T \sum_i r_i Q_i \log Q_i, \quad (17)$$

where  $r_i$  indicates the fraction of  $Q_i$  lost through respiration. Export ( $E$ ) of currency from the system, such as through harvest and removal, is the cumulative extractions  $q_{ie}$  such that

$$E = - T \sum_i q_{ie} Q_i \log Q_i. \quad (18)$$

The cumulative ambiguity in resource-consumer connections, or community-wide niche overlap among competitors,  $R$ , is the equality

$$R = - T \sum_i \sum_j q_{ij} Q_i \log [q_{ij} Q_i / (\sum_k q_{kj} Q_k)]; \quad (19)$$

this quantity has been considered an expression of system-wide trophic redundancy (Ulanowicz, 1980 *sensu* Rutledge *et al.*, 1976).  $R$  works as a measure of actual redundancy because it reflects both similarity in resource-acquisition capability and density-dependent pressure between competitors, based on the probable trophic destination of resource units:

as exploitation increases in intensity, ambiguity in trophic destination will likewise increase. This extends previous interpretations of  $R$  as a phenomenological expression of ambiguity in network exchange (Rutledge *et al.*, 1976; Ulanowicz, 1980) into the more mechanistic context of competition-induced trophic (i.e. functional) compensability. Together,  $S$ ,  $E$ , and  $R$  represent the biological constraints of commerce on  $T$ .

Overall system capacity is quantified as  $\Omega = I_{\max} T$ , where  $\Omega \geq D \geq 0$ . The combination of all ambiguities of connection (i.e. niche overlap among competitors) and impediments to flow ( $S$ ,  $E$ , and  $R$ ),  $\Phi$ , is the quantity

$$\Phi = \Omega - D. \quad (20)$$

$\Phi$ , called the ‘system overhead’ (Ulanowicz, 1995*b*), will approach zero as the system develops, but can never reach zero due in part to the inevitable costs of foraging, metabolism, and maintenance. Thus,  $\Phi$  is expected to be directly proportionate to the amount of community-wide trophic specialization characterizing the system and to  $C$  from equation (8), and inversely proportionate to both  $R$  and  $\Gamma$ . Please note that Ulanowicz (1980, 1986, 1989, 1995*a, b*) limited his treatment of redundancy in trophic dynamics to a variable responding to system development through evolutionary time after perturbation, rather than to a mechanism shaping ecosystem response to perturbation in real (ecological) time. This is important for interpreting the value of the analysis of redundancy presented here, which is the first analysis showing interpopulation compensation (species functional redundancy) as a mechanism of resilience to finite perturbation for dynamic ecosystems.

In addition to thermodynamic costs of living, two other interrelated limitations on the rate at which  $\Phi$  approaches zero occur at the level of (1) the individual and (2) the population. These are the rates of appearance and fixation of a new trait in an evolving population, respectively. New phenotypic traits originate from mutation in individuals. A behavioural trait may well be encoded by several genes comprised within a complex locus, or may otherwise be polygenic but heritable variability in behaviour must arise nonetheless at the level of the allele. The rate at which a successful new trait displaces alternative phenotypes in the population – a process dubbed ‘phyletic evolution’ by Simpson in 1944 – will depend on the strength of selection for the new strategy, relative to biological time. For the present discussion, I assume that the rate of appearance of new genes is basically arbitrary and

equivalent within populations or between populations in whatever systems are being considered. Recalling that the trait with which we are concerned in the context of redundancy is the strategy for acquiring energy, which itself generally limits fitness, the rate of phyletic evolution will depend most directly on the strength of resource limitation. The rate at which the system approaches its maximum ascendancy will likewise depend on the strength of resource limitation. Thus, resource limitation and environmental stochasticity (the latter of which resets ascendancy,  $D$ , toward zero by reducing the evolutionary incentive toward specialization) are both ecosystem legacies, as defined by Vogt *et al.* (1997), influencing the degree to which functional redundancy should emerge. Resource limitation begets redundancy by setting the stage for exploitative competition, but only when disturbance keeps food web commerce – and consequently the evolutionary playing field – sufficiently in the realm of stochasticity to thwart consumer specialization.

## V. GRAPHICAL REPRESENTATION AND DISCUSSION

An overriding goal of ecological modelling is to identify and investigate patterns appearing in nature to understand them better and to generate parsimonious expressions for communicating those ideas to others (Maynard Smith, 1968; Yodzis, 1989; Lawton, 1995; Lawton *et al.*, 1998). The analytical arguments regarding the dynamics of redundancy and resilience (equations 1–20) are graphically summarized, together with the concepts of evolution among and between trophic guilds discussed earlier, in a probabilistic framework for predicting the occurrence of relative functional redundancy in ecosystems (Fig. 3), hereafter referred to as the T-D model. The T-D model offers some qualitative predictions as to what relative degree species may be redundant, and therefore to what degree an ecosystem will be resilient to extinction, based on the mechanism of interspecific compensatory responses to disturbance.

It should be noted up front that the purpose of the T-D model (Fig. 3) is to link some of the general knowledge about the development of generalist *versus* specialist life histories in trophic hierarchy along successional gradients traceable to Lindeman (1942) with the expected resilience of ecosystems to disturbance as mechanistically driven by redundancy, *per* equations (1–20). The classic trophic pyramid is

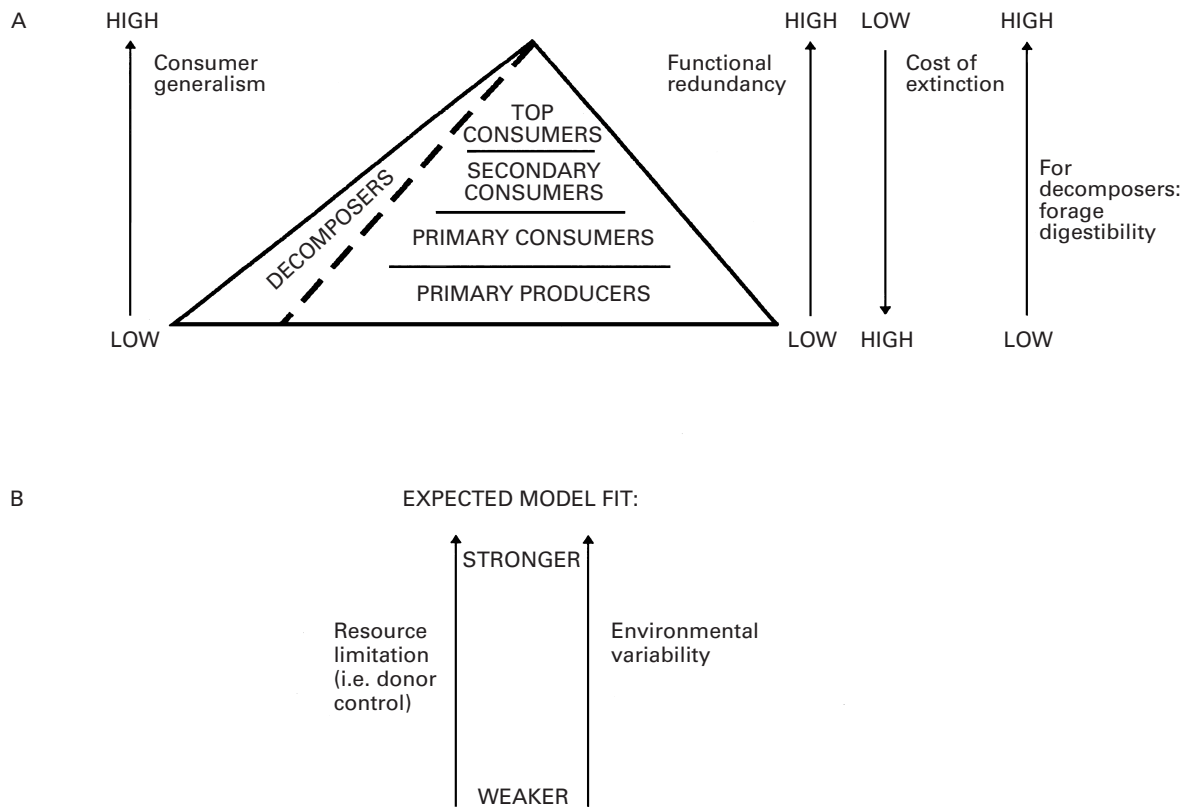


Fig. 3. A trophic–dynamic model of species diversity/ecosystem resilience relations, relative to species richness. The model focuses on productivity and considers consumer generalism as the mechanism generating functional niche shifts throughout the food web in response to environmental change caused by disturbance. The model suggests that niche shifts may predictably be compensatory (*i.e.* that they constitute ‘actual redundancy’ as defined in Section V.1) when they are driven by competition for consumable resources. Cost of perturbation is considered to be directly and inversely related to net compensation, *i.e.* system-wide redundancy. Redundancy is modelled at different trophic levels because the environmental influences on the evolution of resource–acquisition strategies can be shown to operate at the level of the trophic guild; diversity–stability correlations have previously been found to vary with trophic level. Based on existing knowledge about how metabolic energy demands and costs of foraging tend to increase with trophic position, specialization is suggested to progress from lower to higher trophic levels in the simplest scenarios; the predictability of system-wide patterns is discussed in Sections II.3 and V.1. The influence of environmental stochasticity and resource limitation (*i.e.* donor control) on life-history evolution is represented by the arrows in B, which addresses how well part A of the model will fit a particular case in nature. For instance, where environmental stochasticity and donor control are both high throughout the system, the simple relationship depicted in A is most likely because the evolution of consumer generalism among competitors is most predictable and should be strongest among top predators because of their higher energetic demands, *sensu* Lindeman (1942). Rigorous, precisely quantitative examination of specific relationships for particular systems is possible, as shown in Section IV. The graphical model here is intended as a general reference point for refining hypotheses for particular situations.

used as a starting point for graphically discussing the development and consequences of functional redundancy within and between trophic guilds (Fig. 3A). In addition, the environmental conditions (namely, environmental heterogeneity and the relative importance of resource limitation on population and evolutionary trajectories) influencing how and why different patterns may be predicted for different systems are addressed as part of the model (Fig. 3B). The T-D model serves as a framework for generating specific predictions about the system-wide effects of

alterations of species’ relative abundances on the functioning of ecosystems over time because it is based on the mechanism of functional compensability among biota as fostered by relative trophic generalism (equations 1–20). As long as the trends in trophic generalism and specialization as influenced by biotic interactions and the environment gleaned from past ecological research (discussed in Section II.3) may be valid, presenting the implications of generalist *versus* specialist behaviour on the functional dynamics of whole systems (equations 1–20) in



the form of the classic trophic pyramid is defensible. The T-D model should therefore serve ecologists as a helpful – albeit reductionist – framework for formulating hypotheses for testing with experiments, based on generalist *versus* specialist life histories as influences on whole-system dynamics. The mechanistic focus on generalist *versus* specialist behaviour as determinants of redundancy conveyed by the T-D model (Fig. 3) can demystify the manifestation of functional compensation because individual behaviours can be directly measured for experimentation. In the context of productivity, foraging is the relevant behaviour and functional niche adjustment equates to change in net diet, or trophic niche adjustment.

### (1) Trophic hierarchy, environmental influences, and interpopulation compensability

The ability of a species to expand its trophic niche to help compensate for an extinction or reduction in the abundance of a competitor depends on the degree of behavioural plasticity (as it ultimately affects diet plasticity) possessed by the compensating species; niche plasticity for the species will depend first on plasticity in individuals' behaviours. Resource-acquisition strategies of individuals consequently are considered the origin of redundancy. Where a high degree of functional redundancy exists, species will be relatively substitutable in terms of maintaining ecosystem function (Walker, 1992, 1995; Frost *et al.*, 1995). Redundancy among coexisting specialists should be relatively low, as demonstrated with the analysis (equations 1–20). Trophic position may influence the co-evolution of generalist *versus* specialist guilds in a predictable direction, with adaptive generalism likely to prevail increasingly as trophic position increases in many situations (May, 1974, pp. 6–7; Morin, 1995).

Specialization within any one level should increase with successional time. Extreme stochasticity would be characterized by complete uncertainty about dynamics of resources for a given trophic level. Food limitation and environmental variability together make up evolutionary legacies of ecosystems which constrain the approach of  $\Phi$  (system overhead) to zero because they constrain the co-evolution of ecological specialization. As both food limitation and environmental stochasticity increase, the intensity of exploitative competition increases, but the opportunity for specialization decreases because particular resource abundances become unpredict-

able. This situation maximizes redundancy by simultaneously maximizing diet overlap and the intensity of exploitation. Conversely, the predictability of the approach of  $\Phi$  to zero will be minimized where food limitation and stochasticity are both negligible (specialization for life-history attributes other than simple trophic resource acquisition strategy may occur, with the formula complicated by the necessary consideration of what other attributes limit fitness).  $\Phi$  which is inversely related to  $R$  (actual redundancy), therefore becomes a measure of the combined effects of resource limitation and stochasticity legacies on system-wide interspecific redundancy. In reality, resource limitation may well vary inversely or independently of stochasticity, and most systems will probably fall on a continuum between these extremes for  $\Phi$ .

The T-D model accommodates situations in which natural selection operates primarily on life-history attributes other than foraging strategies. This is important because generalist/specialist affinities can develop for resources other than food. An example would include a scenario in which the factor in the environment most limiting to fitness is heterogeneity in the structure or spatial arrangement of physical habitat. Food might not be limiting. Organisms may develop generalist habitat affinities without having generalist diets. If food limitation is less important in the development of evolutionary trajectories than other such influences, the development of generalist life histories may or may not generate trophic generalism. Moreover, it is also possible that coexisting populations which do not interact would exhibit no functional compensation following disturbance because there would be no competition-induced response related to a population change. Generalist foragers, then, with overlapping diets might exhibit no actual redundancy. This could occur, for example, in the density-independent conditions of initial colonization of an empty system where neither food nor space limit population growth. Thus, the presence of environmental heterogeneity favours natural selection for generalist life histories, and this generalism manifests directly as trophic generalism and predictably generates higher probabilities of trophic niche overlap (i.e. actual redundancy) when food availability is the critical limiting factor in the environment. The predominance of these two environmental factors – environmental unpredictability and food limitation – together makes the development of functional compensability predictable; redundancy may develop in heterogeneous environments in which food limitation

is relatively weak, but its occurrence becomes less predictable. In this sense, the T-D model (Fig. 3) is intended to be considered general and probabilistic.

The greater the actual redundancy within a trophic level or guild, the more thoroughly will be recovery of guild – and, therefore, of ecosystem – functioning to normal levels after disturbance. Both the effect of species richness on ecosystem resilience and the likelihood of achieving an alternative functional state (but not an alternative species composition in terms of relative abundances) should thus decrease as consumer generalism predominates. This is to suggest that exploitation interactions, which contribute to food web complexity because their effects are indirect and therefore render the community projection matrix indeterminate (Abrams *et al.*, 1995; Yodzis, 1995), should actually improve the predictability of ecosystem responses to disturbance in two ways. First, relative rates of recovery of ecosystem function will show a positive relationship with redundancy. Second, because redundancy reflects the ability of species to coexist in the face of exploitation through niche adjustment, persistence of suites of species after any single disturbance should correlate positively with redundancy. A ramification of this second notion is that cascading extinctions from the disturbance-induced alteration of background conditions shaping community interactions are more likely where ecosystem resilience is low, as originally suggested by Ehrlich & Ehrlich (1981) and Walker (1992). This is especially intuitive where an initial decrease in *NEP* – which necessarily equates to a removal of energetic quanta from trophic flow – results in an increase in export (*E*) from the system, such as through erosion. If the new system trajectory at dynamic equilibrium is lower than the previous one, it may be that the decrease in system capacity places some additional populations at increased extinction risk.

The T-D model (Fig. 3) suggests that the co-evolution of resource-acquisition strategies is observable at the scale of individual trophic guilds and that the hierarchical relationships between specialization and redundancy will vary depending on environmental conditions as they shape food web interactions. Huston (1994) has observed that interspecific density dependence may indeed vary according to trophic hierarchy, but suggests that its importance may decrease rather than increase with trophic level as a general rule (Huston, 1994, p. 151). This is why it is important to consider the bottom part of the diagram (Fig. 3B). The hierarchical pattern toward increasing generalism,

redundancy, and functional resilience detailed in the top part of the T-D model (Fig. 3A) will be most obvious in a system with both extremely strong food limitation and stochasticity. Conversely, the pattern should be weakest in a community long at equilibrium and in which, for example, top consumers mediate exploitative interactions among their prey. That is, comprehensive top-down regulation (*versus* donor control; Hunter & Price, 1992; Morin & Lawler, 1995) could eliminate the expression of redundancy at intermediate or low trophic levels if food competition there is suppressed to where it no longer regulates those populations. Mutualisms that dilute exploitative competition, such as mycorrhizal symbioses in some mixed species stands of trees (Perry, Bell & Amaranthus, 1992; Johnson *et al.*, 1996), would have the same effect. Where exploitative competition varies inversely with trophic position, specialization (and ultimately redundancy) may likewise vary inversely with trophic position. The exceptional case of black-footed ferrets and prairie dogs discussed earlier involves specialist predation on a generalist herbivore; these life histories reflect the higher degree of resource variability shaping prairie dog foraging evolution in comparison to its predator. This emphasizes an important point: the T-D model should not be misinterpreted as predicting primarily that generalism and redundancy increase with trophic position. It does not. In different systems, environmental heterogeneity may be more of an influence directing selection toward generalism at lower or middle rather than higher trophic levels. Moreover, the availability of consumable resources (in contrast to direct competition, habitat availability, etc.) may not limit the dynamics of top predators' populations as much as it limits those of prey populations in some situations, as already discussed. The case of black-footed ferrets and prairie dogs is offered as an example of such a situation. The consideration of the environmental influences of heterogeneity and resource limitation on life-history evolution as explained above conforms with proper application of the T-D model. The important questions for ecologists are how and why do patterns of generalism and redundancy in trophic hierarchy vary within and between systems, which can be addressed using Fig. 3B. Biodiversity–ecosystem function research has never before been distilled to these mechanistic questions; this refined focus here stems from concentrating on the mechanisms generating functional niche shifts. In the analysis above, the influences of environmental heterogeneity and resource limitation

together on life-history evolution and functional dynamics throughout an ecosystem have been evaluated to the extent that  $\Phi$  can be shown to differ from zero (equation 20), so their combined effects are definite and can actually be measured. And, where quantitative rigour is not the primary modelling objective, ecologists may find more qualitative, general treatments of these factors sufficient to direct the development of hypotheses for experimental testing. So, too, may ecologists use what is already known about trophic hierarchy as an influence on biotic interactions to justify studying relative generalism and redundancy at different trophic levels. Despite these caveats, it remains noteworthy that many ecologists have observed that specialization commonly varies inversely with trophic position, as indicated in Fig. 3A alone (e.g. Lindeman, 1942; May, 1974; Hairston & Hairston, 1993; see also Morin, 1995). Consequently, the top part of the model (Fig. 3A) should serve nonetheless as a useful starting point in general for modelling redundancy.

## (2) How appropriate are trophic level distinctions?

The simple rendering of trophic level progression from primary producers up to top consumers (e.g. Lindeman, 1942) is known as a classic topological food web. Topological food webs have begun to fall somewhat out of fashion in favour of a true web approach showing cross-connections and internal cycling loops (Winemiller & Polis, 1995). Intraguild predation and cannibalism form two obvious internal cycling pathways. A consensus among ecologists as to the prevalence of such loops in nature has long been sought but has not been reached. Pimm (1982) and May (1983) examined published food webs and concluded that such loops are exceedingly rare, especially in large food webs (see also discussions by Polis, 1995 and Ulanowicz, 1995a). More recently, Polis (1995) has taken particular exception to this purported rarity, contending that internal loops and multi-level foraging are quite common in desert food webs. Intraguild predation also occurs in many other systems (Johansson, 1993; Lindstrom *et al.*, 1995; Palomares *et al.*, 1995; see also Holt & Polis, 1997). To accommodate such trophic ambiguities, the T-D model has been drawn with incomplete and perforated lines between trophic guilds (Fig. 3). Recall, however, that a genuine distinction in diversity-stability relations between trophic guilds congruent

with classic topological hierarchy was observed in the historic New York old-field studies reviewed above.

## (3) Decomposers

Decomposers are important to trophic dynamics and should not be neglected in biodiversity and ecosystem function studies (Wardle, Bonner & Nicholson, 1997). Detritivores have therefore been included in the T-D model, although not drawn to scale. Coleman *et al.* (1976) and Coleman (1995) found that detritivores accounted for at least 95 % of the net flow in several terrestrial ecosystems. Decomposers process detritus originating from all trophic levels, but specialization and niche partitioning can be found among their ranks, as well (Coleman, 1995). It can be postulated that specialization is more the ESS among detritivores where dead tissue is extremely difficult to digest. That is, tissue digestibility may constrain donor-controlled trophic dynamics. Woody and other plant tissues high in secondary compounds are among the most indigestible materials. Some detritivore specialization may be for particular species of plants with uniquely structured tissues, as with some species of *Lupinus* (L.) which biomagnify selenium. Tissue digestibility should increase with trophic position, especially in the transition between primary producers and herbivores. This is why animals decompose much more rapidly than wooden logs of equivalent size. And, because trophic ascension necessitates progressive decrease in caloric populations by virtue of the law of conservation of energy, opportunism would seem to be increasingly the ESS for associated decomposers. Decomposers are thus represented in the model (Fig. 3). The T-D model (Fig. 3) predicts some patterns of redundancy among decomposers without strict trophic compartmentalization, but detrital components of ecosystems can be described as mini-food webs with some topological similarities to the rest of Fig. 3 (e.g. Coleman, 1995).

## (4) 'Cost of extinction' qualifier: scaling to species richness

Before we can ask interesting questions about the implications of species diversity reductions, species have to be existing together in the first place. Thus, we are interested here in the phenomenon of differing relative cost of extinctions between guilds and, at a coarser scale, between different ecosystems.

Measuring relative costs of extinctions requires accounting for initial species richness differences between guilds or systems for comparison. ‘Cost’ in the T-D model (Fig. 3) is therefore relative to species richness, as is ‘redundancy’.

In cases where total system productivity might be suppressed as through strong top-down regulation (top-down override of donor control), it is feasible that cumulative niche adjustment after the reduction of such a consumer might exceed the magnitude of the disturbance, allowing post-disturbance productivity ( $NEP'$ ) to be higher than initial  $NEP$ . Therefore, the net result of an extinction can be either a positive or a negative change in  $NEP$ . Increases in  $NEP$  resulting from such alterations of the background conditions shaping trophic interactions can sometimes undermine long-term ecosystem sustainability (see Rosenzweig, 1971; Asner, Seastedt & Townsend, 1997) so deflection away from ground state remains the real economic concern in either case. ‘Cost’ in Fig. 3 therefore refers to the absolute value of  $C$  from equation (8), or the deflection of  $NEP$  from ground state, scaling to species richness.

## VI. SYNOPSIS: CONSIDERATIONS FOR FUTURE RESEARCH

The persistent theme of this paper is that focusing mechanistically on the interactions allowing biotic communities to compensate internally for population changes in terms of contributing to ecosystem function, or their intrinsic functional redundancy, can substantially improve the predictability of ecosystem responses to biodiversity alterations. Distinguishing functional redundancy from functional diversity is a necessary part of such a mechanistic approach, and itself requires successfully modelling biota's capacities to shift functional niches. In the preceding discussion, I have argued that by focusing on generalist resource acquisition as a hypothesized mechanism giving rise to functional redundancy, niche dynamics for biota should be measurable and some important aspects of their cumulative effects should be predictable even in complex systems. This viewpoint differs considerably from previously published works in that it explicitly recognizes that quantifying functional diversity requires clear differentiation of functional niches and that such rigorous differentiation is possible. Furthermore, demonstrating functional redundancy requires explicitly measuring compensatory niche

dynamics following perturbation in a properly designed experiment. While explicit hypothesis testing regarding functional niche dynamics is therefore plausible, these criteria have not yet been met in ecological experiments published to date. There remains much potential for improving the rigour of design and analyses of biodiversity–ecosystem function studies.

### (1) Elaboration on some specific limitations of previous research

Some progressive ecologists have recently attempted to link redundancy with ‘ecosystem reliability’ [*sic*] or predictability in experiments, measuring redundancy as the number of species present in a particular ‘functional group’ and the consistency of ecosystem function over time as the variable responding to different levels of redundancy (e.g. Naeem and Li, 1997, 1998; Naeem, 1998). There are two primary limitations to such treatments of redundancy, and both reflect differences among ecologists in interpretations of redundancy in relation to ecological stability, as mentioned above in Sections II and IV. First, assessing the effects of niche redundancy on system-wide dynamics is prohibitively problematic without first appreciating that actual perturbation is necessary before the compensatory niche shifts attributable to redundancy can be observed. In an important example, Naeem & Li (1997, 1998) assembled communities of microorganism species in microcosms in the laboratory. Variability of standing biomass was compared between unperturbed communities with more *versus* fewer species stocked *per* functional group. Naeem & Li (1997, 1998) concluded that species redundancy (which they synonymized with ‘ecological redundancy’) was shown to improve ecosystem reliability based on the observation that communities with more species per functional group were more consistent in terms of productivity than communities with fewer species per functional group. Perturbation was not included as an experimental manipulation, so communities were never pushed away from baseline conditions. Recalling the standards for rigorously measuring resilience (Holling, 1973; Webster *et al.*, 1974; see also Smedes & Hurd, 1981) already discussed, the conclusion by Naeem & Li (1997, 1998) that redundancy enhances reliability is incongruent with our present definition of redundancy as functional compensability. A system must be perturbed from ground state in order for recovery and hence compensation to be observed. Without a finite



perturbation to push system functioning away from an observed baseline, actual compensation cannot be determined to be the primary stabilizing attribute for the ecosystem. Therefore, the research focus was not on redundancy in the context of compensability. Alternative explanations for such results should be considered. One such possible explanation is that additional species indeed occupy new niche space but without the niche overlap necessary to generate compensation. That is, niches may be completely static and entirely complementary (*sensu* Frost *et al.*, 1995; Hooper & Vitousek, 1997, 1998; Hector, 1998; Hooper, 1998; Loreau, 1998*a, b*), as can occur in plant communities characterized by species with distinctly different phenologies or in the case of system-wide density independence in population dynamics (see Bazzaz, 1986; Johnson *et al.*, 1996). Also, it is clear that the experimental treatments in this case (Naeem & Li, 1997, 1998) basically created different communities characterized by different population dynamics and food web interactions – that is, the communities simply have different dynamical baseline trajectories for ecosystem performance. Intrinsic differences in the variabilities of unperturbed functional trajectories in these experiments (Naeem & Li, 1997, 1998) were compounded further by the fact that the experimental species assemblages never attained any form of equilibrium, including dynamic equilibrium, so the species failed to demonstrate any capacity for long-term coexistence. The most useful insights about the functional significance of biodiversity for real-world conservation will pertain to groups of species capable of coexisting and hence interacting in nature. Perturbing groups of coexisting species to study redundancy as compensability potentially offers improved experimental rigour through the delineation of baselines (control conditions) and hence observable resilience, as well as by making the hypothesized niche-shift mechanism driving resilience observable. These are the advantages of focusing on redundancy as *bona fide* functional compensability in contrast to varying interpretations deliberated by others and discussed above (Walker, 1992, 1995; Morin, 1995; Gitay *et al.*, 1996; Navarette & Menge, 1996; Naeem & Li, 1997, 1998; Ehrlich & Walker, 1998; Ghilarov, 1998; Naeem, 1998; Covich *et al.*, 1999; Yachi & Loreau, 1999).

The second overarching limitation involves the concept of the ‘functional group’ itself. There is considerable vagueness in the way the term is used today by ecologists. Walker (1992, 1995) suggested

lumping species together according to presumed functional similarities in order to approximate which species were most likely to share some redundancy: species from within the same functional group are expected to have a higher likelihood of exhibiting some redundancy than species from different functional groups. This approach implies that redundancy itself might be too abstract to measure in experiments and that a useful standard may exist for designating functional groupings (Walker, 1992, 1995). Subsequently, much discussion of biodiversity and ecosystem function relations has addressed species diversity in relation to numbers of functional groups present in a system (Hooper & Vitousek, 1997, 1998; Naeem & Li, 1997, 1998; Tilman *et al.*, 1997*a*; Hooper, 1998; Lawton *et al.*, 1998; Hodgson *et al.*, 1998; Naeem, 1998; Covich *et al.*, 1999). Unfortunately, designations of functional groupings have remained somewhat arbitrary (an observation with which Lawton *et al.*, 1998 agree – see p. 849) and are based subjectively on characteristics of organisms the researcher assumes to be pertinent; these assumptions typically are not discussed. Plants commonly are grouped according to whether or not they fix nitrogen, by growth form, or both (e.g. Chapin *et al.*, 1997; Hooper & Vitousek, 1997, 1998; Tilman *et al.*, 1997*a*; Hooper, 1998), while other types of organisms are grouped by presumed trophic level (e.g. Naeem & Li, 1997, 1998; Naeem, 1998; Covich *et al.*, 1999). The principal shortcoming of such functional designations is that these functional attributes may not necessarily relate to actual functional niches of organisms in the same context as the specified ecosystem-level measurement variable (conventionally productivity). Nitrogen fixers and non-nitrogen fixers may contribute equally or differently to *NEP* than the degree to which they contribute to nitrogen flux. Yet, productivity has typically served as the ecosystem-level response variable to diversity manipulations in these studies. Species might also exhibit complete compensability in terms of productivity even when grouped differently using the current loose standards. Or, as warned previously by Johnson *et al.* (1996), organisms or species with similar growth forms or from within the same trophic level may have entirely different, unique contributions to *NEP*. That is, biota from the same so-called functional group may be entirely functionally complementary (*sensu* Frost *et al.*, 1995; Hooper & Vitousek, 1997, 1998; Hector, 1998; Hooper, 1998; Loreau, 1998*a, b*) as might be expected with coexisting obligate specialists (as first suggested by Johnson *et al.*, 1996);

this would defeat the purpose of attempted functional grouping in the first place. Thus, functional classification based on subjectively chosen attributes without directly scaling to the ecosystem-level variable may confuse the context in which functional diversity and redundancy should be measured. An alternative is to group species according to relative similarities in their functional niches in the context of the ecosystem-level variable to be measured. For *NEP*, functional groupings should be based on net foraging niches (e.g. growth rate). Potentially related characteristics such as nitrogen-fixation capabilities and growth form may also be examined, but preferably not at the expense of a direct focus on the most directly pertinent measure of the functional niche.

## (2) Rivets *versus* redundancy

Previous discussions about species redundancy (e.g. the recent analytical suggestions of Naeem, 1998) typically have treated redundancy as a static or an instantaneous phenomenon. However, there may be value in considering redundancy to be a process of compensation which requires some time after a disturbance to become complete – an important premise of the present paper. Functional compensation requires time to occur even at the scale of individuals because a perception of change in the interaction environment precedes any potential response by the individual. An individual's response to a stimulus may then occur as behavioural/physiological change, perhaps altering the functional contribution of that individual to the entire system. At the population level, still more time should pass before the responses of individuals can aggregate into a mass population response. Therefore, a theoretical treatment of redundancy should address compensation as a response occurring over time as niche shifts accumulate to re-establish a functional baseline in dynamic equilibrium. The analysis presented above (equations 1–20, Figs 1 and 2) differs from previous theoretical treatments in accomplishing this objective.

The value of future biodiversity–ecosystem function studies, especially those intended to address functional compensability, should be enhanced hereafter by appropriately modelling disturbance-induced niche shifts in dynamical systems rather than drawing on suppositions about niche shifts in absence of perturbation. If rigour and quality are maintained, such studies should benefit ecology in general because functionally compensatory shifts

probably integrate the network of processes across scales which contribute to net ecosystem responses (Johnson *et al.*, 1996).

The study of unperturbed systems or of instantaneous phenomena associated with different levels of biodiversity – such as apparent trends in relationships between diversity and productivity or diversity and the intrinsic variability of dynamical systems (e.g. McGrady Steed *et al.*, 1997; Loreau, 1998a; Yachi & Loreau, 1999) – is not without importance. It is just that these phenomena relate more logically to the concept of ‘rivets’ in an ecosystem (*sensu* Ehrlich & Ehrlich, 1981 & Johnson *et al.*, 1996) than to *bona fide* stability issues such as redundancy in the context of functional compensation used here. The concept of species as rivets was introduced by Ehrlich and Ehrlich (1981), who stated that species effects on the sustainability of an ecosystem could be likened to rivets holding an aeroplane wing together: although loss of a few rivets might go unnoticed, removal of too many rivets could result in sudden collapse of the structure of the wing (or the system). Henceforth, the idea was called the rivet hypothesis (e.g. Lawton, 1994; Johnson *et al.*, 1996). Ehrlich and Ehrlich (1981, preface) used the term ‘redundant’ in describing the existence of rivets which were not immediately necessary to support the wing, so a connection existed between their idea and Walker's (1992) refined ‘redundancy hypothesis’. Only recently (Johnson *et al.*, 1996) were Ehrlich & Ehrlich (1981) recognized as contributing to the origin of the concept of ecological redundancy. Ehrlich & Ehrlich (1981) and Walker (1992, 1995) specified ecosystem ‘resilience’ as the attribute to which their ideas related. Ehrlich & Walker (1998) have now confirmed together that they consider the ideas to be homologous.

Limitations even with this conceptual linkage (rivets, redundancy, and resilience) exist if a naive standard for stability analysis is followed. If the concept of redundancy refers to the ability of biota to compensate functionally for alterations in the abundances of other biota (Walker, 1992, 1995; Johnson *et al.*, 1996; Ehrlich & Walker, 1998), and if the context for ecological function is any process which occurs over time (e.g. productivity), then the compensatory process itself must require time for the adjustments to occur, as explained earlier. The analogy of rivets in an aeroplane wing does not hold up in this sense because the ‘rivet effect’ is essentially an instantaneous shift of stress load onto remaining rivets until the structure of the wing fails entirely. Rivets cannot be taken to drive resilience because

the wing (or the system) remains intact until the structure begins to fail. True compensation in the context of processes through time cannot occur because the system has not been deflected from ground state – the ‘state’ of interest is simply the static position of the wing. The rivets may be structurally complementary to one another to varying degrees, but not functionally compensatory. The degree of structural complementarity declines as more rivets are added to support the same ‘wing’. Functional complementarity (also called ‘species singularity’ by Naeem, 1998, pp. 39, 42), in contrast to structural complementarity, remains a contextually valid concept relative to ecosystem function, but one for which rivets now appear to be a poor metaphor: the additive effects of various components of the biota to overall system function describes their respective unique functional niches (*sensu* Frost *et al.*, 1995; Hooper & Vitousek, 1997, 1998; Hector, 1998; Hooper, 1998; Loreau, 1998*a, b*). One might argue that this is a case of ‘splitting hairs’ in semantics because the ‘function’ of rivets is to support a structure additively, so rivets do perform ‘functions’; however, we are using a precise definition for ecosystem function here, and structural support does not fall within that context. Although important, discussions on the concept of redundancy in relation to rivets to date have not distinguished instantaneous effects of structural complementarity (rivet effects) from functional complementarity (i.e. species singularity or functional uniqueness), or from resilience-driving functional compensability (redundancy). Where resilience has been discussed in relation to redundancy, it is synonymized directly with the effect of structurally complementary rivets (e.g. Ehrlich & Walker, 1998; Naeem, 1998; Covich *et al.*, 1999). Distinguishing between the context of structural complementarity and functional complementarity, and between functional complementarity and functional compensability, is essential if ecologists are to examine the effects of biodiversity on the resilience of ecosystem function because the concepts are not necessarily synonymous or directly related. In as much as redundancy contributes to the resilience of ecosystem function, its effects cannot be likened to those of rivets in an aeroplane wing because rivets are not compensable in the context of ecosystem function. In so far as ‘rivets’ might stabilize a structure, they will not contribute to its functional resilience in the context of their own functions, unlike the way that functional niches of biota contribute to functional niches of ecosystems as suggested here. The effect of functional redundancy

in ecosystems is not a pattern. It is a process. It is possible to study structural complementarity outside the context of functional perturbation through time. Functional complementarity might also be studied in unperturbed systems, but will be most clearly discerned in perturbation studies as the inverse of functional redundancy. Functional redundancy in the context of ecosystem processes, however, cannot be studied in absence of perturbation, and will require time to manifest. Understanding these principals should help ecologists attempting to examine the hypothesized stabilizing effects of redundancy to know what to measure and how to interpret their results.

Mechanistic study of the functional resilience of ecosystems as logically and hypothetically driven by functional redundancy requires perturbation experiments in which it is possible to observe compensatory responses among biota. The generalists-*versus*-specialists approach to modelling the occurrence of compensatory interactions in dynamical systems advocated above applies first principles logic to modelling redundancy. Because of this foundation on these simple principles, the approach has merit for complex as well as simple systems: the processes it addresses relate to the well-known ecological processes of competition and natural selection, which operate to shape life histories predictably in all environmental settings. Essentially, the approach is to model the development and interactions of plasticity envelopes of functional niches in dynamical systems. The key (as analysed in Section IV) is to focus on modelling plasticity envelopes at two temporal scales: real time, in which the potential for compensation may be realized as a function of overlap among fundamental niches (depending on the strength of incentives driving the response potential); and evolutionary time, in which extreme bounds for the potential for plastic responses are delineated. The shifting of realized functional niches in response to perturbation-induced changes in the abundance of one or more neighbors will manifest in net compensability, i.e. resilience. Baseline functional trajectories alone of experimental systems can be compared without perturbing them to examine such aspects of biodiversity–ecosystem function relations as relative intrinsic functional variability (e.g. Tilman & Downing, 1994; Tilman, 1996; Naeem & Li, 1997, 1998; Tilman *et al.*, 1997*a, b*; Hooper, 1998; Hooper & Vitousek, 1997, 1998; Loreau, 1998*a*; Naeem, 1998; Yachi & Loreau, 1999), although such studies are less relevant to ecosystem sustainability under disturbance-inducing

human exploitation than direct investigations into functional resilience.

Rivets do not have evolving plasticity envelopes, but functioning biota do. The present paper advocates the effective modelling of overlap of those functional envelopes for niches as they exist at any given time and as they change in evolutionary time as a means of predicting compensability (the process depicted in equations 1–8), which itself can be likened more to the effect of shock absorbers on perturbed systems than to rivets. The approach need not be restricted to modelling of ecological systems only; it offers promise for improving the modelling of all dynamical systems characterized by consumers with potentials for interaction and adaptation, such as industrial/commercial economies.

### (3) Criteria for measuring redundancy

Successfully modelling ecological redundancy promises to improve the predictability of the functional dynamics of ecosystems. In science, the most successful models tend to be based on mechanistic understanding of phenomena. This mechanistic understanding is developed through a process involving several steps, each progressing toward a more reliable knowledge (*sensu* Romesburg, 1981). Phenomena are identified, ideas about the underlying causes of those phenomena are suggested based on apparent patterns of relationships with other variables (inductive and retroductive reasoning), and those ideas are tested and refined through experiments until successful, mechanistic answers are achieved. This completed process is called hypothetico-deductive reasoning (see Romesburg, 1981 for further discussion about science philosophy and procedure and its application in species conservation). Hypothetico-deductive reasoning generates reliable knowledge in the sense that it generates a tangible, quantitative confidence interval around an experimentally derived conclusion explaining a phenomenon. That confidence interval cannot be generated without replication of experimental units so as to quantify the variance about the mean response. As discussed throughout this paper, a reliable, mechanistic knowledge of biodiversity–ecosystem function relations has not yet been achieved. Research in the field has not yet yielded mechanistic hypotheses capable of successfully explaining widely varying and anomalous observations about the functional significance of biodiversity (Ghilarov, 1998; Lawton *et al.*, 1998; Loreau, 1998a; Yachi & Loreau, 1999). The

development of mechanistic insights has been hampered in part by inconsistencies in use of terms and interpretations of concepts such as redundancy and resilience described above. Without mechanistic direction, it seems unlikely that ecological experiments will be designed properly for developing truly reliable knowledge about the origins and implications of functional redundancy. Above, I have reviewed various semantics and approaches characterizing research on the topic to date, presented arguments for adopting refined definitions of terms, and presented a trophic–dynamic-based, mechanistic framework to direct hypothesis generation for future experiments. Ecological knowledge should benefit from shifting research toward examining how generalist life histories influence potential and actual functional niche overlap and how that overlap influences functional resilience among and between different trophic levels and under different environmental conditions. A new appreciation of functional uniqueness *versus* functional compensability among biota will be critically important to such progress.

Given the tangle of concepts now characterizing the integrative field of biodiversity–ecosystem function science and the resulting necessarily broad, often reiterative aspect of the review and ideas presented above, a reminder of the key criteria to be addressed in experimental resolution of the effects of functional redundancy in ecosystems should be helpful. The five specific criteria summarized below with brief rationales are suggested as a standard for achieving rigour in studying the effects of functional redundancy in ecological communities:

(1) *Demonstrated potential for sustained coexistence among species in the community being studied. Rationale:* combining species into experimental communities without consideration of their capability to coexist and therefore interact over time (e.g. Naeem *et al.*, 1994; Naeem & Li, 1997, 1998; Tilman *et al.*, 1997a) does not necessarily create a sustainable ecosystem capable of representing any attributes of real systems in nature, which are the targets of biodiversity conservation in the first place. Species must be capable of interacting for compensation (i.e. functional redundancy) to be observed, or even to occur. An unstable assemblage of species (e.g. Naeem & Li, 1997, 1998) is open to density-independent influences on population dynamics precluding any unequivocal study of compensatory niche dynamics, regardless of whether or not those communities are replicated. In dynamical systems, such as ecosystems in fluctuating environments, this capability for



sustained coexistence manifests as the persistence of species even as their abundances may fluctuate and constitutes dynamic equilibrium.

(2) *Functional niches of biota must actually be measured – and this means in the same functional units as the chosen ecosystem-level response variable – before it is possible to contrast the effects of functional diversity with functional redundancy. Rationale:* directional, prediction-based hypothesis testing – which is required to generate reliable knowledge through hypothetico-deductive science – about compensatory functional niche dynamics is not possible without first delineating the functional niches of biota in experimental communities. Abstracting the study of functional niche dynamics to the simplified ‘functional group’ approach (e.g. Hooper & Vitousek, 1997, 1998; Naeem & Li, 1997, 1998; Tilman *et al.*, 1997a; Hooper, 1998; Lawton *et al.*, 1998; Hodgson *et al.*, 1998; Naeem, 1998; Covich *et al.*, 1999) as initially recommended by Walker (1992, 1995) may have seemed at first to be a constructive suggestion, given the lack of guidelines then for obtaining more precise niche delineations. However, grouping species by growth form, trophic position, or other traits such as relative nitrogen-fixation capabilities without directly scaling to the context of the ecosystem-level measurement variable will not yield specific observations about functional niche shifts of individuals (and subsequently of populations). For example, if the ecosystem-level response variable is productivity, then the functional niches of biota need to be based on their growth rates; in the complex community setting, growth rates may or may not reflect other traits (such as nitrogen-fixation rates) presumed to characterize their functional role in the ecosystem. And, although measuring functional niches to achieve mechanistic resolution is potentially difficult, it can be accomplished by, for instance, measuring foraging behaviour, as discussed above.

(3) *A system must be perturbed in order for any compensatory response(s) to be observed. Rationale:* the functional resilience of an ecosystem can be ascertained only with reference to recovery to a ground state, and this requires first deflecting the system from that operational baseline. Studying unperturbed systems may facilitate identifying phenomenological patterns of biodiversity–ecosystem function relations, as different combinations of taxa may or may not yield different functional trajectories for the ecosystem. However, redundancy as a hypothetical contributor to resilience cannot be demonstrated unequivocally in unperturbed systems because everything that is observed about ecosystem

functioning occurs within that baseline. That is, compensatory interactions cannot be observed distinctly from, say, the effects of niche partitioning through phenology. Observations about variation in ecosystem function in response to changes in climate or nutrient loading (e.g. pollution) do not necessarily relate to redundancy effects because such ‘treatments’ are not perturbations. Rather, they are changes in background conditions determining the entire system’s functional baseline only. In the absence of perturbation treatments, observations about ecosystem responses simply do not relate to functional resilience and therefore do not demonstrate redundancy.

(4) *Post-disturbance niches must be measured to demonstrate compensation. Rationale:* nothing definite can be said about functional niche shifts as a mechanism underlying ecosystem resilience until post-disturbance niches are measured and compared with pre-disturbance niches; the niche shifts must be observable to confirm or refute a hypothesized relationship.

(5) *Appropriate replication must be achieved to generate the confidence intervals surrounding any experimentally derived conclusions denoting scientifically reliable knowledge about biodiversity–ecosystem function relations. Rationale:* replication is necessary to generate the error terms and hence the estimates of variance used to generate confidence intervals. For experimentally demonstrating functional niche dynamics as detailed in the trophic–dynamic approach with the highest degree of rigour, trophic generalism must be measured with replication at the level of the ecological individual. This can be accomplished, for example, following protocols for measuring phenotypic plasticity, which requires controlling for genotypic variability among experimental subjects in some way in order to evaluate the influence of environment on the expression of genes determining growth form or behaviour (for detailed discussions and examples of proper applications, see Griffiths *et al.*, 1993, pp. 716–718; Schlichting & Pigliucci, 1998). This is simple to do in experiments with plants, for instance, by propagating replicates of clonal species and measuring their rates of productivity along environmental gradients. Niche envelopes describing relative functional generalism *versus* functional specialization can thus be quantified with confidence intervals, and species can either be assembled to achieve communities with varying degrees of niche overlap or niche overlap among already coexisting species can be measured *in situ*. Hypothesis-testing specific to generalism as a mechanism of functional

niche shifts and, potentially, compensation can then be executed; rigorous replication at this scale will prove especially important in the immediate future for initially examining generalism as a mechanism of redundancy. Replication also must be achieved at the scale of experimental ecosystems (i.e. potentially sustainable functional communities) for each level of perturbation treatment, including baselines (controls), so that variance can be measured for the resilience observed.

These criteria have not yet been satisfied in ecological experiments, meaning that functional redundancy and functional diversity have never actually been measured in a manner conducive to relating them to functional compensation or resilience. Satisfying these criteria promises to achieve the goal of improving the design of ecological experiments to generate more reliable knowledge about biodiversity–ecosystem function relations, a need advertised by Johnson *et al.* (1996), Tilman (e.g. 1997), Huston (1997), and others. The trophic–dynamic approach to modelling redundancy presented above is a guide for achieving these objectives.

## VII. CONCLUSIONS

In so far as the evolutionary forces shaping life histories operate simultaneously on multiple populations at the scale of the trophic guild, as suggested by Lindeman (1942), May (1974), Huston (1994, p. 151) and others, ecologists may find it helpful to consider trophic hierarchy when examining biodiversity–ecosystem function relations. The T-D model is thus presented here to provide a framework for predicting the consequences of random species deletions (or any abundance changes) for the resilience of nutrient and energy processing at the ecosystem level to facilitate hypothesis-testing. In prefacing and explaining the trophic–dynamic approach to modelling redundancy in the above text, I have presented refined definitions for terms important to a directed study of redundancy in trophic dynamics, including disturbance, resilience, and redundancy. Proper contextual considerations for applying the T-D model, including for potentially exceptional cases, have been discussed, and relevant recommendations for improving the design of biodiversity–ecosystem function experiments have been specified.

The T-D model (Fig. 3) is predicated on the concept that resource–acquisition strategies of member species, taken together with the environmental conditions (stochasticity and resource limitation)

which give rise to those strategies, will determine the functional uniqueness of particular species in particular ecosystems. Functional redundancy, in turn, will determine ecosystem resilience. Where species are truly functionally unique, their respective populations will be incapable of the compensatory niche shifts defining redundancy. This idea has strong implications for the value of conserving functionally unique species. Recently, Power *et al.* (1996) recommended conserving keystone species, defined as those whose influence is disproportionately large compared to their biomass, in order to conserve ecosystem sustainability. This idea recognizes that losses of functionally irreplaceable species may send ecosystems toward alternative, possibly undesirable functional trajectories, and has not been challenged in the literature. Ecosystem alteration resulting from a species loss could indeed result in additional extinctions under some circumstances, as discussed above (Section V.1). However, a common manifestation of keystone effects is through the mediation of competition, which necessarily reduces redundancy, *R*. This means that conserving keystones in some situations can decrease ecosystem resilience to perturbation. That is, diversity can have pathological properties in that additional species may alter the interaction environment, reducing the resilience and therefore the sustainability of the ecosystem under human use (equations 1–20, Fig. 3). Lawton *et al.* (1998) state directly that no theory to date – including Tilman *et al.* (1997*b*), Loreau (1998*a*), and Naeem (1998); see also Yachi & Loreau (1999) (but see also May, 1974) – acknowledges the possibility that diversity can have negative effects on ecosystem function, so this present paper with its mechanistic focus on compensatory niche shifts as determinants of redundancy and therefore of resilience provides the first such theoretical basis. This should encourage ecologists toward examining behavioural generalism as a mechanism of redundancy, and appreciating that a trade-off potentially exists between the predominant conservation objectives of preserving biodiversity *per se* by preserving keystones *versus* conserving the functional integrity of exploitable ecosystems. The most prudent approach to conserving species for diversity's own sake may indeed be to conserve keystones. Conversely, managing for ecosystem sustainability in the face of consumptive use by humans would call for precisely the opposite approach: managing for redundancy as a driver of ecosystem resilience to disturbance (*sensu* Walker, 1995). Thus, ecosystems characterized by a diversity of functionally unique species (relatively

low  $R$ ) may be least useful for sustaining burgeoning human populations. Indeed, there is a very real and imminent danger to biodiversity conservation in advocating that diversity in any form – whether species diversity or functional diversity – improves the sustainability of ecosystems because this argument can be turned around to justify especially intensive exploitation of the most diverse systems by humans. After all, Aldo Leopold's proclamation that breakfast comes before ethics is vindicated by history. It is functional redundancy *per se* as uniquely defined herein as functional compensability in the face of perturbation and as predictably determined by food web interactions, rather than species composition itself, which should predictably enhance the sustainability of ecosystems under human use.

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## IX. REFERENCES

- AARSSSEN, L. W. (1997). High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos* **80**, 183–184.
- ABRAMS, P. A., MENGE, B. A., MITTELBACH, G. G., SPILLER, D. & YODZIS, P. (1995). The role of indirect effects in food webs. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 371–395. Chapman and Hall, New York.
- ASNER, G. P., SEASTEDT, T. R. & TOWNSEND, A. R. (1997). The decoupling of terrestrial carbon and nitrogen cycles. *BioScience* **47**, 226–234.
- ASSAL, F., BERMAN, A. & GUPTA, R. (1981). Satellite switching center for SS-TDMA systems. *IEEE 1981 International Conference on Communications* **4**, 5.1.1–5.1.8.
- BAZZAZ, F. A. (1986). Life history of colonizing plants: some demographic, genetic, and physiological features. In *Ecology of biological invasions of North America and Hawaii* (ed. H. A. Mooney & J. A. Drake), pp. 96–110. Springer-Verlag, Berlin.
- BELOVSKY, G. E. (1978). Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* **14**, 105–134.
- BIROLINI, A. (1994). *Quality and Reliability of Technical Systems*. Springer-Verlag, Berlin.
- BRAND, A. H., MICKLEM, G. & NASMYTH, K. (1987). A yeast silencer contains sequences that can promote autonomous plasmid replication and transcriptional activation. *Cell* **51**, 709–719.
- CATUNEANU, V. M. & MIHALACHE, A. N. (1989). *Reliability Fundamentals*. Elsevier, Amsterdam.
- CHAPIN, F. S., WALKER, B. H., HOBBS, R. J., HOOPER, D. U., LAWTON, J. H., SALA, O. E. & TILMAN, D. (1997). Biotic control over the functioning of ecosystems. *Science* **277**, 500–504.
- CHASE, J. M. & BELOVSKY, G. E. (1994). Experimental evidence for the included niche. *American Naturalist* **143**, 514–527.
- CHESSON, P. L. & WARNER, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* **117**, 923–943.
- CLARK, R. N., MASRELIEZ, C. J. & BURROWS, J. W. (1976). A functionally redundant altimeter. *IEEE Transactions on Aerospace and Electronic Systems* **12**, 459–463.
- CLARK, R. N. & SETZER, W. (1980). Sensor fault detection in a system with random disturbances (hydrofoil boat lateral axis control system). *IEEE Transactions on Aerospace and Electronic Systems* **16**, 468–473.
- COLEMAN, D. C. (1995). Energetics of detritivory and microbivory in soil in theory and practice. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 39–50. Chapman and Hall, New York.
- COLEMAN, D. C., ANDREWS, R., ELLIS, J. E. & SINGH, J. S. (1976). Energy flow and partitioning in selected man-managed and natural ecosystems. *Agro-Ecosystems* **3**, 45–54.
- COLEMAN, J. S., MCCONNAUGHAY, K. D. M. & ACKERLY, D. D. (1994). Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* **9**, 187–191.
- CONNEL, J. H. (1990). Apparent versus 'real' competition in plants. In *Perspectives on Plant Competition* (ed. J. Grace & D. Tilman), pp. 10–16. Academic Press, New York.
- COTTINGHAM, K. L. & CARPENTER, S. R. (1998). Population, community, and ecosystem variates as ecological indicators – phytoplankton responses to whole-lake enrichment. *Ecological Applications* **8**, 508–530.
- COTTINGHAM, K. L., CARPENTER, S. R. & STAMAND, A. L. (1998). Responses of epilimnetic phytoplankton to experimental nutrient enrichment in three small seepage lakes. *Journal of Plankton Research* **20**, 1889–1914.
- COVICH, A. P., PALMER, M. A. & CROWL, T. A. (1999). The role of benthic invertebrate species in freshwater ecosystems. *BioScience* **49**, 119–127.
- COWLING, R. M., MUSTART, P. J., LAURIE, H. & RICHARDS, M. B. (1994). Species diversity; functional diversity and functional redundancy in fynbos communities. *South African Journal of Science* **90**, 333–337.
- CRICK, F. & KOCH, C. (1990). Towards a neurobiological theory of consciousness. *Seminars in Neuroscience* **2**, 263–275.
- DAILY, G. C. (ed.) (1997). *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, D.C.
- DALL, S. R. X. & CUTHILL, I. C. (1997). The information costs of generalism. *Oikos* **80**, 197–202.
- DOAK, D. F., BIGGER, D., HARDING, E. K., MARVIER, M. A., O'MALLEY, R. E. & THOMSON, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *American Naturalist* **151**, 264–276.
- EHRLICH, P. R. & EHRLICH, A. H. (1981). *Extinction. The Causes and Consequences of the Disappearance of Species*. Random House.
- EHRLICH, P. R. & WALKER, B. (1998). Rivets and redundancy. *BioScience* **48**, 387.
- ELTON, C. (1927). *Animal Ecology*. Macmillan Co., New York.
- ELTON, C. S. (1958). *The Ecology of Invasions by Animals and Plants*. Chapman and Hall, New York. pp. 143–153.

- FOOTE, D. (1995). Patterns of diversity in Island soil fauna: detecting functional redundancy. In *Islands: Biological Diversity and Ecosystem Function* (ed. P. M. Vitousek, L. L. Loope & H. Adersen), pp. 57–71. Springer, Berlin.
- FRANK, D. A. & MCNAUGHTON, S. J. (1991). Stability increases with diversity in plant communities: Empirical evidence from the 1998 Yellowstone drought. *Oikos* **62**, 360–362.
- FROST, T. M., CARPENTER, S. R., IVES, A. R. & KRATZ, T. K. (1995). Species compensation and complementarity in ecosystem function. In *Linking Species and Ecosystems* (ed. C. G. Jones & J. H. Lawton), pp. 224–239. Chapman and Hall, London.
- GHILAROV, A. M. (1998). Species redundancy versus non-redundancy: is it worth further discussion? *Žhurnal Obshchei Biologii* **58**, 100–105.
- GITAY, H., WILSON, J. B. & LEE, W. G. (1996). Species redundancy: a redundant concept? *Journal of Ecology* **84**, 121–124.
- GRANT, R. & GRANT, P. (1993). Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London Series B* **251**, 111–117.
- GRIFFITHS, A. J. F., MILLER, J. H., SUZUKI, D. T., LEWONTIN, R. C. & GELBART, W. M. (1993). *An Introduction to Genetic Analysis*, 5th Edition. W. H. Freeman and Company, New York.
- GRIME, J. P. (1974). Vegetation classification by reference to strategies. *Nature* **250**, 26–31.
- GRIME, J. P. (1979). *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York.
- HAIRSTON, N. G., JR. & HAIRSTON, N. G., SR. (1993). Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* **142**, 379–411.
- HARR, M. E. (1987). *Reliability-based Design in Civil Engineering*. McGraw-Hill, New York.
- HECTOR, A. (1998). The effect of diversity on productivity: detecting the role of species complementarity. *Oikos* **82**, 599.
- HODGSON, J. G., THOMPSON, K., WILSON, P. J. & BOGAARD, A. (1998). Does biodiversity determine ecosystem function? The Ecotron experiment reconsidered. *Functional Ecology* **12**, 843–852.
- HOLLING, C. S. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**, 1–23.
- HOLT, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**, 197–229.
- HOLT, R. D. (1995). Food webs in space: an island biogeographic perspective. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 313–323. Chapman and Hall, New York.
- HOLT, R. D. & POLIS, G. A. (1997). A theoretical framework for intraguild predation. *American Naturalist* **149**, 745–764.
- HOOPER, D. U. (1998). The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* **79**, 704–719.
- HOOPER, D. U. & VITOUSEK, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science* **277**, 1302–1305.
- HOOPER, D. U. & VITOUSEK, P. M. (1998). Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**, 121–149.
- HOYLAND, A. & RAUSAND, M. (1994). *System Reliability Theory: model and Statistical Methods*. John Wiley & Sons, New York.
- HUNTER, M. D. & PRICE, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724–732.
- HURD, L. E., MELLINGER, M. V., WOLF, L. L. & MCNAUGHTON, S. J. (1971). Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science* **173**, 1134–1136.
- HURD, L. E. & WOLF, L. L. (1974). Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. *Ecological Monographs* **44**, 465–482.
- HUSTON, M. A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge, MA.
- HUSTON, M. A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**, 449–460.
- JAKSIC, F. M., FEINSINGER, P. & JIMENEZ, J. E. (1996). Ecological redundancy and long-term dynamics of vertebrate predators in semiarid Chile. *Conservation Biology* **10**, 252–262.
- JARMAN, P. J. & SINCLAIR, A. R. E. (1979). Feeding strategy and the pattern of resource partitioning in ungulates. In *Serengeti: Dynamics of an Ecosystem* (ed. A. R. E. Sinclair & M. Norton-Griffiths), pp. 135–143. University of Chicago Press, Chicago.
- JOHANSSON, F. (1993). Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. *Oikos* **66**, 80–87.
- JOHNSON, K. H., VOGT, K. A., CLARK, H. J., SCHMITZ, O. J. & VOGT, D. J. (1996). Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution* **11**, 372–377.
- KAREIVA (1994). Diversity begets productivity. *Nature* **368**, 686–687.
- KISS, G. B., AMIN, A. A. & PEARLMAN, R. E. (1981). Two separate regions of the extrachromosomal ribosomal deoxyribonucleic acid of *Tetrahymena thermophila* enable autonomous replication of plasmids in *Saccharomyces cerevisiae*. *Molecular and Cellular Biology* **1**, 535–543.
- KLOPPER, P. H. & MACARTHUR, R. H. (1960). Niche size and faunal diversity. *American Naturalist* **94**, 293–300.
- KOHEN, E., SANTUS, R. & HIRSCHBERG, J. G. (1996). *Photobiology*. Academic Press, San Diego.
- LAWTON, J. (1994). What do species do in ecosystems? *Oikos* **71**, 367–374.
- LAWTON, J. (1995). Ecological experiments with model systems. *Science* **269**, 328–331.
- LAWTON, J. H. & BROWN, V. K. (1993). Redundancy in ecosystems. In *Biodiversity and Ecosystem Function* (ed. E. D. Schulze & H. A. Mooney), pp. 255–270. Springer-Verlag, Berlin.
- LAWTON, J. H., NAEEM, S., THOMPSON, L. J., HECTOR, A. & CRAWLEY, M. J. (1998). Biodiversity and ecosystem function: getting the Ecotron experiment in its correct context. *Functional Ecology* **12**, 848–852.
- LEVINS, R. & MACARTHUR, R. (1969). An hypothesis to explain the incidence of monophagy. *Ecology* **50**, 910–911.
- LEWIS, E. E. (1987). *Introduction to Reliability Engineering*. Wiley, New York (sic).
- LINDEMAN, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–417.
- LINDSTROM, E. R., BRAINERD, S. M., HELDIN, J. O. & OVERSKAUG, K. (1995). Pine marten-red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici* **32**, 123–130.



- LOREAU, M. (1998a). Biodiversity and ecosystem functioning – a mechanistic model. *Proceedings of the National Academy of Sciences of United States of America* **95**, 5632–5636.
- LOREAU, M. (1998b). Ecosystem development explained by competition within and between material cycles. *Proceedings of the Royal Society of London*, **B 265**, 33–38.
- LUNDBERG, P. & FRODIN, P. (1998). Ecosystem resilience and productivity – are predictions possible? *Oikos* **81**, 603–606.
- MACARTHUR, R. (1955). Fluctuations of animal populations and a measure of community stability. *Ecology* **36**, 533–536.
- MACARTHUR, R. & LEVINS, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* **101**, 377–385.
- MACGILLIVRAY, C. W. & GRIME, J. P. (1995). Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Functional Ecology* **9**, 640–649.
- MARGALEF, R. (1969). Diversity and stability: a practical proposal and a model of interdependence. *Brookhaven Symposium on Biology* **22**, 25–37.
- MARTIN, T. E. (1996). Fitness costs of resource overlap among coexisting bird species. *Nature* **380**, 338–340.
- MAY, R. M. (1974). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.
- MAY, R. M. (1975). Some notes on estimating the competition matrix,  $\alpha$ . *Ecology* **56**, 737–741.
- MAY, R. M. (1983). The structure of foodwebs. *Nature* **301**, 566–568.
- MAYNARD SMITH, J. (1968). *Mathematical Ideas in Biology*. Cambridge University Press, Oxford. 152 pp.
- MAYNARD SMITH, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Oxford.
- MCCANN, K., HASTINGS, A. & HUXEL, G. (1998). Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- MCGRADY STEED, J., HARRIS, P. M. & MORIN, P. J. (1997). Biodiversity regulates ecosystem predictability. *Nature* **390**, 162–165.
- MCNAUGHTON, S. J. (1977). Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. *American Naturalist* **111**, 515–525.
- MCNAUGHTON, S. J. (1993). Biodiversity and the function of grazing ecosystems. In *Biodiversity and Ecosystem Function* (ed. E. D. Schulze & H. A. Mooney), pp. 361–383. Springer-Verlag, Berlin.
- MELLINGER, M. V. & MCNAUGHTON, S. J. (1975). Structure and function of successional vascular plant communities in central New York. *Ecological Monographs* **45**, 161–182.
- MINTA, S. C. (1993). Sexual differences in spatio-temporal interaction among badgers. *Oecologia* **96**, 402–409.
- MORIN, P. J. (1995). Functional redundancy, non-additive interactions, and supply-side dynamics in experimental pond communities. *Ecology* **76**, 133–149.
- MORIN, P. J. & LAWLER, S. P. (1995). Effects of food chain length and omnivory on population dynamics in experimental food webs. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 218–230. Chapman and Hall, New York.
- NAEEM, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology* **12**, 39–45.
- NAEEM, S. & LI, S. (1997). Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.
- NAEEM, S. & LI, S. (1998). Consumer species richness and autotrophic biomass. *Ecology* **79**, 2603–2615.
- NAEEM, S., THOMPSON, L. J., LAWLOR, S. P., LAWTON, J. H. & WOODFIN, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.
- NAVARRETTE, S. A. & MENGE, B. A. (1996). Keystone predation and interaction strength: interactive effects of predators and prey. *Ecological Monographs* **66**, 409–430.
- ODUM, E. P. (1969). The strategy of ecosystem development. *Science* **164**, 262–270.
- ODUM, E. P. (1985). Trends expected in stressed ecosystems. *BioScience* **35**, 419–422.
- ODUM, E. P., FLINN, J. T. & FRANZ, E. H. (1979). Perturbation theory and the subsidy-stress gradient. *BioScience* **29**, 349–352.
- PAINE, R. T. (1966). Food web complexity and species diversity. *American Naturalist* **100**, 65–75.
- PAINE, R. T. (1969). A note on trophic complexity and community stability. *American Naturalist* **103**, 91–93.
- PALOMARES, F., GAONA, P., FERRERAS, P. & DELIBES, M. (1995). Positive effects on game species of top predators by controlling small predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology* **9**, 295–305.
- PERRY, D. A., BELL, T. & AMARANTHUS, M. P. (1992). Mycorrhizal fungi in mixed-species forests and other tales of positive feedback, redundancy, and stability. In *The Ecology of Mixed-species Stands of Trees* (ed. M. G. R. Cannell, D. C. Malcom & P. A. Robertson), pp. 151–179. Blackwell Scientific, London.
- PIMM, S. L. (1982). *Food Webs*. Chapman and Hall, London.
- PIMM, S. L. (1991). *The Balance of Nature?* University of Chicago Press, Chicago.
- PIGLIUCCI, M. & SCHLICHTING, C. D. (1995). Reaction norms of *Arabidopsis* (Brassicaceae). III. Response to nutrients in 26 populations from a worldwide collection. *American Journal of Botany* **82**, 1117–1125.
- POLIS, G. A. (1995). Complex food webs. In *Complex Ecology: The Part-whole Relation in Ecosystems* (ed. B. C. Patten & S. E. Jorgensen), pp. 513–548. Prentice Hall, Englewood Cliffs, New Jersey.
- POWER, M. E., TILMAN, D., ESTES, J. A., MENGE, B. A., BOND, W. J., MILLS, L. S., DAILEY, G., CASTILLA, J. C., LUBCHENCO, J. & PAINE, R. T. (1996). Challenges in the quest for keystones. *BioScience* **49**, 465–471.
- PRACH, K., PYSEK, P. & SMLAUER, P. (1997). Changes in species traits during succession: a search for pattern. *Oikos* **79**, 201–205.
- READING, R. P. & MILLER, B. J. (1994). The black-footed ferret recovery program: unmasking professional and organizational weaknesses. In *Endangered Species Recovery: Finding the Lessons, Improving the Process* (ed. T. W. Clark, R. P. Reading & A. L. Clarke), pp. 73–100. Island Press, Washington, D. C.
- ROMESBURG, H. C. (1981). Wildlife science: gaining reliable knowledge. *Journal of Wildlife Management* **45**, 293–313.
- ROSENZWEIG, M. L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**, 385–387.
- RUTLEDGE, R. W., BASORE, B. L. & MULHOLLAND, R. J. (1976). Ecological stability: an information theory viewpoint. *Journal of Theoretical Biology* **57**, 355–371.
- SCHLICHTING, C. D. & PIGLIUCCI, M. (1998). *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland, MA.
- SCHOENER, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**, 369–404.

- SCHOENER, T. W. (1974). Competition and the form of habitat shift. *Theoretical Population Biology* **6**, 265–307.
- SIMPSON, G. G. (1944). *Tempo and Mode in Evolution*. Columbia University Press, New York.
- SMEDES, G. W. & HURD, L. E. (1981). An empirical test of community stability: resistance of a fouling community to a biologically patch-forming disturbance. *Ecology* **62**, 1561–1572.
- SULTAN, S. E. (1987). Evolutionary implications of phenotypic plasticity in plants. In *Evolutionary Biology 21* (ed. M. K. Hecht, B. Wallace & G. T. Prance), pp. 127–178. Plenum Press, New York.
- STEARNS, S. C. (1989). The evolutionary significance of phenotypic plasticity. *BioScience* **39**, 436–447.
- TILMAN, D. (1985). The resource-ratio hypothesis of plant succession. *American Naturalist* **125**, 827–852.
- TILMAN, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350–363.
- TILMAN, D. (1997). Distinguishing between the effects of species diversity and species composition. *Oikos* **80**, 185.
- TILMAN, D. & DOWNING, J. A. (1994). Biodiversity and stability in grasslands. *Nature* **367**, 363–365.
- TILMAN, D., KNOPS, J., WEDIN, D., REICH, P., RITCHIE, M. & SIEMANN, E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302.
- TILMAN, D., LEHMAN, C. L. & THOMSON, K. T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 1857–1861.
- TILMAN, D., LEHMAN, C. L. & C. E. BRISTOW. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist* **151**, 277–282.
- TURKINGTON, R. & MEHRHOFF, L. A. (1990). The role of competition in structuring pasture communities. In *Perspectives on Plant Competition* (ed. J. Grace & D. Tilman), p. 309. Academic Press, New York.
- ULANOWICZ, R. E. (1980). An hypothesis on the development of natural communities. *Journal of Theoretical Biology* **85**, 223–245.
- ULANOWICZ, R. E. (1986). *Growth and Development: Ecosystems Phenomenology*. Springer-Verlag, New York.
- ULANOWICZ, R. E. (1989). A phenomenology of evolving networks. *Systems Research* **6**, 209–217.
- ULANOWICZ, R. E. (1995a). Ecosystem trophic foundations: Lindeman exonerata. In *Complex Ecology: the Part-whole Relation in Ecosystems* (ed. B. C. Patten & S. E. Jorgensen), pp. 549–560. Prentice-Hall, Englewood Cliffs, NJ.
- ULANOWICZ, R. E. (1995b). Trophic flow networks as indicators of ecosystem stress. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 358–368. Chapman and Hall, New York.
- VIA, S., GOMULKIEWICZ, R., DE JONG, G., SCHEINER, S. M., SCHLICHTING, C. D. & VAN TIENDEREN, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends in Ecology and Evolution* **10**, 212–217.
- VOGT, K. A., GORDON, J. C., WARGO, J. P., VOGT, D. J., ASBJORNSEN, H., PALMIOTTO, P. A., CLARK, H. J., O'HARA, J. L., KEATON, W. S., PATEL-WEYNAND, T. & WITTEN, E. (1997). *Ecosystems: Balancing Science with Management*. Springer, New York.
- WALKER, B. (1992). Biodiversity and ecological redundancy. *Conservation Biology* **6**, 18–23.
- WALKER, B. (1995). Conserving biological diversity through ecosystem resilience. *Conservation Biology* **9**, 747–752.
- WALLACE, J. L. (1989). Gastric resistance to acid: is the mucus-bicarbonate barrier functionally redundant? *American Journal of Physiology* **256**, G31–G38.
- WARDLE, D. A., BONNER, K. I. & NICHOLSON, K. S. (1997). Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. *Oikos* **79**, 247–258.
- WEBSTER, J. R., WAIDE, J. B. & PATTEN, B. C. (1974). Nutrient recycling and the stability of ecosystems. In *Mineral Cycling in Southeastern Ecosystems* (ed. F. G. Howell, J. B. Gentry & M. H. Smith); reprinted in 1979 in *Systems Ecology* (ed. H. H. Shugart & R. V. O'Neill), pp. 136–162. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PE, U.S.A.
- WEDIN, D. A. & TILMAN, D. (1996). Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* **274**, 5293–5295.
- WINDHOLZ, G. & GRIMSLEY, D. L. (1992). Pavlov's position on the effects of decortication on conditional reflexes. *Integrative Physiological and Behavioral Science* **27**, 170–181.
- WINEMILLER, K. O. & POLIS, G. A. (1995). Food webs: what do they tell us about the world? In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis & K. O. Winemiller), pp. 1–22. Chapman and Hall, New York.
- YACHI, S. & LOREAU, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences, U.S.A.* **96**, 1463–1468.
- YODZIS, P. (1978). *Competition for Space and the Structure of Ecological Communities*. Springer-Verlag, Berlin.
- YODZIS, P. (1989). *Introduction to Theoretical Ecology*. Harper and Row, New York.
- YODZIS, P. (1995). Food webs and perturbation experiments: theory and practice. In *Food Webs: Integration of Patterns and Dynamics* (ed. G. A. Polis and K. O. Winemiller), pp. 192–200. Chapman and Hall, New York.
- ZARKOWER, D. & WICKENS, M. (1988). A functionally redundant downstream sequence in SV-40 late pre-messenger RNA is required for messenger RNA 3'-end formation and for assembly of a precleavage complex *in vitro*. *Journal of Biochemistry* **263**, 5780–5788.