

Phenotypic Diversity and Stability of Ecosystem Processes

Michel Loreau¹ and Narayan Behera²

Laboratoire d'Ecologie, UMR 7625, Ecole Normale Supérieure, 46 rue d'Ulm,
F-75230 Paris Cedex 05, France

Received March 2, 1998

The resistance of an ecosystem to perturbations and the speed at which it recovers after the perturbations, which is called resilience, are two important components of ecosystem stability. It has been suggested that biodiversity increases the resilience and resistance of aggregated ecosystem processes. We test this hypothesis using a theoretical model of a nutrient-limited ecosystem in a heterogeneous environment. We investigate the stability properties of the model for its simplest possible configuration, i.e., a system consisting of two plant species and their associated detritus and local resource depletion zones. Phenotypic diversity within the plant community is described by differences in the nutrient uptake and mortality rates of the two species. The usual measure of resilience characterizes the system as a whole and thus also applies to aggregated ecosystem processes. As a rule this decreases with increased diversity, though under certain conditions it is maximum for an intermediate value of diversity. Resistance is a property that characterizes each system component and process separately. The resistance of the inorganic nutrient pools, hence of nutrient retention in the ecosystem, decreases with increased diversity. The resistance of both total plant biomass and productivity either monotonically decreases or increases over part of the parameter range with increased diversity. Furthermore, it is very sensitive to parameter values. These results support the view that there is no simple relationship between diversity and stability in equilibrium deterministic systems, whether at the level of populations or aggregated ecosystem processes. We discuss these results in relation to recent experiments. © 1999 Academic Press

Key Words: biodiversity; ecosystem processes; energy flow; productivity; nutrient cycling; perturbation; resilience; resistance; stability.

INTRODUCTION

A variety of ecological interpretations have been given to the term “stability.” The most generally used concept refers to the stability in the vicinity of an equilibrium point in a deterministic system. Webster *et al.* (1975) and Pimm (1984) distinguished two aspects of this stability: “resilience,” the speed at which a system returns to its

equilibrium following a perturbation, and “resistance,” the ability of a system to withstand displacement by a disturbance in its environment. These two properties are usually held to be responsible for the persistence of ecosystems in an unpredictable environment (but see Neubert and Caswell (1997) for new alternative measures of ecosystem stability). The diversity–stability hypothesis holds that increased biodiversity leads to greater ecological stability (Elton, 1958). In particular, more diverse ecosystems are more likely to contain some species that can survive during a given environmental disturbance and thus compensate for reduced competitors. Therefore, biodiversity should enhance resistance to perturbation.

¹ To whom correspondence should be addressed. E-mail: Loreau@ens.fr.

² Present address: Center for Ecological Research, Kyoto University, Kitashirakawa Nishimachi, Sakyo, Kyoto 606, Japan.

McNaughton (1977) presented data on plant productivity that supported this hypothesis. King and Pimm (1983) found that higher plant diversity led to greater biomass stability in response to changes in herbivory, and Tilman and Downing (1994) found a similar effect in response to drought. Recent experiments in laboratory microcosms showed increased predictability of ecosystem processes at a higher species diversity (McGrady-Steed *et al.*, 1997; Naeem and Li, 1997).

But there has been continuing debate about the diversity–stability hypothesis (MacArthur, 1955; Gardner and Ashby, 1970; May, 1972, 1973; McNaughton, 1977; Armstrong, 1982; Pimm, 1984). May (1972) showed that randomly connected systems were less likely to be stable as the number of their components (i.e., species) and the number and strength of the connections between them (i.e., species interactions) increased; therefore there should not be any simple relationship between diversity and stability. DeAngelis (1975, 1992) and Gilpin (1975) reached similar conclusions using different models. The debate is now regaining vigour because of the potential importance of biodiversity in the maintenance of ecosystem services (Schulze and Mooney, 1993; Tilman and Downing, 1994; Givnish 1994; “Global Biodiversity Assessment,” 1995). A reconciliation of the opposing views would, however, be possible if these proved to apply to different scales: populations might be less stable, whereas the aggregated compartments and processes at the ecosystem level might be more stable in more diverse systems. Tilman (1996) recently provided some evidence for this hypothesis in a long-term study of grassland experimental plots. But there has been as yet little rigorous theoretical investigation of this issue.

In this paper, we explore the resilience and resistance of ecosystem compartments and processes in a simple nutrient-limited ecosystem model, and we show that there is also no simple relationship between diversity and stability at the aggregated ecosystem level. The role of material cycling in ecosystem stability has been investigated and discussed thoroughly by DeAngelis *et al.* (1989), DeAngelis (1992), and Loreau (1994), but the latter did not consider species diversity within functional groups or trophic levels. In an attempt to establish an explicit link between community properties and ecosystem processes, Loreau (1996, 1998) recently analysed a nutrient-limited ecosystem model containing an arbitrary number of parallel plant–detritus or plant–herbivore–detritus food chains in a heterogeneous environment. Here we investigate the stability properties of his model for its simplest possible configuration, i.e., a system consisting of two plant species or genotypes and their associated detritus and local resource depletion

zones. Phenotypic diversity within the plant community is described by differences in the nutrient uptake and mortality rates of the two species. These are traits that are measurable experimentally and likely to be directly affected by changes in the environment.

MODEL

1. Dynamical Equations

The model is based on the conceptual framework first presented by Huston and DeAngelis (1994) and further developed by Loreau (1996, 1998). Plant growth is assumed to be limited by a single nutrient. As a result of plant nutrient uptake, a small-scale spatial heterogeneity is created in their vicinity. The rate of nutrient transport between the common regional pool and local resource depletion zones around the plants determines the competitive interactions between plants through their effect on the shared nutrient pool (Fig. 1). An increase in the rate of nutrient transport has the effect of homogenising the medium and thus intensifying competition. Each plant species produces detritus, part of which is decomposed locally and recycles the nutrient directly to the local resource depletion zone, while another part is dispersed and is assumed to recycle the nutrient to the regional pool (Fig. 1).

Let R and V_R be the nutrient concentration and volume, respectively, of the regional pool, and L_i and V_i the nutrient concentration and volume, respectively, of the local resource depletion zone of plant species i . Nutrient transport between the regional pool and the local zones is assumed to be proportional to the product of the difference between the nutrient concentrations R and L_i and the volume V_i , the proportionality constant being k , a constant characteristic for the medium. The nutrient flows in and out of the regional pool at a rate q ; the input flux of new nutrient per unit volume is then qR_0 , where R_0 is the input nutrient concentration.

The local biological compartments are expressed in units of nutrient concentration per volume of the local resource depletion zone; their biomass is assumed to be proportional to their nutrient content. Thus P_i and D_i represent the local nutrient concentrations of plant i and its detritus, respectively. The uptake rate of nutrient by plant species i is modelled by a Lotka–Volterra function $a_i L_i P_i$. This has the property of leading to recipient control of resource concentration at equilibrium. Nutrient recycling through decomposition of detritus is assumed to be a linear donor-controlled process; b_i is the rate at which plants produce detritus; l_i and r_i are the rates at

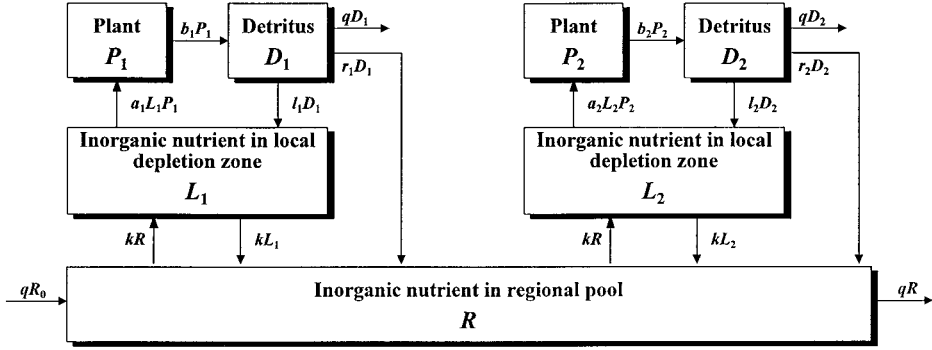


FIG. 1. Flow diagram of the model ecosystem.

which nutrient is released from the plant to the local resource depletion zone and regional pool, respectively. The recycled nutrient, on returning to the regional pool, is assumed to be subject to the same loss rate q as the nutrient in the pool.

The dynamical equations for the model are then

$$\frac{dR}{dt} = q(R_0 - R) - k \sum_i \sigma_i (R - L_i) + \sum_i \sigma_i r_i D_i, \quad (1)$$

$$\frac{dL_i}{dt} = k(R - L_i) - a_i L_i P_i + l_i D_i, \quad (2)$$

$$\frac{dP_i}{dt} = a_i L_i P_i - b_i P_i, \quad (3)$$

$$\frac{dD_i}{dt} = b_i P_i - (l_i + r_i + q) D_i, \quad (4)$$

where

$$\sigma_i = V_i / V_R. \quad (5)$$

2. Equilibrium

Let X^* denote the equilibrium value of variable X . The equilibrium of the system is obtained by solving Eqs. (1) to (4) after the time derivatives have been set equal to zero. Since outputs balance inputs at equilibrium, Eq. (1) for the regional pool may be conveniently replaced with the mass-balance equation for the whole ecosystem:

$$R_0 - R^* - \sum_i \sigma_i D_i = 0. \quad (6)$$

The equilibrium concentrations of the various compartments are found to be

$$R^* = \frac{R_0 + k \sum_i \alpha_i L_i^*}{1 + k \sum_i \alpha_i}, \quad (7)$$

$$L_i^* = \frac{b_i}{a_i}, \quad (8)$$

$$P_i^* = \frac{k(R^* - L_i^*)}{v_i b_i}, \quad (9)$$

$$D_i^* = \frac{k(R^* - L_i^*)}{r_i + q}, \quad (10)$$

where

$$v_i = \frac{r_i + q}{l_i + r_i + q}, \quad (11)$$

$$\alpha_i = \frac{\sigma_i}{r_i + q}. \quad (12)$$

The persistence of plant species i and its associated detritus at equilibrium requires (from Eq. (9))

$$R^* - L_i^* > 0. \quad (13)$$

Since all the energy flowing in the ecosystem enters through the plants and drives the flow of nutrient from the inorganic pools to the plants, we assume, as in Loreau (1995, 1996, 1998), that the energy flow E or primary productivity is measured by the total flow of nutrient to the plants, assuming an appropriate transformation of units. At equilibrium, it is equal to

$$E^* = V_R \sum_i \sigma_i a_i L_i^* P_i^*. \quad (14)$$

3. Stability

Resilience is fairly well defined mathematically since it corresponds to the concept of Lyapunov asymptotic stability. It depends on the eigenvalues of the Jacobian matrix of the system linearised about its equilibrium. All the eigenvalues must have negative real parts to ensure stability. Following a perturbation, the return time of the system variables will ultimately be governed by the dominant eigenvalue, λ_d , that which is closest to zero. The absolute value of the dominant eigenvalue is taken as a measure of ecosystem resilience (Webster *et al.*, 1975; DeAngelis, 1992).

The analysis of resistance, even for linear models, is not as well understood. Harrison (1979) showed that the resistance of a system to stress can be measured by the inertia of the state of the system caused by a change in the flow parameters. Stress does not change the system at once but only after perturbations of the flow rates have lasted for some time. Harrison and Fekete (1980) extended the mathematical framework for analysing resistance to linear nutrient cycling models. These linear models are used as a good first approximation to natural processes and, also, they are mathematically tractable.

Following Harrison and Fekete (1980), consider a linear ecosystem model of the form

$$\frac{d\mathbf{X}}{dt} = \mathbf{A}\mathbf{X} + \mathbf{Z}, \quad (15)$$

where \mathbf{X} is the vector of nutrient concentrations in the various compartments, \mathbf{Z} is the vector of inflow rates from outside the system, and \mathbf{A} is the matrix containing the flow rates a_{ij} between compartments and the outflows from the system. Suppose that in the system initially at equilibrium, the flow rates a_{ij} are perturbed by an amount δa_{ij} . If the onset of the perturbation is set to time $t = 0$, the dynamics of the perturbed system is given by

$$\frac{d\mathbf{X}}{dt} = (\mathbf{A} + \delta\mathbf{A})\mathbf{X} + \mathbf{Z}, \quad \mathbf{X}(0) = \mathbf{X}^*. \quad (16)$$

The displacement of the perturbed trajectory from the equilibrium state,

$$\delta\mathbf{X}(t) = \mathbf{X}(t) - \mathbf{X}^*, \quad (17)$$

is then an inverse measure of the resistance of the ecosystem to the perturbation of the flow rates over the

time interval 0 to t . Harrison and Fekete (1980) showed that its dynamics are given by

$$\delta\mathbf{X}(t) = \delta\mathbf{X}^* - \sum_i c_i \mathbf{u}_i e^{-\mu_i t}, \quad (18)$$

where $\delta\mathbf{X}^*$ is the ultimate displacement, μ_i are the eigenvalues of $\mathbf{A} + \delta\mathbf{A}$, \mathbf{u}_i are the corresponding eigenvectors, and c_i are constants. Thus the disturbed system approaches a new equilibrium $\mathbf{X}^* + \delta\mathbf{X}^*$ at a rate decided by the eigenvalues μ_i , along a path determined by the weighted eigenvectors $c_i \mathbf{u}_i$.

4. Implementation of the Model

We investigated the stability properties of a system comprising two plant species with respect to changes in two of their traits, namely their nutrient uptake rate, a_i , and their rate of detritus production from mortality or other causes, b_i , which we shall call mortality rate in short. All other model parameters were kept constant and chosen to be equal between the species. The difference between the trait values of the two species was taken as a measure of phenotypic diversity with respect to that trait. In the case of nutrient uptake rate, $a_1 + a_2$ and $a_1 - a_2$ uniquely specify the system; here, $a_1 + a_2$ is a measure of the average nutrient uptake rate, while $a_1 - a_2$ is a measure of its diversity. The same holds true for mortality rates.

Resilience was investigated both as a function of $a_1 - a_2$ while $a_1 + a_2$ was kept constant and as a function of $a_1 + a_2$ while $a_1 - a_2$ was kept constant, and similarly for mortality rates. Keeping the other variable constant is the only way to study the system's behaviour systematically and unambiguously. Resilience was calculated from the Jacobian matrix of the system (see Appendix 1) over the whole range of parameters ensuring feasibility of the equilibrium. The feasibility conditions, obtained from inequality (13), are here

$$a_2(R_0 a_1 - b_1) + k\alpha(a_1 b_2 - a_2 b_1) > 0, \quad (19)$$

$$a_1(R_0 a_2 - b_2) + k\alpha(a_2 b_1 - a_1 b_2) > 0, \quad (20)$$

where $\alpha_1 = \alpha_2 = \alpha$.

For the analysis of resistance, we limit ourselves here to studying the ultimate displacement in Eq. (18); the full trajectories were found to be too variable for a systematic investigation. In studying resistance as a function of diversity in uptake rates, a_1 was perturbed by an amount δa_1 while a_2 was perturbed by $-\delta a_1$, so that $a_1 + a_2$ was

kept constant. In studying resistance as a function of the average nutrient uptake rate, a_1 and a_2 were both altered by an amount δa_1 , so that $a_1 - a_2$ remained constant. A similar analysis was performed for mortality rates. It was ensured that the perturbed system also satisfied the feasibility conditions. We calculated relative displacements to have comparable measures of resistance, for the following aggregated compartments and processes:

$$\frac{\delta R^*}{R^*} \quad (\text{soil inorganic nutrient pool}) \quad (21)$$

$$\frac{\delta L^*}{L^*} = \frac{\delta L_1^* + \delta L_2^*}{L_1^* + L_2^*} \quad (\text{total inorganic nutrient in local depletion zones}) \quad (22)$$

$$\frac{\delta P^*}{P^*} = \frac{\delta P_1^* + \delta P_2^*}{P_1^* + P_2^*} \quad (\text{total plant biomass}) \quad (23)$$

and

$$\frac{\delta E^*}{E^*} = \frac{\delta L_1^* P_1^* + \delta P_1^* L_1^* + \delta L_2^* P_2^* + \delta P_2^* L_2^*}{L_1^* P_1^* + L_2^* P_2^*} \quad (\text{total primary productivity}). \quad (24)$$

The analytical expressions for these measures are given in Appendix 2.

RESULTS

1. Resilience as a Function of Nutrient Uptake Rates

When $b_1 \geq b_2$, resilience decreases slowly in the beginning when diversity in nutrient uptake rates is increased, but falls sharply as the limit of equilibrium feasibility is approached (Fig. 2A). It is higher when the average nutrient uptake rate is larger. When $b_1 < b_2$, there is generally an intermediate value of diversity that maximises resilience (Fig. 2B). As the difference in the mortality rates of the two species increases, the maximum shifts to larger diversity values; when b_1 tends to zero, it shifts toward the largest value compatible with equilibrium feasibility (data not shown). But at the same time resilience decreases (Fig. 2B). The maximum disappears for large values of b 's.

Resilience increases toward saturation as the average nutrient uptake rate increases, but is relatively lower with higher diversity, when $b_1 \geq b_2$ (Fig. 2C). No general trend was found when $b_1 < b_2$ (data not shown). The variation of resilience in a single-plant-species system is qualitatively similar to Fig. 2C.

2. Resilience as a Function of Mortality Rates

The diversity in mortality rates affects resilience in much the same way as does the diversity in nutrient uptake rates (see Fig. 2D when $a_1 \geq a_2$). When $a_1 < a_2$, there is again generally an intermediate value of diversity for which resilience is maximised, but it tends toward zero as $a_1 - a_2$ becomes too small or too large (data not shown). There is also an intermediate value of the average mortality rate that maximises resilience, and resilience is relatively lower with higher diversity, when $a_1 \geq a_2$ (Fig. 2E). No general trend was found when $a_1 < a_2$. The variation of resilience in a single-plant-species system is again qualitatively similar to Fig. 2E.

3. Resistance as a Function of Nutrient Uptake Rates

The resistance of the inorganic nutrient pools in both the local resource depletion zones and the regional pool decreases with higher levels of diversity in nutrient uptake rates (data not shown). The lower the perturbation, the smaller the relative displacement, as expected.

The resistance of total plant biomass decreases with increased diversity when mortality rates are equal; and the higher the average nutrient uptake rate, the lower the relative displacement (Fig. 3A). (Recall that resistance is highest when the relative displacement is zero, and decreases as the relative displacement grows toward either positive or negative values.) However, for some specific values of b_1 and b_2 (see Eq. A7), resistance of plant biomass can increase with higher diversity up to a certain level beyond which it decreases, but this is dependent on the amount of perturbation (Fig. 3B). Large perturbations destroy this property. The relative displacement crosses zero for some values of a_1 and a_2 within the region of feasible equilibria for certain levels of perturbation (see Eq. A7). Resistance of plant biomass increases with the average nutrient uptake rate, and this increase is larger when diversity is lower (Fig. 3C).

As regards energy flow or total primary productivity, complex behaviours are observed when diversity increases, even for equal mortality rates (Fig. 3D). In some cases, resistance at first decreases, then increases, and eventually decreases again (solid curve). But it decreases monotonically when the average nutrient uptake rate is higher (dashed curve), and it always does so for large perturbations, irrespective of the average nutrient uptake rate (data not shown). The resistance of productivity as a function of diversity is very sensitive to model parameters. For example, Fig. 3E shows a peculiar type of behaviour for some specific values of b_1

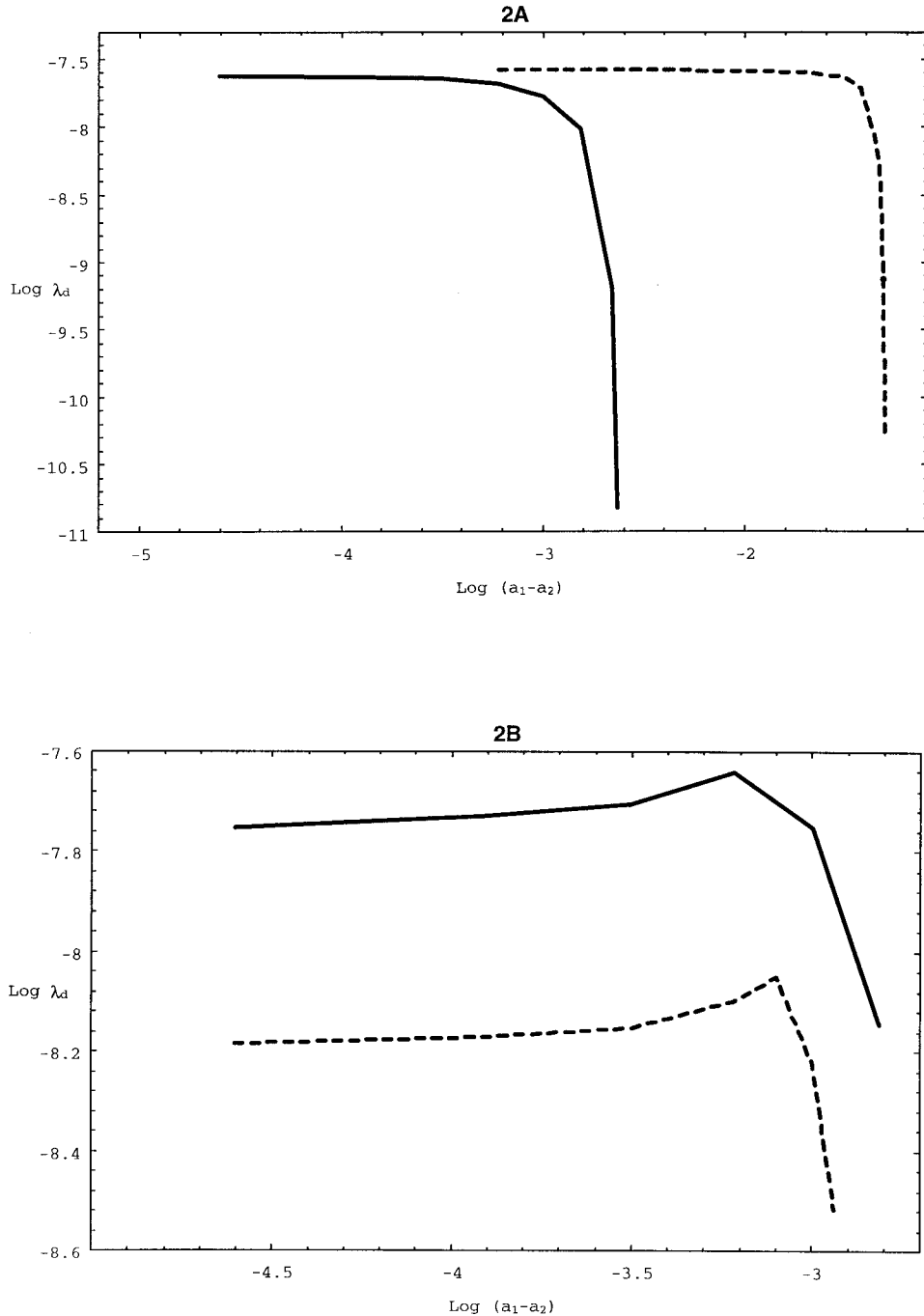


FIG. 2. Effects of nutrient uptake and mortality rates on resilience. (A) Resilience (as measured by the log-transformed absolute value of the dominant eigenvalue) as a function of the diversity in nutrient uptake rates (as measured by the log-transformed difference between the nutrient uptake rates of the two species), for two values of the average uptake rate, when $b_1 = b_2$. (B) Resilience as a function of diversity in nutrient uptake rates, for two values of the difference in mortality rates, when $b_1 < b_2$. (C) Resilience as a function of the log-transformed average nutrient uptake rate, for two values of the diversity in uptake rates. (D) Resilience as a function of the diversity in mortality rates, for two values of the average mortality rate. (E) Resilience as a function of the log-transformed average mortality rate, for two values of the diversity in mortality rates. Parameter values: $k = 0.8$, $R_0 = 1.2$, $q = 0.06$, $l = 0.06$, $r = 0.06$, $\sigma = 0.3$. (A) $b_1 = b_2 = 0.009$, $a_1 + a_2 = 0.1$ (solid line) or 0.3 (dashed line). (B) $a_1 + a_2 = 0.1$, $b_1 + b_2 = 0.018$, $b_1 - b_2 = -0.003$ (solid line) or -0.009 (dashed line). (C) $b_1 = b_2 = 0.009$, $a_1 - a_2 = 0.1$ (solid line) or 0.5 (dashed line). (D) $a_1 = a_2 = 0.3$, $b_1 + b_2 = 0.1$ (solid line) or 0.3 (dashed line). (E) $a_1 = a_2 = 0.3$, $b_1 - b_2 = 0.05$ (solid line) or 0.1 (dashed line).

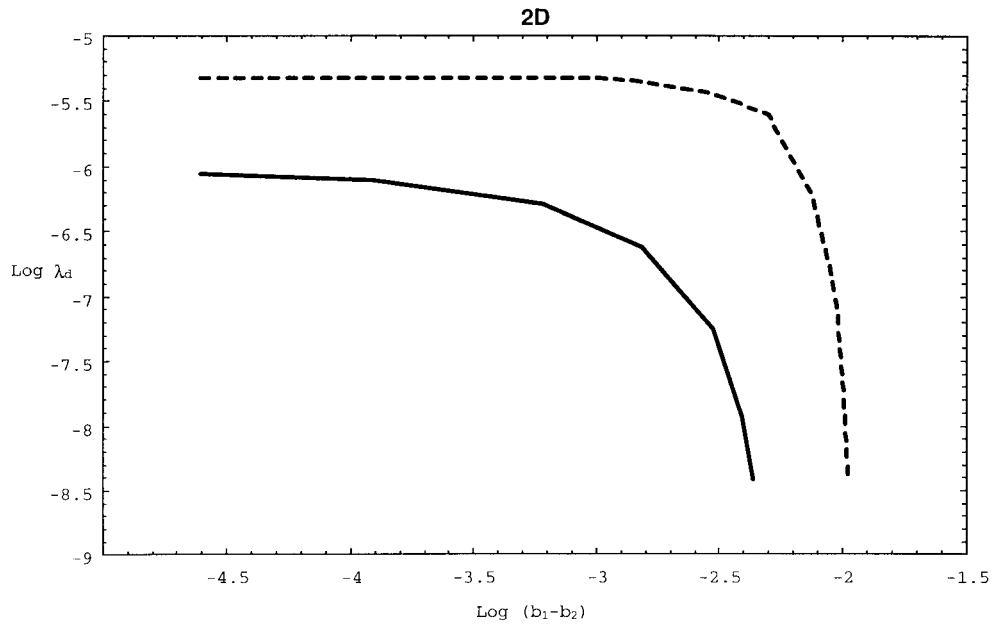
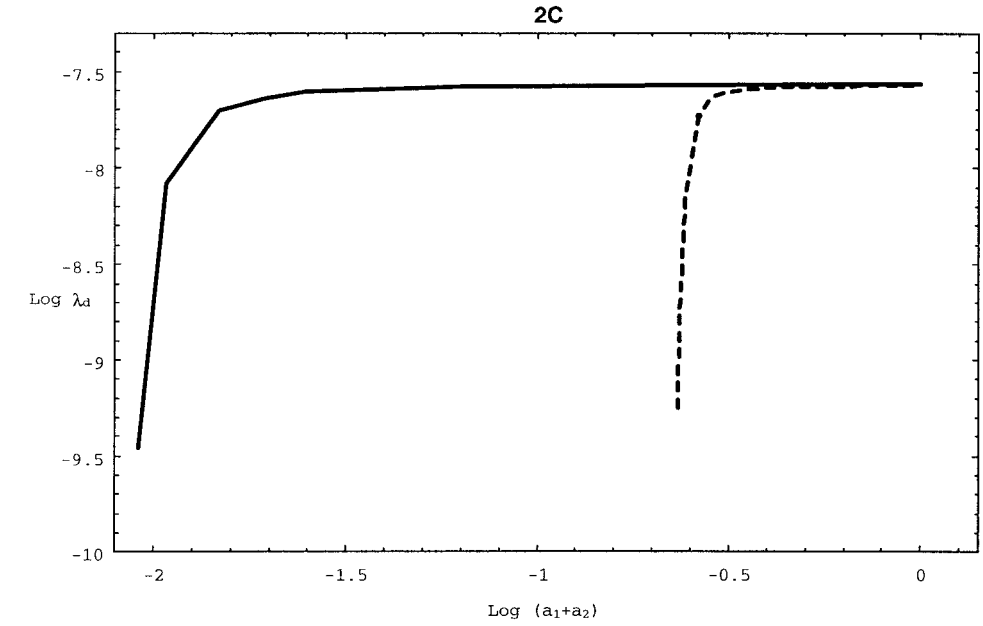


FIG. 2.—Continued

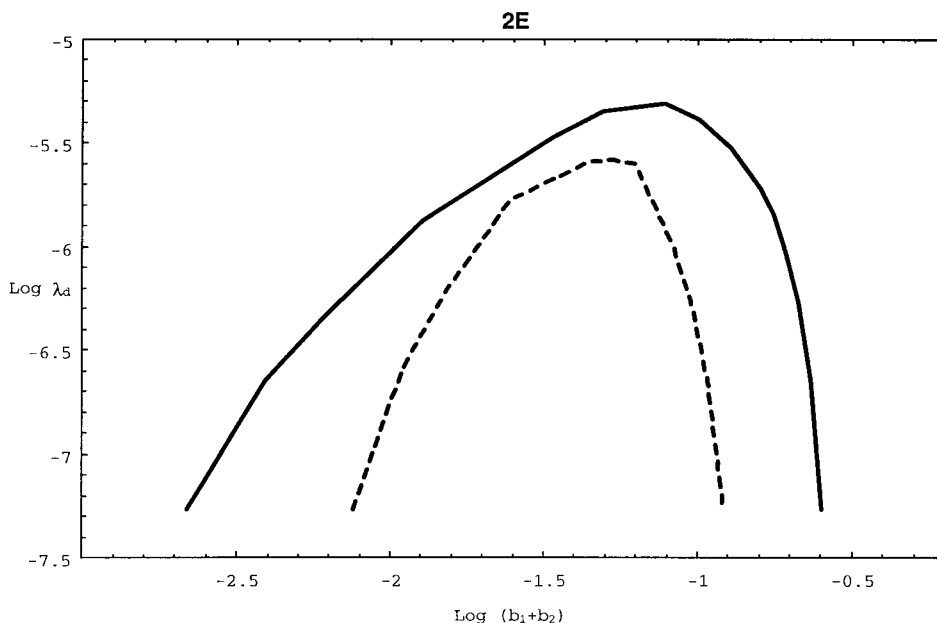


FIG. 2.—Continued

and b_2 . Another special type of behaviour is observed for the resistance of energy flow as a function of the average nutrient uptake rate: it increases at first, then decreases, and finally increases again (Fig. 3F). This behaviour is observed for all values of the perturbation (data not shown).

4. Resistance as a Function of Mortality Rates

The resistance of the inorganic nutrient pools in both the local resource depletion zones and the regional pool decreases with higher levels of diversity in mortality rates, just as for nutrient uptake rates (data not shown). However, the relative displacements of these compartments become zero when $a_1 = a_2$ (see Eqs. A9 and A10).

The resistance of plant biomass generally decreases with increased diversity, and is relatively higher for a lower average mortality rate only up to certain level of diversity (Fig. 4A). These observations hold good irrespective of the amount of perturbation (data not shown). However, for some specific values of a_1 and a_2 , resistance can increase with diversity (Fig. 4B). The relative displacement becomes zero at a lower level of diversity when the perturbation is larger. In other words, the range of diversity for which resistance increases with diversity is reduced for larger perturbations. This initial increase in resistance is sometimes destroyed by very large perturbations (data not shown). Finally, the resistance of plant biomass has a maximum at an intermediate value of the average mortality rate (Fig. 4C).

The resistance of energy flow decreases with increased diversity when $a_1 = a_2$ (Fig. 4D). But it may slightly increase initially and later decrease for a small perturbation and some specific values of a_1 and a_2 (Fig. 4E). An increased average mortality increases resistance in the initial phase only (Fig. 4F).

DISCUSSION

The present model abstracts some of the fundamental effects of diversity on ecosystem stability. Phenotypic diversity is here defined as variability in plant traits. This definition presents the advantage of being amenable to direct translation in terms of model parameters and experimental measurement, and of being general enough to apply to several hierarchical levels of biodiversity. Although our model was here applied to plants grouped in two species, it is built on an individual-based approach (Huston and DeAngelis, 1994; Loreau, 1996, 1998); therefore, both our model and our definition of phenotypic diversity can apply to any type of grouping of individuals with similar traits, whether functional groups, species, genotypes, or the individuals themselves. In this study, we limited ourselves to a simple system with two species (or other groupings), because it can be analysed systematically. This investigation could obviously be generalised to any number of species, though at the expense of its systematic nature. One alternative would be to choose a particular distribution of traits and study the effect of the number of species or the

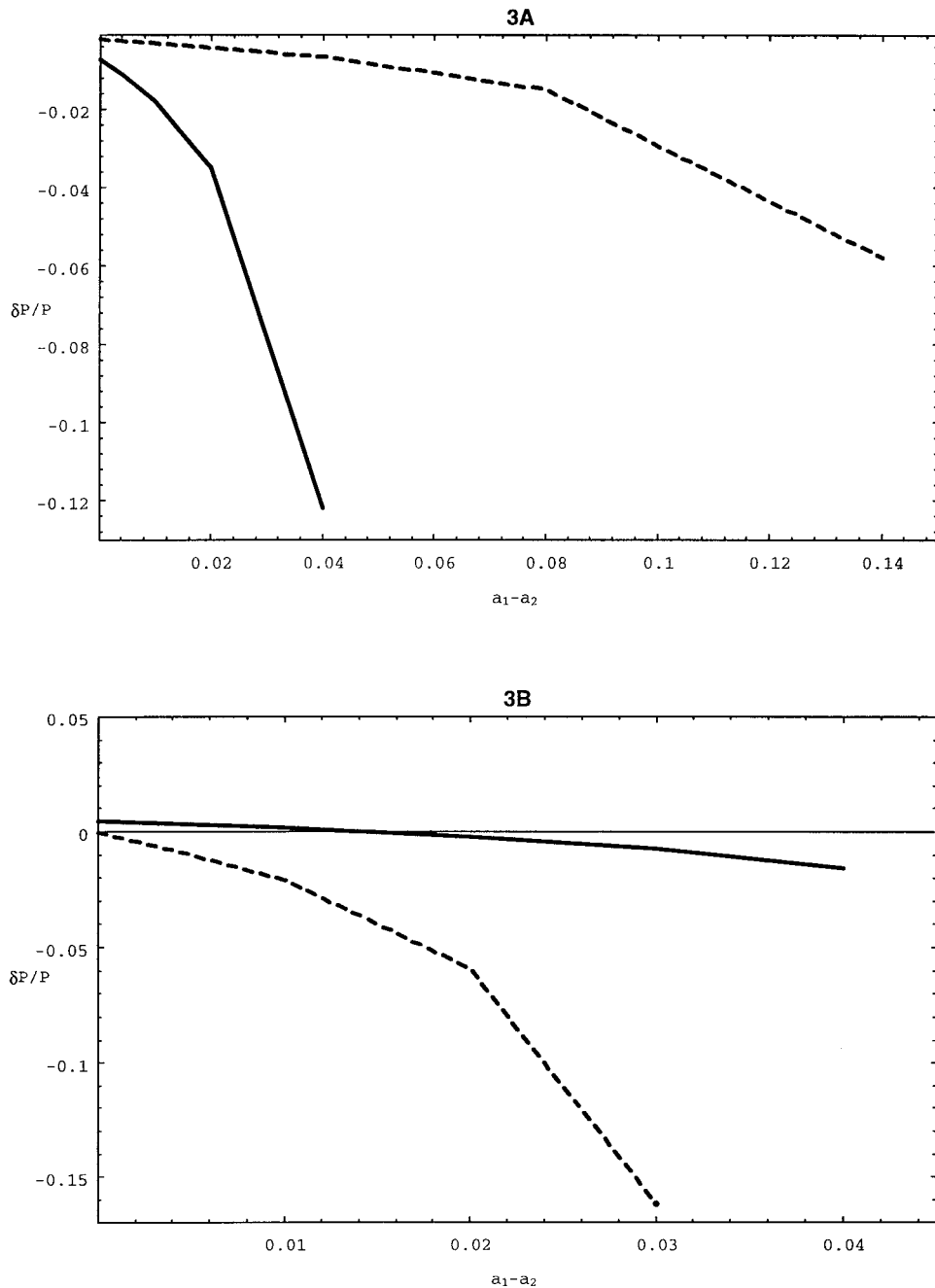


FIG. 3. Effects of nutrient uptake rates on resistance. (A) Resistance (as measured by the relative ultimate displacement) of total plant biomass as a function of the diversity in nutrient uptake rates (as measured by the difference between the nutrient uptake rates of the two species), for two values of the average uptake rate. (B) Resistance of total plant biomass as a function of the diversity in nutrient uptake rates, for two perturbation magnitudes. (C) Resistance of total plant biomass as a function of the average nutrient uptake rate, for two values of diversity. (D) Resistance of total plant productivity as a function of the diversity in nutrient uptake rates, for two values of the average uptake rate. (E) Resistance of total plant productivity as a function of the diversity in nutrient uptake rates, for two perturbation magnitudes. (F) Resistance of total plant productivity as a function of the average nutrient uptake rate, for two values of diversity. Parameter values: $k = 0.8$, $R_0 = 1.2$, $q = 0.06$, $l = 0.06$, $r = 0.06$, $\sigma = 0.3$. (A) $b_1 = b_2 = 0.009$, $\delta = 0.2$, $a_1 + a_2 = 0.1$ (solid line) or 0.3 (dashed line). (B) $a_1 + a_2 = 0.1$, $b_1 = 0.007$, $b_2 = 0.01$, $\delta = 0.1$ (solid line) or 0.4 (dashed line). (C) $b_1 = b_2 = 0.009$, $\delta = 0.2$, $a_1 - a_2 = 0.1$ (solid line) or 0.5 (dashed line). (D) $b_1 = b_2 = 0.009$, $\delta = 0.1$, $a_1 + a_2 = 0.1$ (solid line) or 0.3 (dashed line). (E) $a_1 + a_2 = 0.1$, $b_1 = 0.001$, $b_2 = 0.01$, $\delta = 0.2$ (solid line) or 0.4 (dashed line). (F) $b_1 = b_2 = 0.009$, $\delta = 0.2$, $a_1 - a_2 = 0.1$ (solid line) or 0.5 (dashed line).

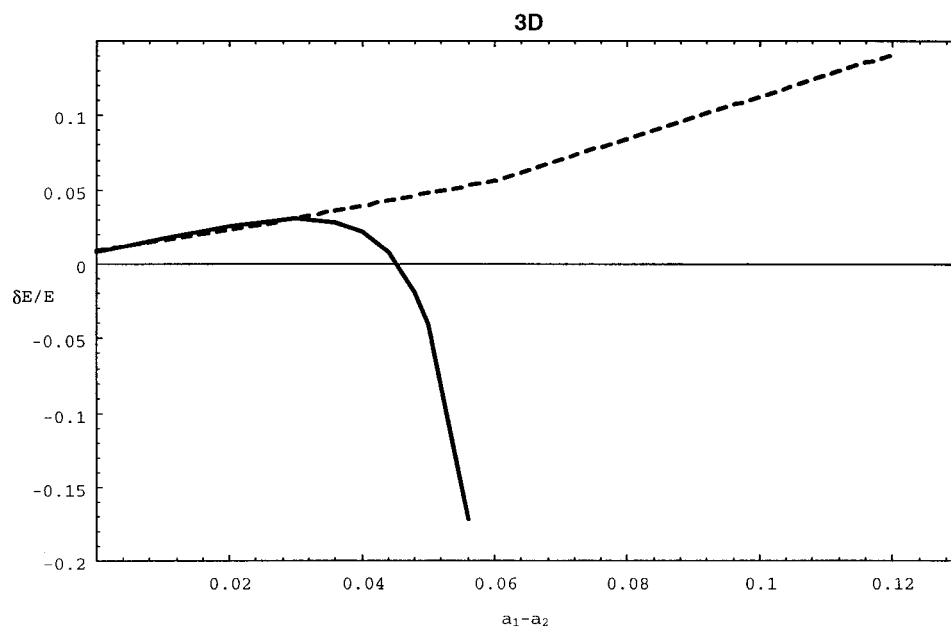
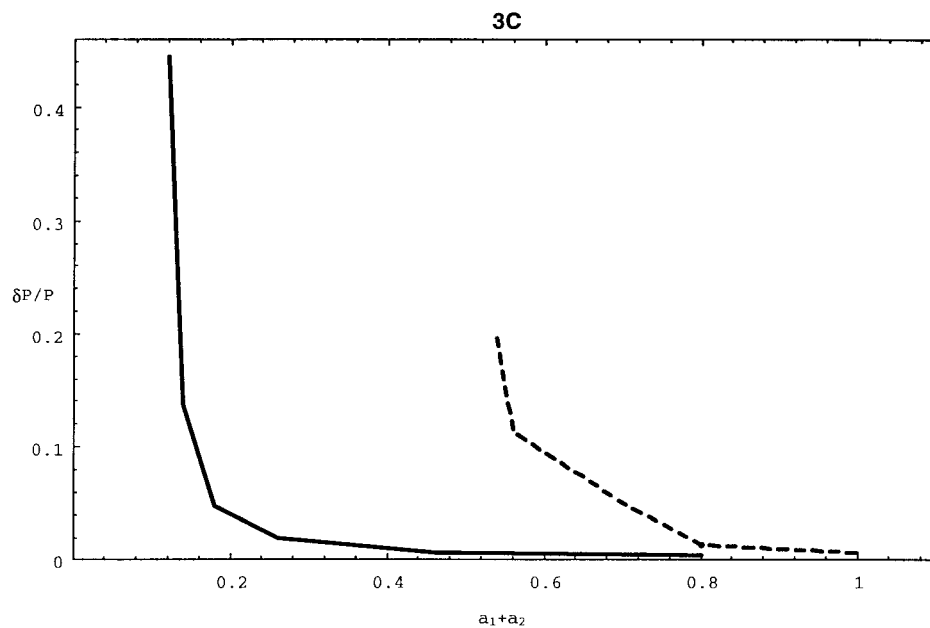


FIG. 3.—Continued

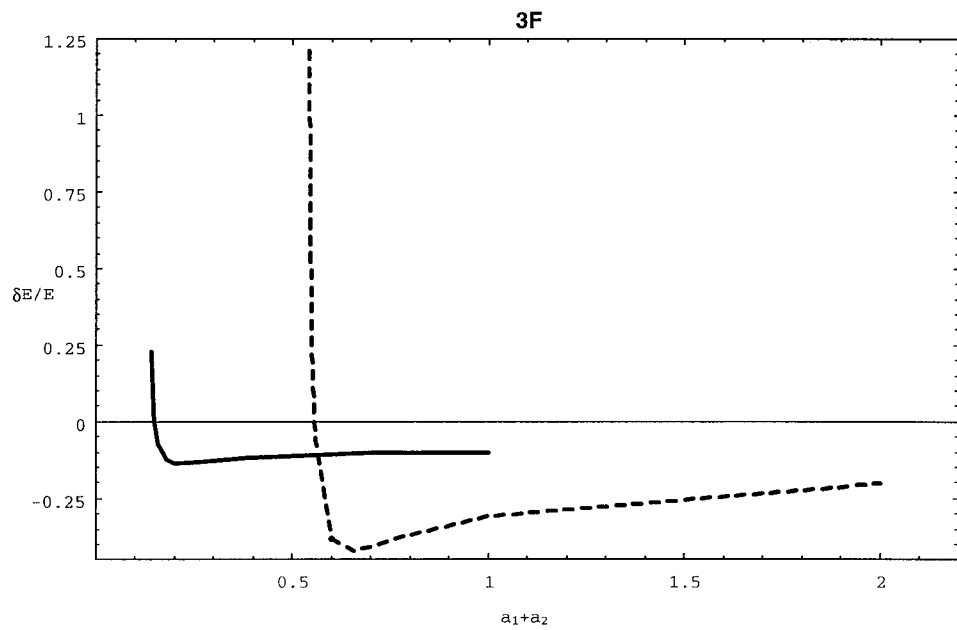
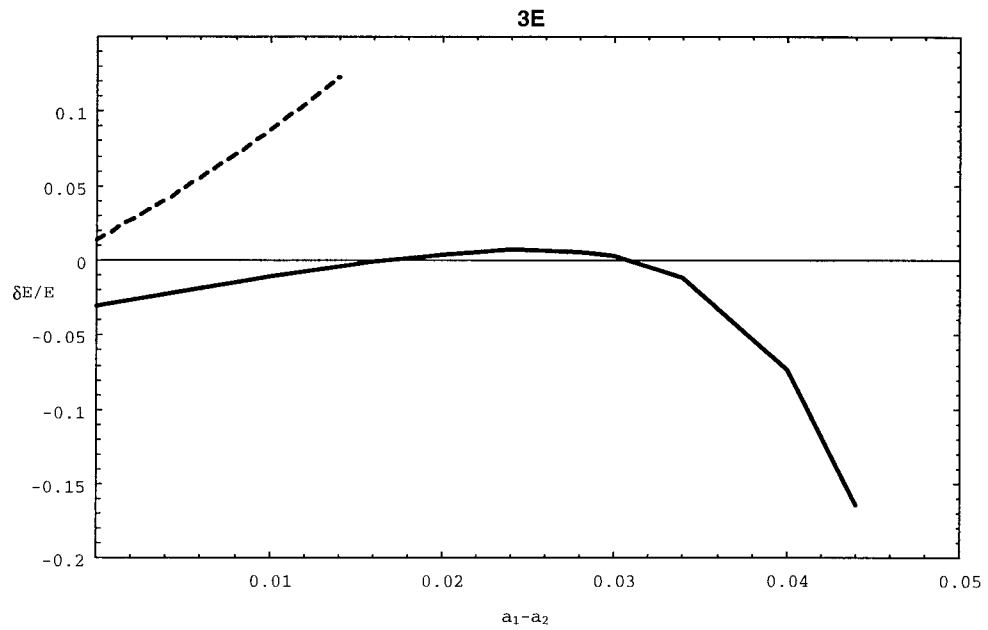


FIG. 3.—Continued

type of distribution on ecosystem stability. Our analysis of the simple two-species system shows that the relationship between diversity and stability of ecosystem processes is very complex; it is highly doubtful that it would be any simpler with more species.

Resilience, as is commonly measured by the dominant eigenvalue of the Jacobian matrix of the system at equilibrium, has the pleasing property of characterising the system as a whole and applying to any system component. It is then easy to show that any aggregated ecosystem process that is a function of several components, as is energy flow in (14), has the same measure of resilience, unless there are special symmetries in the system (Appendix 3). This alone makes hopes vanish that the resilience of aggregated processes in ecosystems in general changes with diversity in a different direction from that of their constituent populations—at least as far as the classical measure of resilience is concerned.

In the context of the present model, resilience was found to increase with the nutrient uptake rate and to peak at an intermediate value of the mortality rate in a single-plant-species system. It generally follows the same patterns as a function of the average nutrient uptake or mortality rate in the two-plant-species system. There is often an intermediate value of diversity for a trait (either nutrient uptake rate or mortality rate) that maximises resilience when one species has a higher nutrient uptake rate and the other a higher mortality rate. But resilience decreases as the diversity for the other trait increases, and it always decreases with diversity when the species with the higher nutrient uptake rate (or mortality rate) also has a mortality rate (or nutrient uptake rate) that is equal to or greater than that of the other species. As a result, the ecosystem can return to its equilibrium value faster following a perturbation if the two species have identical traits, i.e., if diversity is zero. This conclusion of our spatially structured model is opposite to that usually obtained for spatially homogeneous systems, in which resilience tends to zero as two species tend to be functionally similar (e.g., Armstrong, 1982). However, this difference is explained by a difference in the conceptual approach to diversity or similarity. In spatially homogeneous systems, where coexistence of several species in the same niche or on the same resource at equilibrium is impossible, similarity is usually defined in terms of similarity of ecological niche or resource use. In the present spatially structured system, coexistence on the same limiting nutrient is made possible by the spatial distinction of the resource depletion zones of the various species (or genotypes, individuals, etc.). Alternatively, this spatial distinction may be viewed as a built-in difference in the resources used by the various species (Abrams, 1988),

although it is only a partial one, governed by the rate of nutrient transport from the common regional pool. Similarity is here defined directly in terms of the parameters that govern plant growth.

The generally negative effect of diversity on resilience can then be explained as follows. The dominant eigenvalue of the linearized system at equilibrium is determined by those compartments and processes which are slowest to return to equilibrium. Thus, when there are two plant species with different parameter values, the system's resilience will be essentially limited by that plant whose parameters tend to decrease resilience most. Now, resilience is a concave function of both the nutrient uptake and mortality rates (Figs. 2C and 2E). Therefore, as diversity for one trait increases while the average value of the trait is kept constant, at least one plant will have its trait changed in the direction of decreased resilience, and this effect will generally be dominant. However, resilience can reach a maximum for an intermediate value of diversity if the two plants have different values for the other trait in such a way that there is a shift in the species that limits resilience as diversity is increased. For instance, in Fig. 2B, $b_2 > b_1$. But resilience increases with b over a large part of the range of feasible b values (Fig. 2D). If b_1 and b_2 lie in that part of the range, resilience is limited by species 1 when diversity in a is zero ($a_1 - a_2 = 0$). When this diversity is increased, resilience at first increases, because a_1 increases and this has a positive effect on resilience (Fig. 2C). However, a_2 also decreases, so that eventually species 2 comes to limit resilience, and any further increase in diversity then decreases resilience. This generates the pattern observed in Fig. 2B. The other results can be explained similarly.

Resistance is a property that characterises each system component and process separately; accordingly its relation to diversity is complex. The resistance of the inorganic nutrient pools in both the local resource depletion zones and the regional pool, and hence the resistance of nutrient retention in the ecosystem, always decreases with increased diversity. The resistance of total plant biomass also decreases with increased diversity in nutrient uptake rates (or mortality rates) when the two species have equal mortality rates (or nutrient uptake rates). This can be observed directly from Eqs. (A7) and (A11). However, the resistance of plant biomass can increase with diversity for some parameter values when the two species differ in both traits. In such a situation, the relative displacement curve was always found to cross zero. It can be seen from Eq. (A7) that this occurs when

$$\frac{a_2(a_2 - \delta a_1)}{a_1(a_1 + \delta a_1)} = \frac{(1 + k\alpha) b_1 b_2 - k\alpha b_2^2}{(1 + k\alpha) b_1 b_2 - k\alpha b_1^2}. \quad (25)$$

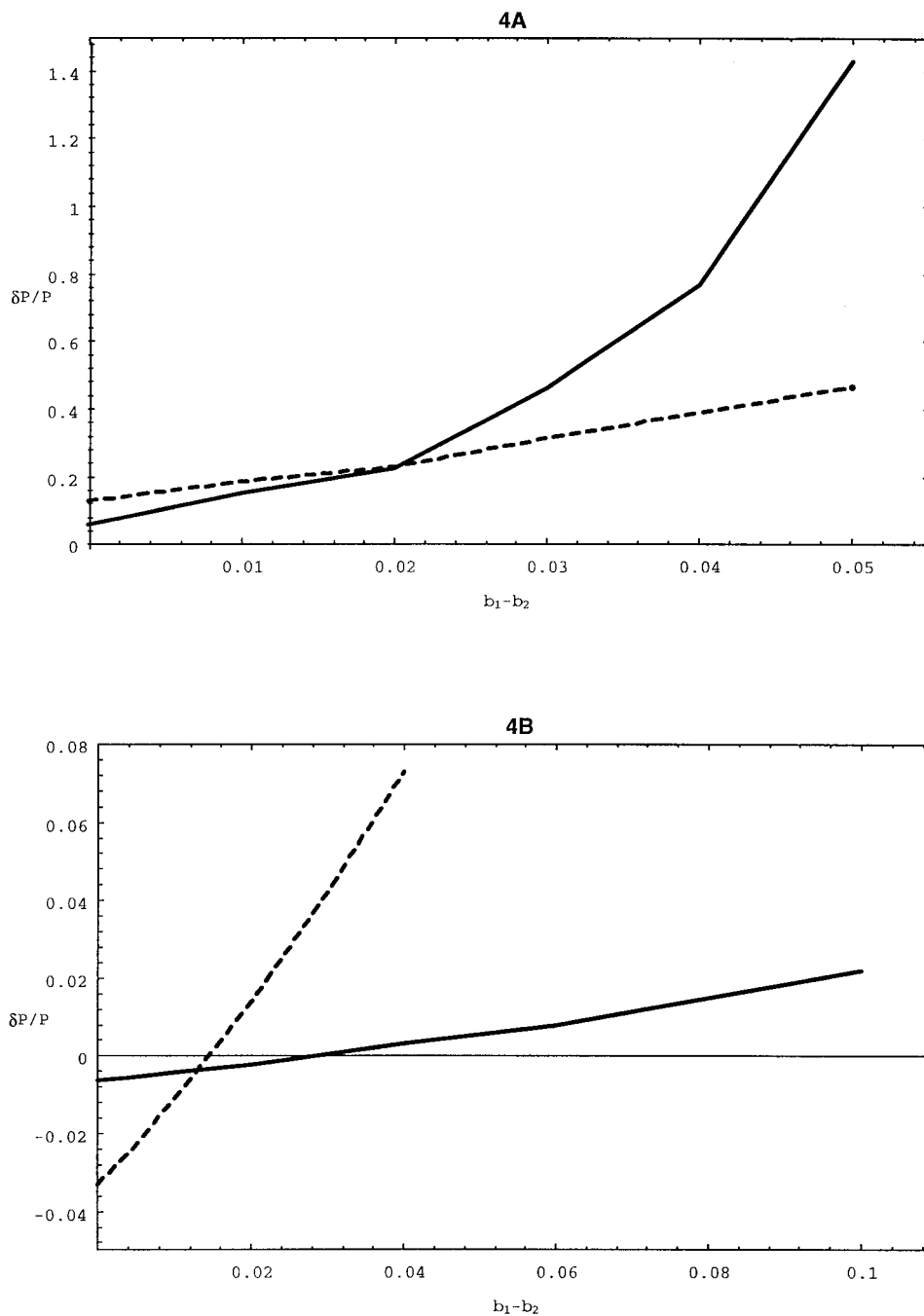


FIG. 4. Effects of mortality rates on resistance. Legend as in Fig. 3, except that mortality rates replace nutrient uptake rates. Parameter values: $k = 0.8$, $R_0 = 1.2$, $q = 0.06$, $l = 0.06$, $r = 0.06$, $\sigma = 0.3$. (A) $a_1 = a_2 = 0.3$, $\delta = 0.2$, $b_1 + b_2 = 0.1$ (solid line) or 0.3 (dashed line). (B) $a_1 = 0.5$, $a_2 = 0.2$, $b_1 + b_2 = 0.3$, $\delta = 0.01$ (solid line) or 0.1 (dashed line). (C) $a_1 = a_2 = 0.3$, $\delta = 0.2$, $b_1 - b_2 = 0.05$ (solid line) or 0.1 (dashed line). (D) $a_1 = a_2 = 0.3$, $\delta = 0.2$, $b_1 + b_2 = 0.1$ (solid line) or 0.3 (dashed line). (E) $a_1 = 0.28$, $a_2 = 0.32$, $b_1 + b_2 = 0.1$, $\delta = 0.01$ (solid line) or 0.1 (dashed line). (F) $a_1 = a_2 = 0.3$, $\delta = 0.2$, $b_1 - b_2 = 0.05$ (solid line) or 0.1 (dashed line).

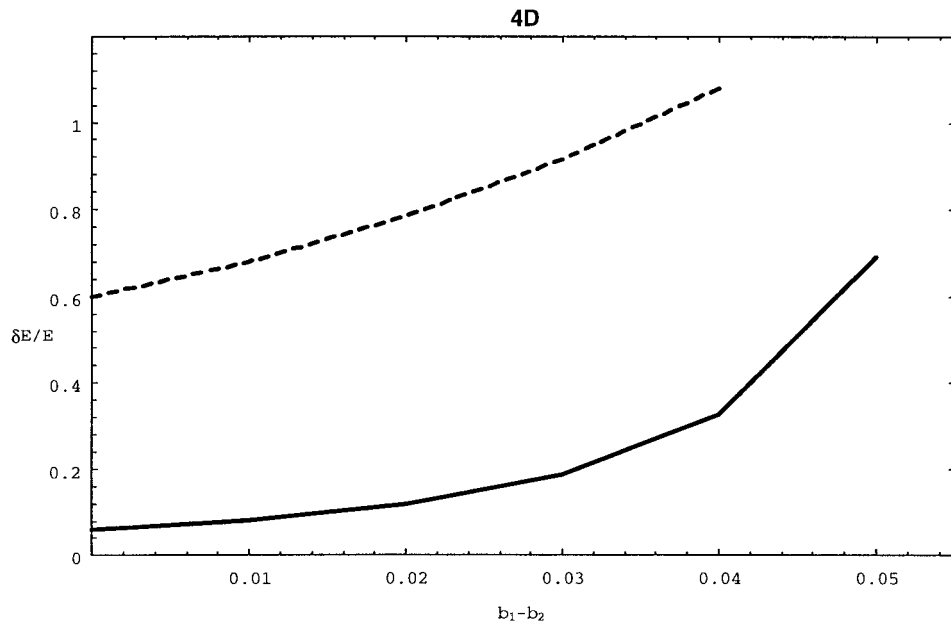
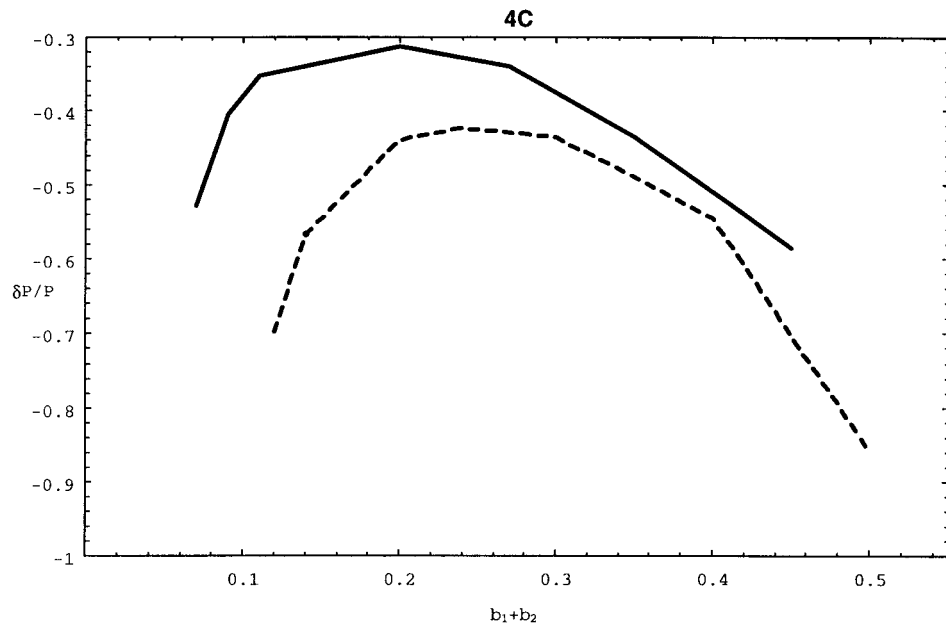


FIG. 4.—Continued

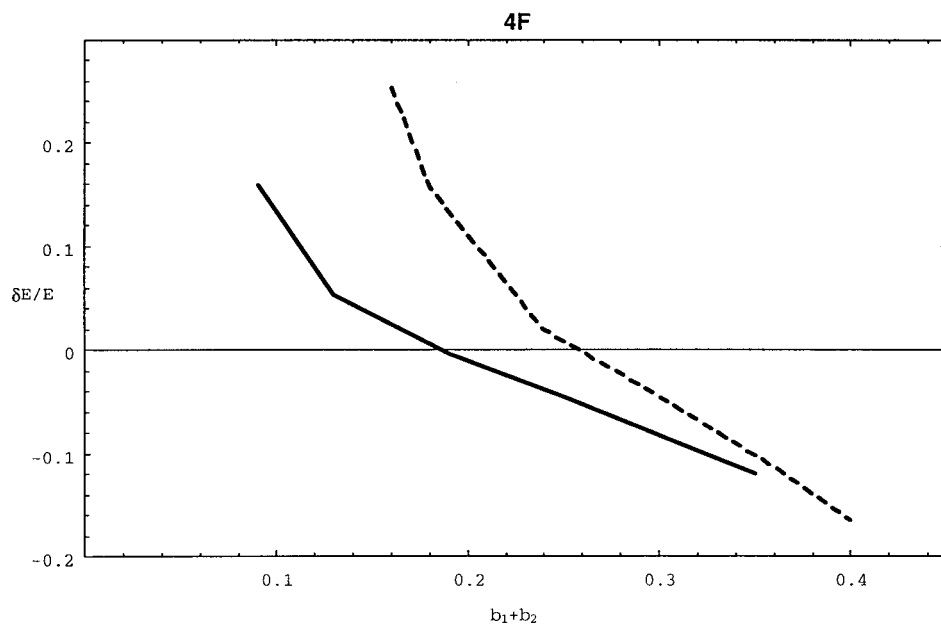
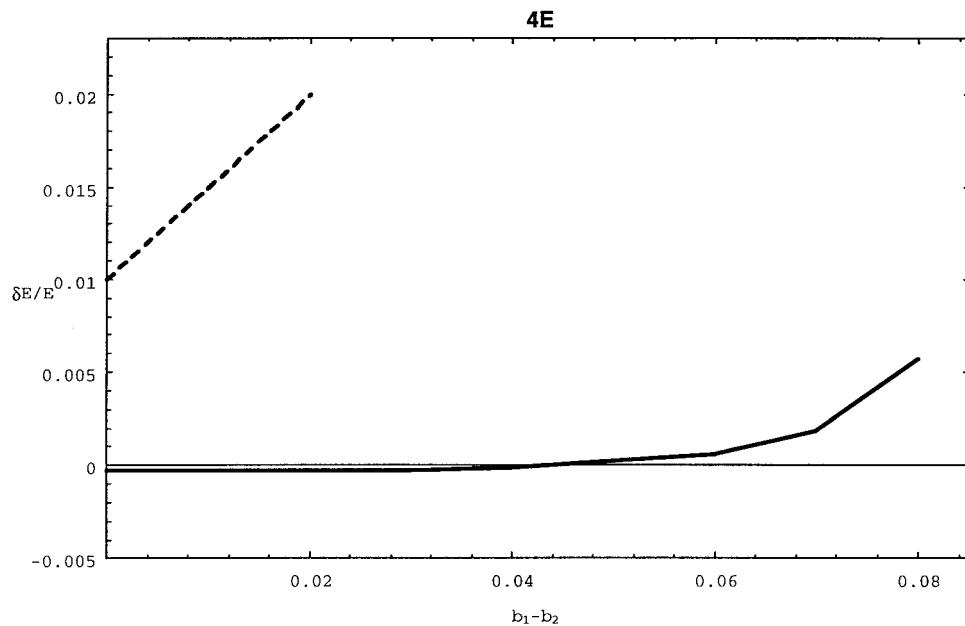


FIG. 4.—Continued

A similar condition can be found from Eq. (A11). This property of increased resistance with a higher diversity can, however, be destroyed by large perturbations.

The resistance of energy flow or total primary productivity can either increase or decrease with increased diversity. This can also be observed directly from Eqs. (A8) and (A12). When it increases with diversity, it is always over a limited range of diversity. Further, its behaviour is extremely sensitive to parameter values. Finally, the resistance of both plant biomass and productivity can also increase, under certain conditions, as the average nutrient uptake and mortality rates are increased.

It may be worthwhile to mention an alternative approach to studying the behaviour of resistance as a function of biodiversity. Diversity could also be defined here as variability, not in the plant traits themselves, but in the perturbations of these traits. Resistance would then be studied as a function of the difference between the perturbations of some trait for fixed initial trait parameter values. Given the sensitivity of resistance to parameter values, including parameter δ determining the relative magnitude of the perturbation, we expect that basic conclusions similar to the present ones would emerge from such a study.

There is always a potential for discrepancy between a model and a real experimental situation. Therefore model limitations have to be borne in mind. In particular, the present model applies to ecosystems in which the nutrient supply is low enough for light or other factors not to become major limiting factors on plant growth (Loreau, 1996). We need to understand how exactly environmental stresses affect flow rates in order to develop a complete theory of resistance of nutrient stocks and fluxes to such stresses. Our study assumes that the ecosystem is perturbed from its equilibrium state and that the ultimate displacement is recorded after a new equilibrium is reached. There may not be any consistent relationship between the relative displacement of a compartment or process and diversity over the entire displacement trajectory, as our own observations suggest. Also, the volume of the local resource depletion zones may not remain constant as the environment changes; in particular, in the long run some species should increase the amount of space they occupy at the expense of others, whether by vegetative growth or reproduction and dispersal. Thus, our work clearly does not cover all potential mechanisms of compensation between species.

The most critical limitation of this and most previous theoretical works on the relationship between ecosystem stability and diversity, however, may lie in their deterministic, equilibrium approach to this issue. If ecosystems

are nonequilibrium systems at the timescale implicitly considered in this modelling work or in recent experiments, the classical equilibrium analysis of resilience and resistance may be inappropriate for addressing the relationship between diversity and stability or predictability as it is observed in the field or in the laboratory (Tilman, 1996; McGrady-Steed *et al.*, 1997; Naeem and Li, 1997). Reduced variability of aggregated ecosystem processes at a high species diversity may occur because of simple statistical properties of population fluctuations (Doak *et al.*, 1998; Tilman *et al.*, 1998). Statistical effects generated by asynchronicity of species responses to a fluctuating environment are very robust (Yachi and Loreau, 1999), and have little to do with a system's equilibrium properties.

An equilibrium analysis might, however, be relevant to Tilman and Downing's (1994) experimental system, because this experienced a single perturbation in time. Why then did they find an increase in resistance and resilience of total plant biomass with increased diversity while our theoretical analysis suggests this to be unlikely? First, their measure of resilience was inadequate because it was dependent on the size of the perturbation; once corrected for this factor, the effect of diversity on resilience of total biomass disappeared (Tilman, 1996). If anything, resilience may have been lower, rather than higher, in more diverse ecosystems, as suggested by the (weakly) higher variability of the biomass of individual plant species, in agreement with our model. Second, our model is able to reproduce the positive effect of diversity on the resistance of total plant biomass, which was still significant after controlling for confounding factors (Tilman, 1996), for a region of parameter space. But it also shows that this outcome is very sensitive to parameter values, so that the explanation is likely to lie elsewhere. There is an important difference between Tilman and Downing's (1994) experimental system and our model. In our model, the effect of phenotypic diversity was studied *per se*, while keeping average parameter values constant. In their experiment, drought was a "negative" perturbation overall, which had a negative effect on most species simultaneously. This amounts to changing both the difference and the average of trait values simultaneously. There are good reasons to believe that diversity should have a positive effect on the resistance of total plant biomass in the case of a "negative" perturbation. Increasing phenotypic diversity increases the probability to have a species that is less negatively affected by the perturbation, and this species should tend to become dominant in the community because it is best adapted to the conditions prevailing during the perturbation. But the same argument suggests

that the resistance of plant biomass should also be lower in the case of a “positive” perturbation, i.e., a perturbation that has an intrinsically positive effect on the biomass of most species (before competition has taken place), such as might be the case with nitrogen addition for instance. In this case indeed, increasing phenotypic diversity increases the probability to have a species that is more positively affected by the perturbation, and this species should tend to become dominant in the community. Thus, resistance of ecosystem processes may still either increase or decrease depending on the type of perturbation.

The main lesson from the present work is that the classical approaches to resilience and resistance in the neighborhood of the equilibrium in conceptually simple systems are unlikely to reveal a systematic positive relationship between diversity and the stability of ecosystem processes. This suggests that (1) the currently available experimental data may be insufficient to draw general conclusions on the relationship between diversity and the stability of ecosystem processes; or (2) the observed relationships may have little to do with the theoretical insights from equilibrium deterministic systems.

APPENDIX 1

Resilience of the Model Ecosystem

The local stability of the equilibrium of model ecosystem (1)–(4) for two plant species is determined by the eigenvalues of its Jacobian matrix, which has the form

$$\mathbf{J} = \begin{bmatrix} -q - k \sum_{j=1}^2 \sigma_j & \mathbf{B}_1 & \mathbf{B}_2 \\ \mathbf{C}_1 & \mathbf{A}_1 & \mathbf{0} \\ \mathbf{C}_2 & \mathbf{0} & \mathbf{A}_2 \end{bmatrix}, \quad (\text{A1})$$

Perturbation of Nutrient Uptake Rates

$$\frac{\delta R^*}{R^*} = \left(\frac{-\delta}{1+\delta} \right) \frac{k\alpha [b_1 a_2 (a_2 \pm \delta a_1) \pm b_2 a_1 (a_1 + \delta a_1)]}{(a_2 \pm \delta a_1) [R_0 a_1 a_2 + k\alpha (b_2 a_1 + b_1 a_2)]} \quad (\text{A5})$$

$$\frac{\delta L^*}{L^*} = \left(\frac{-\delta}{1+\delta} \right) \frac{b_1 a_2 (a_2 \pm \delta a_1) \pm b_2 a_1 (a_1 + \delta a_1)}{(a_2 \pm \delta a_1) (b_2 a_1 + b_1 a_2)} \quad (\text{A6})$$

where $\mathbf{0}$ is the zero matrix,

$$\mathbf{A}_i = \sigma_i \begin{bmatrix} -(k + a_i P_i^*) & -b_i & l_i \\ a_i P_i^* & 0 & 0 \\ 0 & b_i & -(l_i + r_i + q) \end{bmatrix}, \quad (\text{A2})$$

$$\mathbf{B}_i = \sigma_i [k \quad 0 \quad r_i], \quad (\text{A3})$$

and

$$\mathbf{C}_i = \sigma_i \begin{bmatrix} k \\ 0 \\ 0 \end{bmatrix}. \quad (\text{A4})$$

The matrix \mathbf{A}_i describes the interactions within local subsystem i , while the vectors \mathbf{B}_i and \mathbf{C}_i describe its coupling with the regional pool. Note that they are multiplied by a factor σ_i because Eqs. (2)–(4) have to be multiplied by this same factor to obtain the mass-balance equation (6).

Loreau (1996) proved that a more general form of this system containing herbivores and their associated detritus was qualitatively stable. Therefore the dominant eigenvalue of \mathbf{J} is negative and its absolute value can be used as a measure of resilience.

APPENDIX 2

Relative Ultimate Displacements after Perturbation

Here we provide the analytical expressions for the relative ultimate displacements of the aggregated compartments and processes after perturbation of the model ecosystem, as described in Eqs. (21)–(24), in both the case where nutrient uptake rates are perturbed and the case where mortality rates are perturbed. When a \pm or \mp sign appears in the equations, it should be understood that the upper and lower sign correspond to perturbations of parameters in the same and opposite directions, respectively, in the two species.

$$\frac{\delta P^*}{P^*} = \left(\frac{\delta}{1+\delta} \right) \frac{a_2(a_2 \pm \delta a_1)[(1+k\alpha) b_1 b_2 - k\alpha b_1^2] \pm a_1(a_1 + \delta a_1)[(1+k\alpha) b_1 b_2 - k\alpha b_2^2]}{(a_2 \pm \delta a_1)[k\alpha(b_1 - b_2)(b_1 a_2 - b_2 a_1) + R_0 a_1 a_2 (b_1 + b_2) - b_1 b_2 (a_1 + a_2)]} \quad (A7)$$

$$\frac{\delta E^*}{E^*} = \left(\frac{\delta}{1+\delta} \right) \frac{a_2(a_2 \pm \delta a_1)[2(1+k\alpha) a_2 b_1 - k\alpha a_1 (b_1 + b_2) - R_0 a_1 a_2] \pm a_1(a_1 + \delta a_1)[2(1+k\alpha) a_1 b_2 - k\alpha a_2 (b_1 + b_2) - R_0 a_1 a_2]}{(a_2 \pm \delta a_1)[k\alpha a_1 a_2 (b_1 + b_2) - (1+k\alpha)(b_1 a_2^2 + b_2 a_1^2) + R_0 a_1 a_2 (a_1 + a_2)]}. \quad (A8)$$

Perturbation of Mortality Rates

$$\frac{\delta R^*}{R^*} = \frac{\delta b_1 k\alpha (a_2 \pm a_1)}{k\alpha (b_1 a_2 + b_2 a_1) + R_0 a_1 a_2} \quad (A9)$$

$$\frac{\delta L^*}{L^*} = \frac{\delta b_1 (a_2 \pm a_1)}{b_1 a_2 + b_2 a_1} \quad (A10)$$

$$\frac{\delta P^*}{P^*} = \left(\frac{\delta}{1+\delta} \right) \frac{a_1 b_2 (b_2 \pm \delta b_1)[k\alpha (\pm b_1 - b_2) - R_0 a_2] + a_2 b_1 (b_1 + \delta b_1)[k\alpha (\mp b_1 + b_2) \mp R_0 a_1]}{(b_2 \pm \delta b_1)[k\alpha (a_1 b_2^2 + a_2 b_1^2) - (1+k\alpha) b_1 b_2 (a_1 + a_2) + R_0 a_1 a_2 (b_1 + b_2)]} \quad (A11)$$

$$\frac{\delta E^*}{E^*} = \left(\frac{\delta}{1+\delta} \right) \frac{\left[a_2 b_2 (b_2 \pm \delta b_1) [(b_1 + \delta b_1) \{ k\alpha a_1 b_2 - (1+k\alpha) a_2 b_1 + R_0 a_1 a_2 \} + a_1 b_1 (\pm k\alpha b_1 - k\alpha b_2 - R_0 a_2)] \pm a_1 b_1 (b_1 + \delta b_1) [(b_2 \pm \delta b_1) \{ k\alpha a_2 b_1 - (1+k\alpha) a_1 b_2 + R_0 a_1 a_2 \} \pm a_2 b_2 (\mp k\alpha b_1 + k\alpha b_2 \mp R_0 a_1)] \right]}{b_1 b_2 (b_2 \pm \delta b_1) [k\alpha a_1 a_2 (b_1 + b_2) - (1+k\alpha)(b_1 a_2^2 + b_2 a_1^2) + R_0 a_1 a_2 (a_1 + a_2)]}. \quad (A12)$$

APPENDIX 3

Resilience of Aggregated Ecosystem Processes

Here we prove that aggregated ecosystem processes generally have the same measure of resilience as do all system compartments.

Denote by $X_i(t)$ the size of compartment i in the model ecosystem, by X_i^* its equilibrium value, and by $x_i(t) = X_i(t) - X_i^*$ a small perturbation from the equilibrium. Provided that the equilibrium is locally stable, in the long run this perturbation will decay exponentially according to

$$x_i(t) = C_i e^{-|\lambda_d|t}, \quad (A13)$$

where C_i is a constant that depends on initial conditions and λ_d is the dominant eigenvalue of the Jacobian matrix of the system at equilibrium. Resilience is measured by the rate of this long-term exponential decay, $|\lambda_d|$ (e.g., Webster *et al.*, 1975; DeAngelis, 1992).

Energy flow, as given by Eq. (14), is a sum of products of compartment sizes, which we may rewrite in a more general form as

$$E(t) = \sum_{i,j} c_{ij} X_i(t) X_j(t). \quad (A14)$$

Simple algebra shows that the perturbation to energy flow is then

$$\begin{aligned} E(t) - E^* &= \sum_{i,j} c_{ij} [X_i(t) X_j(t) - X_i^* X_j^*] \\ &= \sum_{i,j} c_{ij} [x_i(t) x_j(t) + X_i^* x_j(t) + X_j^* x_i(t)]. \end{aligned} \quad (A15)$$

It is easily seen from (A13) that the products $x_i(t) x_j(t)$ eventually decay at a rate $2|\lambda_d|$ while the linear terms in $x_i(t)$ and $x_j(t)$ decay at a slower rate $|\lambda_d|$. Therefore the latter is the long-term decay rate, hence the measure of resilience, of energy flow.

More generally, a small perturbation to any ecosystem process that is a complex function $f[X_1(t), X_2(t), \dots, X_n(t)]$ of n compartments can be approximated, by Taylor development of f , as

$$\begin{aligned} f[X_1(t), \dots, X_n(t)] - f[X_1^*, \dots, X_n^*] \\ = \sum_j \left(\frac{\partial f}{\partial X_j} \right)^* x_j(t) + O[x^2(t)] \end{aligned} \quad (A16)$$

in the vicinity of the equilibrium. Unless there are special symmetries in the system that lead to the linear terms associated with the dominant eigenvalue cancelling each other out, the long-term exponential decay rate of the perturbation to the ecosystem process will be the same as that of the perturbations to the system compartments; their resilience will therefore be the same.

ACKNOWLEDGMENTS

We thank D. L. DeAngelis, J. H. Lawton, S. Naeem, and two anonymous reviewers for their comments on the manuscript. N. Behera acknowledges a postdoctoral fellowship from the French Government (Centre International des Etudiants et Stagiaires, Paris). This work was partly supported by the Commission of the European Communities within the *Environment and Climate* programme.

REFERENCES

- Abrams, P. A. 1988. How should resources be counted? *Theor. Popul. Biol.* **33**, 226–242.
- Armstrong, R. A. 1982. The effects of connectivity on community stability, *Am. Nat.* **120**, 391–402.
- DeAngelis, D. L. 1975. Stability and connectance in food web models, *Ecology* **56**, 238–243.
- DeAngelis, D. L. 1992. “Dynamics of Nutrient Cycling and Food Webs,” Chapman & Hall, London, England.
- DeAngelis, D. L., Mulholland, P. J., Palumbo, A. V., Steinman, A. D., Huston, M. A., and Elwood, J. W. 1989. Nutrient dynamics and food-web stability, *Annu. Rev. Ecol. Syst.* **20**, 71–95.
- Doak, D. F., Bigger, D., Harding, E. K., Marvier, M. A., O'Malley, R. E., and Thomson, D. 1998. The statistical inevitability of stability–diversity relationships in community ecology, *Am. Nat.* **151**, 264–276.
- Elton, C. S. 1958. “The Ecology of Invasions by Animals and Plants,” Methuen, London, England.
- Gardner, M. R., and Ashby, W. R. 1970. Connectance of large dynamic (cybernetic) systems: Critical values for stability, *Nature* **228**, 784.
- Gilpin, M. E. 1975. Limit cycles in competition communities, *Am. Nat.* **109**, 51–60.
- Givnish, T. J. 1994. Does diversity beget stability? *Nature* **371**, 113–114.
- “Global Biodiversity Assessment,” 1995. Cambridge Univ. Press, Cambridge.
- Harrison, G. W. 1979. Stability under environmental stress: Resistance, resilience, persistence, and variability, *Am. Nat.* **113**, 659–669.
- Harrison, G. W., and Fekete, S. 1980. Resistance of nutrient cycling systems to perturbations of the flow rates, *Ecol. Model.* **10**, 227–241.
- Huston, M. A., and DeAngelis, D. L. 1994. Competition and coexistence: The effect of resource transport and supply rates, *Am. Nat.* **144**, 954–977.
- King, A. W., and Pimm, S. L. 1983. Complexity, diversity and stability: A reconciliation of empirical and theoretical results, *Am. Nat.* **122**, 229–239.
- Loreau, M. 1994. Material cycling and the stability of ecosystems, *Am. Nat.* **143**, 508–513.
- Loreau, M. 1995. Consumers as maximizers of matter and energy flow in ecosystems, *Am. Nat.* **145**, 22–42.
- Loreau, M. 1996. Coexistence of multiple food chains in a heterogeneous environment: Interactions among community structure, ecosystem functioning and nutrient dynamics, *Math. Biosci.* **134**, 153–188.
- Loreau, M. 1998. Biodiversity and ecosystem functioning: A mechanistic model, *Proc. Natl. Acad. Sci. USA* **95**, 5632–5636.
- MacArthur, R. H. 1955. Fluctuations of animal populations, and a measure of community stability, *Ecology* **35**, 533–536.
- May, R. M. 1972. What is the chance that a large complex system will be stable? *Nature* **237**, 413–414.
- May, R. M. 1973. “Stability and Complexity in Model Ecosystems,” Princeton Univ. Press, Princeton, NJ.
- McGrady-Steed, J., Harris, P. M., and 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, *Am. Nat.* **111**, 515–525.
- Naeem, S., and Li, S. 1997. Biodiversity enhances ecosystem reliability, *Nature* **390**, 507–509.
- Neubert, M. G., and Caswell, H. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations, *Ecology* **78**, 653–665.
- Pimm, S. L. 1984. The complexity and stability of ecosystems, *Nature* **307**, 321–326.
- Schulze, E. D., and Mooney, H. A. 1993. “Biodiversity and Ecosystem Function,” Springer-Verlag, Berlin, Germany.
- Tilman, D. 1996. Biodiversity: Population versus ecosystem stability, *Ecology* **77**, 350–363.
- Tilman, D., and Downing, J. A. 1994. Biodiversity and stability in grasslands, *Nature* **367**, 363–365.
- Tilman, D., Lehman, C. L., and Bristow, C. E. 1998. Diversity–stability relationships: Statistical inevitability or ecological consequences? *Am. Nat.* **151**, 277–282.
- Webster, J. R., Waide, J. B., and Patten, B. C. 1975. Nutrient recycling and the stability of ecosystems, in “Mineral Cycling in Southeastern Ecosystems” (F. G. Howell, J. B. Jentry, and M. H. Smith, Eds.), ERDA Conference 740513, National Technical Information Service, U.S. Department of Commerce, Springfield, VA.
- Yachi, S., and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis, *Proc. Natl. Acad. Sci. USA* **96**, 1463–1468.