Effects of Disturbance on Species Diversity: A Multitrophic Perspective

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ABSTRACT: Models of the effects of disturbance on ecological communities have largely considered communities of competing species at a single trophic level. In contrast, most real communities have multiple interacting trophic levels. I explored several versions of simple single- and multitrophic models to determine whether predictions of the intermediate disturbance hypothesis (IDH), derived from considering only a single trophic level, apply to multitrophic situations. The IDH was predicted by models of competing species at a single trophic level but did not hold in many situations with more natural trophic structure. In general, basal species in a food web tended to follow the IDH, whereas competitors at top trophic levels did not. Additional analyses indicated that outside immigration interacted with trophic structure to produce widely differing predictions about the consequences of disturbance and that density-dependent disturbance events could recapture the IDH in some multiple trophic level situations. Model predictions matched the results of empirical studies to date: the IDH has generally been supported for species competing for nondynamic basal resources but not for mobile aquatic invertebrates at higher trophic levels. The model analysis also verified basic predictions of verbal models addressing the effects of physical stress. Three different aspects of disturbance and their contributions to species coexistence were identified: changes in average mortality rates, changes in temporal variability, and changes in spatial heterogeneity. The results indicate that the IDH should be applied with caution to real multitrophic communities.

Keywords: competition, food webs, nonequilibrium, spatial structure, species coexistence, stress.

In the past several decades, it has become increasingly clear that disturbance plays a critical role in determining the abundance and diversity of species in ecological com-

munities (Watt 1947; Dayton 1971; Horn 1975; Connell 1978; Paine and Levin 1981; Sousa 1984; Pickett and White 1985). A central theory to emerge from this discovery is the intermediate disturbance hypothesis (Paine and Vadas 1969; Dayton 1971; Horn 1975; Connell 1978; Lubchenco 1978; Sousa 1979). It posits that agents of mortality (physical disturbance or consumers) at intermediate intensity enhance diversity by reducing competitive exclusion because they prevent competitively superior species from attaining population sizes that are large enough to monopolize all of the limiting resources. At low levels of disturbance, one species can effectively monopolize limiting resources, leading to reduced diversity because of competitive exclusion. At high levels of disturbance, species diversity declines because some species cannot reproduce fast enough to compensate for the increased mortality imposed by the disturbance.

Many studies now suggest that intermediate disturbance levels can enhance diversity. For example, intermediate levels of windfalls, fire, and animal digging in the soil enhance terrestrial plant diversity (Platt 1975; Keeley et al. 1981; Sprugel and Bormann 1981; Sousa 1984; Denslow 1985). Similarly, wave disturbance, rolling boulders, and consumers enhance the diversity of sessile intertidal organisms (Paine 1966; Paine and Vadas 1969; Dayton 1971; Lubchenco 1978; Sousa 1979; Paine and Levin 1981; Dethier 1984). Indeed, the intermediate disturbance hypothesis has become sufficiently established in ecological thought that it now exerts a major influence on many management plans (e.g., Yellowstone National Park fire policy).

Although the intermediate disturbance hypothesis seems well supported in some studies, it has not fared well in all settings. For example, experimental studies of freshwater invertebrates have generally failed to uncover important effects of disturbance of species diversity (Thorp and Bergey 1981; Reice 1984, 1985; Robinson and Minshall 1986; Resh et al. 1988; Doeg et al. 1989; Lake et al. 1989; Lake 1990; Death and Winterbourn 1995; but see Hemphill and Cooper 1983; McAuliffe 1984). Considering its current importance in environmental man-

agement plans, there is both practical and theoretical interest in determining whether the intermediate disturbance hypothesis applies generally to some situations and not to others.

Comparing the characteristics of situations where the intermediate disturbance hypothesis receives strong support with those where it fails suggests several factors that may control its operation. The best experimental examples of the intermediate disturbance hypothesis, including the few demonstrations arising in aquatic invertebrates (Hemphill and Cooper 1983; McAuliffe 1984), come from studying species competing for space or some space-associated resource. Counterexamples come largely from studying mobile consumers. These situations differ in two basic ways. First, the organisms in question tend to have different mobility in the two situations. In fact, when interpreting why their results tend not to support the intermediate disturbance hypothesis, investigators in streams have focused on the mobility of their study organisms and have suggested that immigration swamps the effects of local disturbance (Reice 1985; Doeg et al. 1989; Frid and Townsend 1989; Townsend 1989; Lake 1990). Because individuals lost to disturbance are replaced quickly, competition is not alleviated. The second major difference between systems is that sessile species tend to be collectors of outside energy (either photons or plankton) at the bottom of the food web, whereas mobile species are generally consumers embedded within the food web at higher trophic levels. The implications of this second difference have yet to be addressed within the context of the intermediate disturbance hypothesis. In this article, I consider how interactions among multiple trophic levels may affect the predicted consequences of disturbance. Specifically, I show that the intermediate disturbance hypothesis often does not hold when interactions among multiple trophic levels are taken into account.

Disturbance in Multitrophic Systems—Some General Considerations

The intermediate disturbance hypothesis was originally posed in response to the prevailing view that competition primarily structured ecological communities (e.g., MacArthur and Levins 1964; MacArthur 1972; Cody 1974; Schoener 1974; Diamond 1975). As a consequence, the intermediate disturbance hypothesis considers competing species within a single trophic level and largely abstracts organisms at other trophic levels as static factors in the environment. Real communities, of course, contain species that occupy many different trophic positions, and all of these species have their own dynamical behavior that depends in part on the dynamics of species at higher and lower trophic positions. Indeed, experimental manipulations have now convincingly established that understand-ing the direct and indirect interactions among trophic levels is critical in determining many patterns in ecological communities (e.g., Paine 1966; Davidson et al. 1984; Carpenter et al. 1985; Sih et al. 1985; Schmitt 1987; Power 1990; Wootton 1992, 1994a, 1994b; Schoener 1993; Menge 1995; Wootton et al. 1996). Thus, when considering the effects of disturbance, it seems most appropriate (1) to consider consumers and resources, as well as potential competitors, as dynamic entities and (2) to consider effects of consumers ("keystone predation," e.g., Paine 1966) as separate from effects of physical disturbance because the biota of the community is less likely to directly control the dynamics of the latter (e.g., Menge and Sutherland 1987). How might interactions among trophic levels affect the consequences of disturbance?

A simple graphical model assuming well-defined trophic levels suggests some ways in which multitrophic interactions could alter the intermediate disturbance hypothesis (fig. 1). One implication is that disturbance can directly impact organisms at multiple trophic levels. At one extreme (fig. 1, *top*), disturbance might affect each trophic level in proportion to its abundance. Under such circumstances, each individual will experience the same supply of resources and the same predation intensity immediately following the disturbance as it did prior to disturbance. As a consequence, competition will not be alleviated as the intermediate disturbance hypothesis assumes. At the other extreme, disturbance may be concentrated at one trophic level (fig. 1, *bottom*). In this case, individuals of the affected trophic level would experience relatively more resources immediately after the disturbance, hence less competition as suggested by the intermediate disturbance hypothesis. Thus on the surface, the intermediate disturbance might apply to situations where disturbance acts only on one trophic level.

Further consideration of the situation where disturbance affects a single trophic level, however, yields several complications that make it uncertain that the intermediate disturbance hypothesis applies to the entire community. First, the affected trophic level experiences higher predation intensity, which might further stress populations within the trophic level and push them out of the community. Second, although disturbance may temporarily relieve the affected trophic level from competition, it can intensify competition elsewhere in the food web, both because the food resources of higher trophic levels have been reduced and because the lower trophic level has been released from predation. As a consequence, diversity on other trophic levels might decline because of competitive exclusion. Third, any reduced diversity at lower and higher levels might cause reduced diversity at the disturbance-affected trophic level if differences in resource use and predation pressure partially mediate coexistence. Finally, the depicted situation does not account
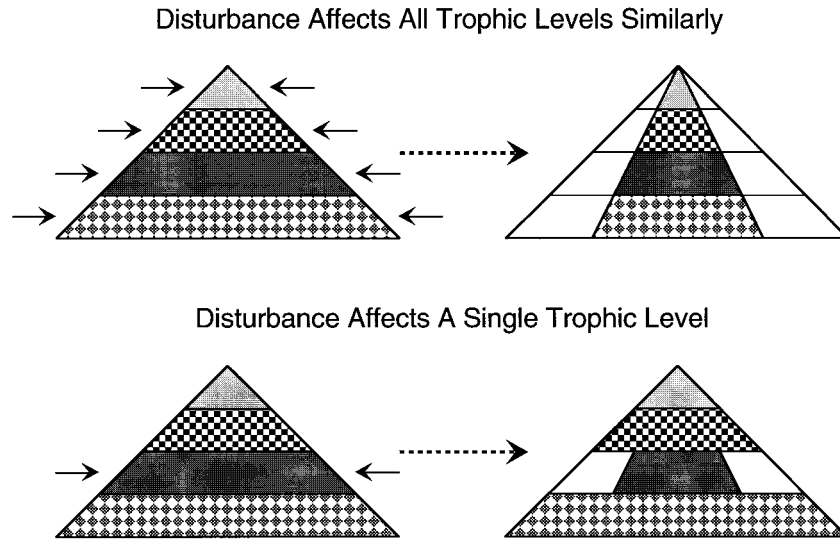
Disturbance Affects All Trophic Levels Similarly

Disturbance Affects A Single Trophic Level

Figure 1: Conceptual model of the effects of disturbance in a multiple trophic level community. Solid arrows represent action of disturbance on a particular trophic level; areas of different shading patterns represent abundance of different trophic levels. *Top,* Disturbance acts proportionally on species at all trophic levels, yielding no short-term change in relative abundance. *Bottom,* Disturbance acts selectively at a single trophic level, at a middle-trophic position.

for the compensatory dynamics of other trophic levels as time passes following a disturbance. For example, in simple food chain models with three species, chronically removing individuals from the intermediate trophic level ultimately causes declines in its consumers, whereas the affected trophic level does not necessarily change (app. A). Thus, reducing a single trophic level ultimately causes its predation pressure to decline, allowing it to return to higher population sizes and, thus, higher competitive intensity.

On the basis of some simple graphical and verbal arguments, therefore, it is easy to envision how changing the level of disturbance in a system with multiple trophic levels may not follow the predictions of the intermediate disturbance hypothesis. Because of the numerous possibilities that could arise from compensatory effects among trophic levels, however, I have chosen a more formal mathematical treatment to explore the role of disturbance in multitrophic communities. In the following section, I consider whether predicted effects of disturbance change with differences in the structure of simple multitrophic models. I also consider the potential role of immigration in affecting these predictions.

Simple Models with Varying Trophic Structure

Methods

To examine whether multitrophic interactions can alter the predictions of the intermediate disturbance hypothesis, I present graphical analyses of some simple models in which the trophic level of interest has two competing

species. My intent here is not to exhaustively consider how disturbance acts in multitrophic systems but simply to explore whether the predictions of the intermediate disturbance hypothesis might change with changes in trophic structure. Clearly these analyses only begin to address this issue, but it is beyond the scope of this article to consider more complicated versions.

In the following examples, I take a graphical analysis approach to show that the conclusions from the simple models I analyze can potentially be extended to certain nonlinear cases. I used two basic types of graphical analysis, exploring in each how changing disturbance (increasing mortality) changes the existence of feasible equilibrium points (i.e., points where all populations have positive sizes). For two- or three-species situations, I applied standard isocline (or isosurface) analysis (e.g., Rosenzweig and MacArthur 1963), where isoclines or isosurfaces are defined as the combination of species abundances in which the rate of change in a species is 0. The point or points at which isoclines or isosurfaces for all species intersect represent potential equilibrium points where all species coexist.

For most four-species situations, I applied the alternative zero net growth isocline approach (ZNGI; e.g., Tilman 1982; Leibold 1996). When the isoclines of two species (here termed "abstracted species") can be expressed entirely in terms of the other two species (here termed "graphed species"), this approach allows graphical exploration of species coexistence by reducing the analysis from four to two dimensions. In this approach, coexistence is possible when two conditions are met: (1) the

isoclines of the abstracted species must intersect in positive phase space of the graphed species (indicating that the densities of the abstracted species will not change at that combination of densities of the graphed species), and (2) at the point of intersection, some combination of the impacts of individual members of the abstracted species must offset the expected density changes of the graphed species in the absence of the abstracted species (indicating that the densities of the graphed species will also not change at that combination of their positive densities). The second condition is tested by determining whether adding some combination of vectors describing the joint impact of each individual of an abstracted species (called the "impact vectors") to the vector describing the joint change in the graphed species in the absence of the abstracted species (termed the "supply vector") yields a vector of 0. The number of impact vectors of each abstracted species added to the supply vector to reach 0 gives the expected equilibrium numbers of the abstracted species. In practice, the second condition is analyzed graphically by determining whether the supply vector falls between the smaller of the angles delineated by the inverses of the two impact vectors of the abstracted species (inverse vectors point in the opposite direction of the impact vectors). If this condition is met, then some combination of impact vectors can cancel the supply vector.

The graphical conditions just described only identify feasible equilibria; they do not determine the stability of the equilibria. To determine the stability of any feasible equilibrium, I applied loop analysis (Puccia and Levins 1985), a method that analyzes the conditions required for local stability (the tendency of the system to return back to the equilibrium point when perturbed slightly away from it) given a qualitative picture of the per capita positive and negative effects of each species on itself and other species.

In this analysis, I consider first a model of two competitors at a single trophic level under varying disturbance conditions. I also explore the interplay of immigration and disturbance by comparing cases where recruits to the population arise from either local births or outside immigration. I then examine a variety of models with two trophic levels, including cases with competitors at either the top, bottom, or both trophic levels, with outside immigration supplementing competitor populations and with density-dependent disturbance. Finally, I consider a system with three trophic levels and examine how the effects of disturbance on the coexistence of competitors vary with trophic position.

Case 1: Single Trophic Level Model. I first consider two species competing for a nondynamic resource (e.g., space). Under these conditions, the traditional Lotka-Volterra competition equations apply (Schoener 1973), with an added term expressing disturbance-induced mortality. The equations for this two-species system are

$$dN_1/dt = r_1 N_1 (1 - \alpha_{11} N_1/S - \alpha_{12} N_2/S) - mN_1$$

and   (1)

$$dN_2/dt = r_2 N_2 (1 - \alpha_{22} N_2/S - \alpha_{21} N_1/S) - \delta mN_2,$$

where N_i is the abundance of competitor i, r_i is the intrinsic rate of increase in the absence of disturbance, α_{ij} is the effect of species j on species i, S is the total amount of a limiting resource (e.g., space), m is the mortality rate of species 1 due to disturbance, and δ is the ratio of disturbance-induced mortality on species 2 divided by that on species 1. I define N_1 competitively superior to N_2 in the absence of disturbance in this and all subsequent examples. In competition for space, this assumption implies displacement of species 2 by species 1, but not the reverse (although N_2 may slow down the invasion of N_1). This analysis assumes disturbance is a chronic event, and I obtain steady-state solutions for whether species can coexist. I examine below the possible differences in behavior between models with constant versus fluctuating disturbance.

Solving this system of equations for equilibrium yields the following isoclines (combinations of species abundances in which the rate of change in the focal species is 0; fig. 2, *top*):

$$\text{for } N_1: \quad N_1 = (S - \alpha_{12} N_2 - mS/r_1)/\alpha_{11}$$

and   (2)

$$\text{for } N_2: \quad N_1 = (S - \alpha_{22} N_2 - \delta mS/r_2)/\alpha_{21}.$$

Initially the N_1 isocline is completely above the N_2 isocline because of the assumed dominance of N_1 in the absence of disturbance. In the equations describing the isoclines, increasing disturbance (m) lowers the Y-intercept of the isocline. The intermediate disturbance hypothesis is predicted in this situation for a restricted set of conditions. First, the ratio of mortality on the inferior to superior competitor caused by disturbance must be lower than the ratio of rates of increase of the inferior to superior species (i.e., when $\delta < r_2/r_1$). When $\delta < r_2/r_1$, the isoclines initially do not cross, but as disturbance increases, the isocline of species 1 drops more quickly and catches that of species 2. As a consequence, the isoclines cross, permitting a two-species equilibrium. As disturbance continues to increase, however, the lines fail to intersect once again, and diversity drops. If $\delta \geq r_2/r_1$, the isocline of species 1 will drop more slowly than the isocline of species 2, and consequently the isoclines can never cross. In addition, competitive interactions must be such that $\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$ to produce a stable equilibrium
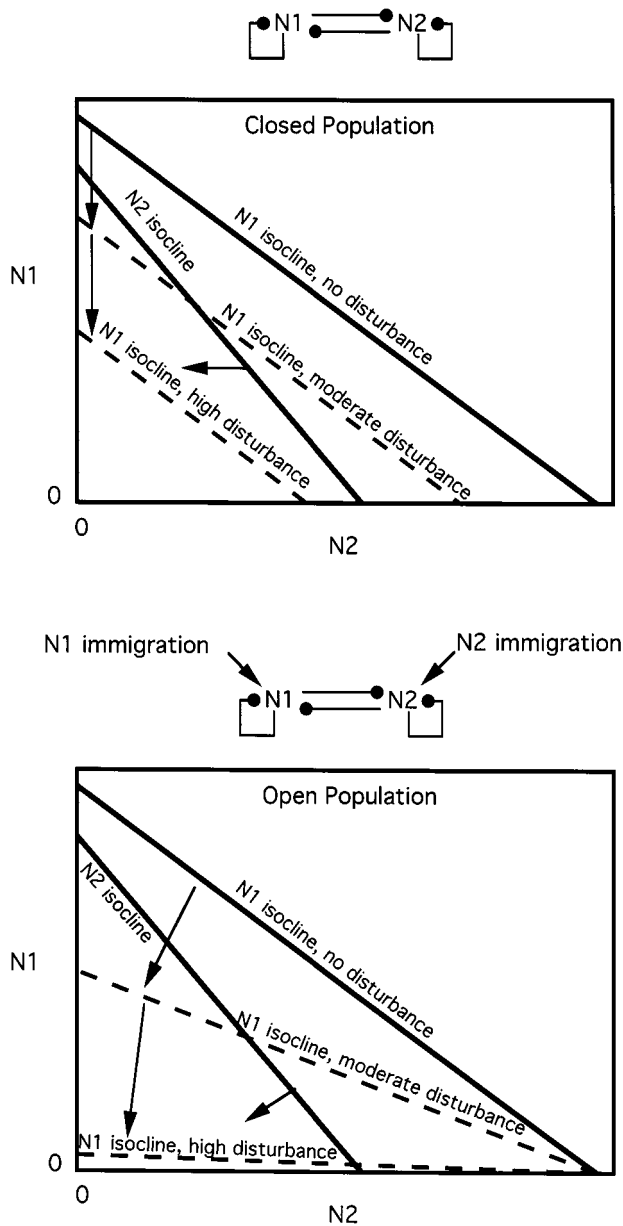
Figure 2: Isocline analysis for two competitors for a single, non-dynamic resource. Solid arrows in graph indicate direction of movement of isoclines as disturbance increases, with dashed lines representing position of isoclines of the competitive dominant (N_1) at successively higher disturbance levels. *Top,* Closed population model. *Bottom,* model with outside immigration. Diagrams above graphs represent the pattern of species interactions, where positive effects of one species on another are denoted by arrows pointing to the affected species and negative effects are denoted by a line with a terminal dot adjacent to the affected species.

point. This condition occurs when the product of the per capita intraspecific competitive intensities is greater than the product of per capita interspecific competitive intensities. Otherwise the equilibrium is unstable, and the intermediate disturbance hypothesis does not hold.

Disturbance Effects: Nonequilibrial or Mortality-Induced Causes? A key feature of arguments associated with the intermediate disturbance hypothesis is that disturbance removes individuals, thereby preventing monopolization of resources and the attainment of the equilibrium condition of competitive exclusion expected in the absence of the disturbance (Paine and Vadas 1969; Connell 1978). Some discussions have taken this statement to imply that nonequilibrium per se favors species coexistence (e.g., Connell 1978; Huston 1979). This idea runs counter to the analyses that I present here, where I examine long-term consequences of disturbance by considering it as a chronic factor and then looking at changes in equilibrium points. There is no specific reason, however, for nonequilibrium conditions in general to favor species coexistence. Competitively inferior species are just as likely as competitive dominants to be negatively affected when a community is away from its equilibrium. Furthermore, equilibrial and nonequilibrial systems form a continuum depending on the scale of observation; a variety of analyses indicate that systems with underlying nonequilibrial properties obtain equilibria when scaled up in time or space (e.g., MacArthur and Wilson 1967; Horn 1975; Paine and Levin 1981; Shugart and West 1981; Chesson and Case 1986; DeAngelis and Waterhouse 1987; Petraitis et al. 1989; Chesson 1990; Levin 1992).

To illustrate and explore this issue, I compared the deterministic trajectory of equations (1) under chronic low-level disturbance with 400 simulations under randomly occurring strong disturbance. Although simulations of the effects of periodic disturbance events on diversity have been reported (e.g., Huston 1979), average mortality rates increased as nonequilibrium conditions were added, potentially confounding the interpretation that nonequilibrium conditions promote coexistence. I disentangled the effects of elevated mortality and stochastic movement away from equilibrium by scaling mortality to the inverse of the frequency of disturbance (i.e., disturbance-induced mortality was 16 times as great when the chance of disturbance occurring at any given time was one-sixteenth as great). I chose parameters such that species 1 excluded species 2 under the deterministic scenario after a reasonably long time period (126 generations) to increase the chances of nonequilibrial coexistence. I further biased the simulation to favor coexistence in the nonequilibrium case in two ways: (1) by inflicting distur-
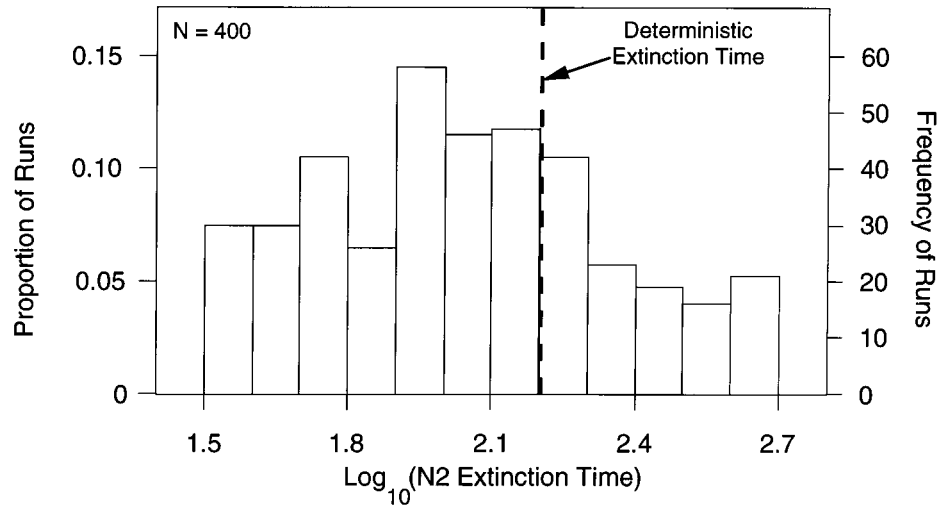
Figure 3: Comparison of the expected extinction time of a competitively inferior species from a deterministic model with constant disturbance intensity (eqq. [1]), with the distribution of extinction times from 400 simulations of a stochastic model of two competitors for a single nondynamic resource where disturbance produces the same average mortality over time but occurs at random on average once every 16 time steps with 16 times the mortality rate of the deterministic model (the maximum intensity possible without a disturbance event causing extinction of the competitive dominant). Parameters defined as in equations (1) are $r_1 = 0.5$, $r_2 = 1.0$, $\alpha_{12}/S = 0.8$, $\alpha_{21}/S = 1.2$, $\alpha_{11}/S = 1.0$, $\alpha_{22}/S = 1.0$, $m = 0.06$, and $\delta m = 0$.

bance only on the competitive dominant to prevent the competitively inferior species from going extinct as a result of stochastic processes and (2) by giving the competitively inferior species a higher intrinsic rate of growth ($r_2 > r_1$), which Huston (1979) suggested should promote coexistence in the face of nonequilibrium conditions.

Under these conditions, trajectories with random episodic disturbance did not behave qualitatively differently from the trajectory with deterministic disturbance: the competitively inferior species always went extinct (fig. 3). The extinction times for the inferior species clustered around 126 generations (median extinction time = 109.5 generations), the time that the deterministic trajectory approached 0. Although extinction times were longer than expected in 174 of the runs, they were shorter in 225 of the model runs. Goldwasser et al. (1994) came to similar conclusions after examining stochastic models of competition for space of a different form, and I have obtained similar results for stochastic forms of the models involving two competitors for a dynamic resource described below (J. T. Wootton, unpublished analyses). These results show that the intermediate disturbance hypothesis can be obtained in equilibrial analyses with changing disturbance-induced mortality rates and that introducing nonequilibrial dynamics while holding long-term mortality rates constant does not facilitate coexistence. As a consequence, the changes in mortality rates induced by disturbance appear much more central to en-

hanced coexistence of competitors than nondeterministic characteristics introduced to the dynamics, at least for the situations considered here.

Case 2: Single Trophic Level, Immigration Driven. The lack of evidence for the intermediate disturbance hypothesis in some experiments has been attributed to the communities under investigation being dominated more by immigration than by local dynamics. To investigate the impact of outside immigration, I modified the models described above as follows:

$$dN_1/dt = I_1(1 - \alpha_{11}N_1/S - \alpha_{12}N_2/S) - mN_1$$

and $\quad(3)$

$$dN_2/dt = I_2(1 - \alpha_{21}N_1/S - \alpha_{22}N_2/S) - \delta mN_2,$$

where notation is the same as in equations (1), except that local birth terms (the r_iN_i terms in eqq. [1] have been replaced by constant immigration rates of species i (I_i). In this scenario, immigrants become established in relationship to how much resource is available (e.g., new settlers to rock in the intertidal zone). Isoclines derived for these equation are

for N_1: $\quad N_1 = I_1S/\alpha_{11}(1 - mS)$

$$- [I_1\alpha_{12}/\alpha_{11}(1 - mS)]N_2$$

and $\quad(4)$

for N_2: $\quad N_1 = I_2S/\alpha_{21} - (I_2/\alpha_{21} + \delta mS/\alpha_{21})N_2.$

In contrast to previous suggestions, when recruitment is driven by outside immigration, conditions favoring the intermediate disturbance hypothesis are enhanced rather than eliminated (fig. 2, *bottom*). As in case 1, the isoclines do not cross without disturbance. When disturbance increases, the slopes of the isoclines change, rotating the isocline to form a smaller angle with the axis of the other species. As the isoclines rotate, the lines necessarily cross (fig. 2, *bottom*), and coexistence is possible, regardless of whether disturbance is concentrated on the competitively superior species (although it still must affect that species to some extent). Therefore, recruitment from outside immigration relaxes the conditions under which disturbance promotes coexistence. In addition, when a clear competitive dominant exists in the absence of disturbance, the equilibrium formed by the rotating isoclines is always stable, regardless of the relative magnitude of the α_{ij} terms. This conclusion arises graphically (fig. 2, *bottom*) because when the isoclines cross, the isocline of a target species always crosses its own axis at a lower value than does the isocline of the competitor. In this circumstance, negative intraspecific effects on the growth rate of a species caps the species at a population size low enough to permit competitors to increase from low density. As disturbance increases further, the angle between the isocline of a species and the axes of its competitor approaches 0, although the isocline and axis are never superimposed precisely. As a consequence, the equilibrium abundance of one or both species approaches 0 at high disturbance levels, and although deterministic extinction does not occur, populations become sufficiently low that stochastic processes can easily eliminate species from the community.

Case 3: Two Trophic Levels, Competitors at Top. In the one trophic level case, the resource was modeled as a nondynamic entity; hence it was more analogous to interference competition (e.g., competition for space, Schoener 1973). Mechanistic models of exploitative competition are appropriately described as a two trophic level system, particularly when the shared resource is a species at a lower trophic level. In this case, the system can be modeled with standard predator-prey equations, such as

$$dR/dt = [r(1 - \alpha_{rr}R/S) - \rho m - c_{r1}N_1 - c_{r2}N_2]R,$$

$$dN_1/dt = (b_{r1}c_{r1}R - \mu_1 - m)N_1,$$

and

$$dN_2/dt = b_{r2}c_{r2}R - \mu_2 - \delta m)N_2,$$

where the population of resource species (R) exhibits density-dependent growth (per capita birth rate of r, space-limitation term of α_{rr}/S); loses individuals because

of disturbance at a per capita rate (ρm), where ρ is the relative per capita effect of disturbance on the resource population relative to its effect on consumer 1; and loses individuals to consumers N_x at a per capita rate of c_{rx}. Competing consumers (N_x) convert a consumed resource individual into new individuals at a rate b_{rx}, lose individuals at a per capita rate of m (species 1) or δm (species 2) to disturbance, and die at a per capita rate μ_x from other causes (e.g., starvation).

The system of equations (5) can be solved for equilibrium, which allows graphing of isoplanes in three dimensions (fig. 4). The equations for the isoplanes are

for R: $R = S(r - \rho m - c_{r1}N_1 - c_{r2}N_2)/\alpha_{rr}r,$

for N_1: $R = (\mu_1 + m)/b_{r1}c_{r1},$

and (6)

for N_2: $R = (\mu_2 + \delta m)/b_{r2}c_{r2}.$

The conditions under which N_1 and N_2 do not change depend only on resource levels and occur at specific, constant resource concentrations. Therefore, the N_1 and N_2 isoplanes parallel each other and do not intersect, and stable coexistence is not possible. Increasing disturbance only changes the constant resource values of each isoplane, but the isoplanes remain parallel, so disturbance does not promote coexistence under these circumstances, and the intermediate disturbance hypothesis does not hold.

This analysis raises the issue of whether the shared resource must be biotic or whether competition for dynamic abiotic resources (e.g., nutrients) behaves like a one or two trophic level system. To reflect the dynamics of nutrients rather than a locally reproducing resource species, we need only alter the resource portion in equations (5) as follows:

$$dR/dt = \sigma - (\lambda + c_{r1}N_1 + c_{r2}N_2)R, \quad (7)$$

where σ is the nutrient supply rate and λ is the per nutrient leaching rate from the system. The competitor equations remain the same. Notice that the conditions producing the parallel isoplanes in equations (6) derive from the equations describing the isoclines for N_1 and N_2, not the resource. Therefore, altering the equations to reflect a dynamic abiotic resource does not affect the results of the analysis: exploitative competition for a dynamic abiotic resource behaves as a two trophic level system, with no effect of disturbance on species coexistence.

Case 4: Two Trophic Levels, Competitors at Top, Density-Dependent Disturbance. Disturbance is usually considered as a density-independent process because local biological conditions are unlikely to affect climatic or geological
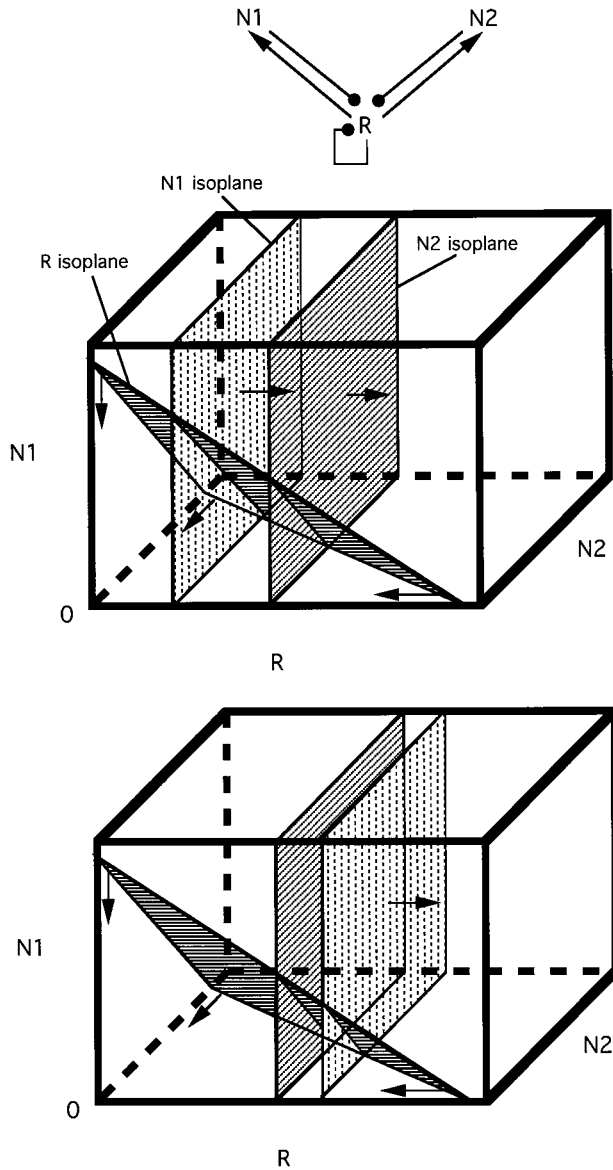
Figure 4: Isoplane analysis for a two trophic level model with competitors on the top (exploitative competition for a dynamic resource). Symbols in species interaction diagram at top of page, as in figure 2. The isoplane belonging to each species has shading running parallel to the axis of that species. Arrows in the graph indicate the direction of movement in response to increased disturbance. Lower graph shows resulting situation with disturbance directed toward the dominant competitor.

processes typically associated with physical disturbance. The effects of such processes, however, might interact with density in some circumstances to affect the rate of disturbance. I explored the effects of density-dependent disturbance on coexistence of competitors in a two trophic level system by multiplying the disturbance (m) terms in equations (5) by species density, yielding

$$dR/dt = [r(1 - \alpha_{rr}R/S) - \rho mR - c_{r1}N_1 - c_{r2}N_2]R,$$

$$dN_1/dt = (b_{r1}c_{r1}R - \mu_1 - mN_1)N_1,$$

and

$$dN_2/dt = (b_{r2}c_{r2}R - \mu_2 - \delta mN_2)N_2. \tag{8}$$

I applied a three-dimensional isoplane analysis to these equations to predict long-term coexistence. The isoplanes for equations (5) are (fig. 5)

$$\text{for } R: \quad R = (r - c_{r1}N_1 - c_{r2}N_2)/(\alpha_{rr}r/S + \rho m),$$

$$\text{for } N_1: \quad R = (\mu_1 + mN_1)/b_{r1}c_{r1},$$

and

$$\text{for } N_2: \quad R = (\mu_2 + \delta mN_2)/b_{r2}c_{r2}. \tag{9}$$

As in the density-independent disturbance case (case 3), competitors do not coexist without disturbance ($m = 0$) because the isoplanes for N_1 and N_2 are constant values of R and, therefore, do not cross. As disturbance increases, the N_1 and N_2 isoplanes tilt at an angle away from the N_1 and N_2 axes, respectively, and the resource isoplane moves proportionally along all axes toward the origin. The competitor isoplanes tilt because disturbance mortality increases with increasing density: higher resource levels permitting more reproduction are required to offset the greater disturbance-induced mortality at high density. Because no isoplanes are parallel, they can all intersect, and coexistence is possible. For feasible coexistence (i.e., all three species have positive densities at the intersection of isoplanes), disturbance must affect the competitive dominant (N_1) with sufficient strength that at $N_2 = 0$, the N_1 isoplane intersects the N_2 isoplane below where the N_2 and R isoplanes intersect (i.e., below the value $r - [m_2(\alpha_{rr}r/S + \rho m)/b_{r2}c_{r2}c_{r1}]$). This condition occurs when the following quadratic equation holds:

$$f(m) = [\mu_1 - (b_{r1}c_{r1}\mu_2)/b_{r2}c_{r2}]$$
$$+ [r/c_{r1}(1 - \mu_2\alpha_{rr}/Sb_{r2}c_{r2})m] - (\rho m^2) > 0. \tag{10}$$

Loop analysis (Puccia and Levins 1985) indicates that when an equilibrium exists it will be stable.

Several possible consequences of varying disturbance emerge, depending on the relative susceptibility to disturbance of the different elements of the system. The effects of disturbance on N_2 do not matter qualitatively because δ does not enter into the coexistence conditions. First, note that because competitors do not coexist in the absence of disturbance (when $m = 0$, the isoclines are parallel, as in fig. 5, *top*), and I have defined N_1 as the competitive dominant in the absence of disturbance, the first term in square brackets ($\mu_1 - (b_{r1}c_{r1}\mu_2)/b_{r2}c_{r2}$) is negative. Subtraction of the third term in square brackets also contributes negatively to $f(m)$ because ρ and m are
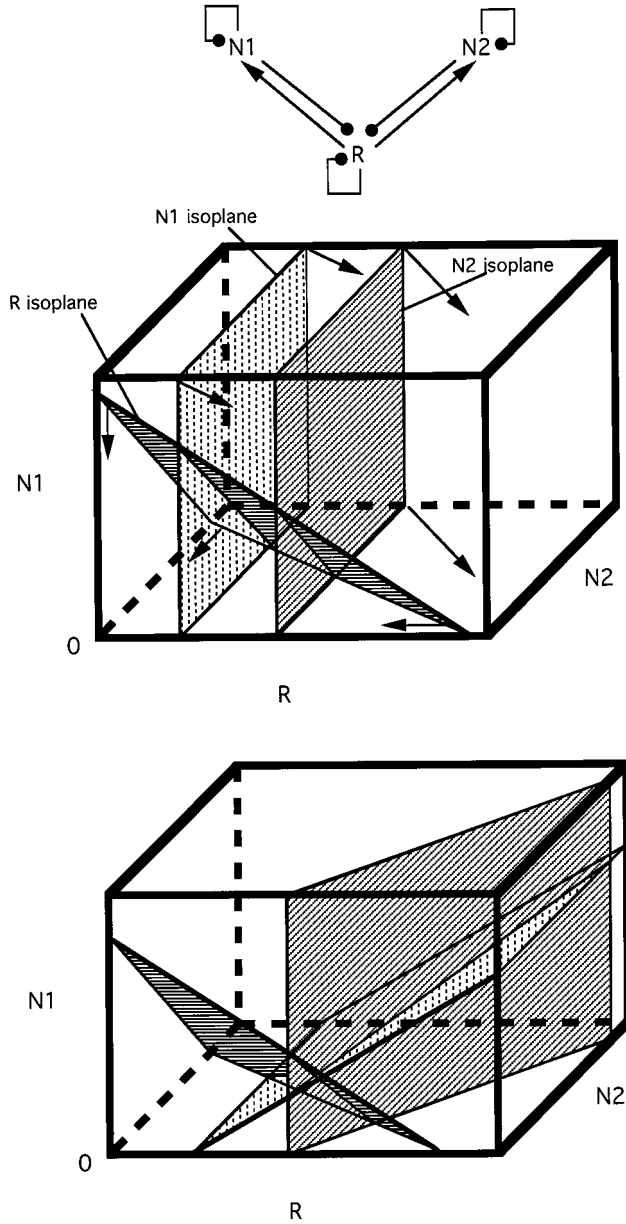
Figure 5: Isoplane analysis for a two trophic level model with competitors on the top level and disturbance acting in a density-dependent manner. Symbols in species interaction diagram at top of page, as in figure 2. Other graph symbols follow figure 4. Bottom graph indicates effects of increasing disturbance on both competitor species.

always positive. Therefore, disturbance can only facilitate coexistence if the second term is positive, which occurs when $\mu_2 \alpha_{rr}/Sb_{r2}c_{r2} < 1$. This condition will be met only if the resource has little self-limitation or species 2 has a low rate of background mortality relative to its efficiency of converting resources into offspring. If this condition is met and disturbance does not affect the resource ($\rho =$

0), then disturbance promotes coexistence, but the intermediate disturbance hypothesis does not strictly hold. There is no drop-off at high levels of disturbance in the absence of stochastic events because it takes infinite disturbance to rotate the N_1 isoplane so that the angle between it and the N_1 axis is 0. Because of density-dependent disturbance, when densities of N_1 are low, disturbance is also low and cannot push the competitive dominant out of the system. The equilibrium density of some competitors at high disturbance levels may be so low, however, that stochastic processes may knock them out of the community, reducing diversity as predicted by the intermediate disturbance hypothesis.

When disturbance affects the resource, as well as the competitors, the intermediate disturbance hypothesis also might hold, but for different reasons than originally envisioned. When $\rho > 0$, a negative quadratic term is introduced that affects the coexistence conditions most strongly at high disturbance levels, yielding coexistence at intermediate disturbance levels if the second term in square brackets in equation (10) is positive. In this scenario, high disturbance levels inhibit coexistence by suppressing the resource population, rather than either competitor population. This can cause three progressively severe scenarios: (1) an unstable equilibrium develops, such that one or the other competitors persists, depending on initial conditions; (2) resource levels become too low for the competitively inferior species to persist; or (3) disturbance drives the resource to low levels where it can no longer persist, causing the entire system to collapse. Finally, if disturbance acts too strongly on the resource (ρ is large), the third term in square brackets (eq. [10]) can overshadow the second term in square brackets such that $f(m)$ is never positive and the conditions of coexistence never obtain. In summary, the intermediate disturbance will work in a two trophic level system when disturbance is density dependent under a limited set of conditions.

Case 5: Two Trophic Levels, Competitors on Top, Outside Immigration. As previously discussed, the interaction of outside immigration and disturbance has been proposed to affect patterns of coexistence. Can immigration change the effects of disturbance in a two trophic level situation? To examine this, I modified equations (5) by adding outside immigration by the competitors, yielding the following equations:

$$dR/dt = [r(1 - \alpha_{rr}R/S) - \rho m - c_{r1}N_1 - c_{r2}N_2]R,$$

$$dN_1/dt = I_1 + (b_{r1}c_{r1}R - \mu_1 - m)N_1,$$

and

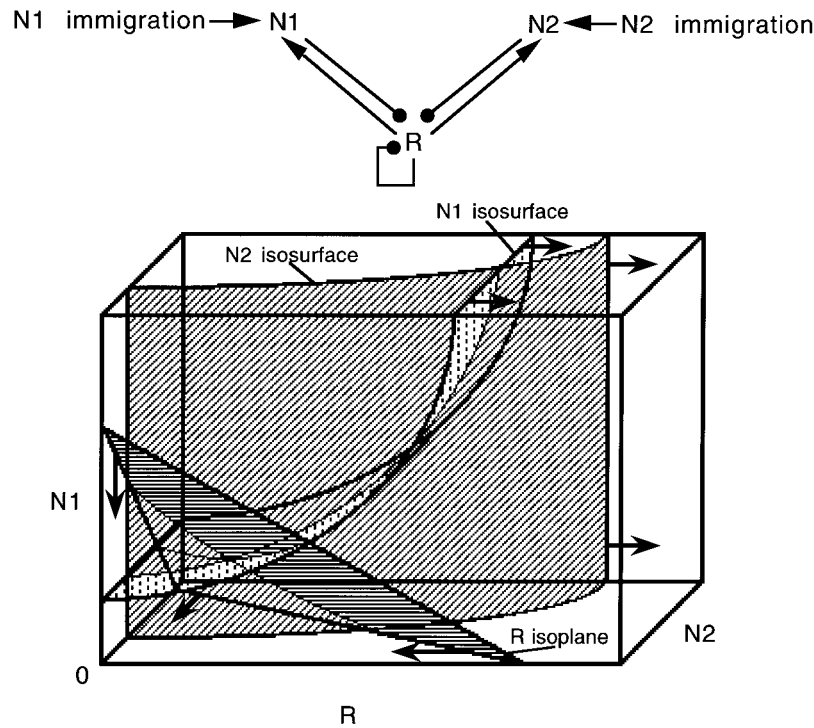$$dN_2/dt = I_2 + (b_{r2}c_{r2}R - \mu_2 - \delta m)N_2.$$

$$(11)$$

Figure 6: Isosurface analysis for a two trophic level model with competitors on the top level and outside immigration supplementing competitor populations. Symbols in species interaction diagram at top of page, as in figure 2. Other graph symbols, as in figure 4.

Since N_1 and N_2 are assumed exploitative competitors, resources positively affect their populations through some combination of local births, reductions in local mortality via declines in starvation, or resource-dependent immigration (e.g., Wootton and Power 1993). Solving these equations for steady state yields the following isosurfaces:

for R: $R = S(r - \rho m - c_{r1} N_1 - c_{r2} N_2)/r\alpha_{rr}$,

for N_1: $R = (\mu_1 + m - I_1/N_1)/b_{r1} c_{r1}$,

$$(12)$$

and

for N_2: $R = (\mu_2 + \delta m - I_2/N_2)/b_{r2} c_{r2}$.

The nonlinear isosurface (fig. 6) of each competitor never reaches 0 and runs perpendicular to the isosurface of the other competitor. As a consequence, the competitor isosurfaces always cross, and there is no competitive exclusion, regardless of the disturbance level. Increasing disturbance does lower the R isoplane, and if it is sufficiently high, the resource will drop out of the system. Therefore, disturbance either has no effect or simply reduces overall community diversity, so the intermediate disturbance hypothesis does not hold.

Case 6: Two Trophic Levels, Competitors at Bottom. The previous three cases have considered a two trophic level system with exploitative competitors at the top trophic level. Basal species in the food web might also compete in a two trophic level system and, additionally, may exhibit apparent competition (Holt 1977) by virtue of having a shared predator. Does the intermediate disturbance hypothesis still hold when basal competitors are placed within a two-level food web? A hybrid set of equations, similar to equations (1) and (5) can be written as follows, assuming resource species 1 (R_1) to be the competitive dominant:

$$dN/dt = (b_{1n} c_{1n} R_1 + b_{2n} c_{2n} N_{2n} R_2 - \mu - \delta m) N,$$

$$dR_1/dt = [r_1(1 - \alpha_{11} R_1/S - \alpha_{12} R_2/S) - c_{1n} N - m] R_1,$$

$$(13)$$

and

$$dR_2/dt = [r_2(1 - \alpha_{22} R_2/S - \alpha_{21} R_1/S) - c_{2n} N - \rho m] R_2.$$

Solving for steady state yields the following isoplanes (fig. 7):

for N: $R_1 = (\mu + \delta m - b_{2n} c_{2n} R_2)/b_{1n} c_{1n}$,

for R_1: $N = [r_1(1 - \alpha_{11} R_1/S - \alpha_{12} R_2/S) - m]/c_{1n}$, (14)
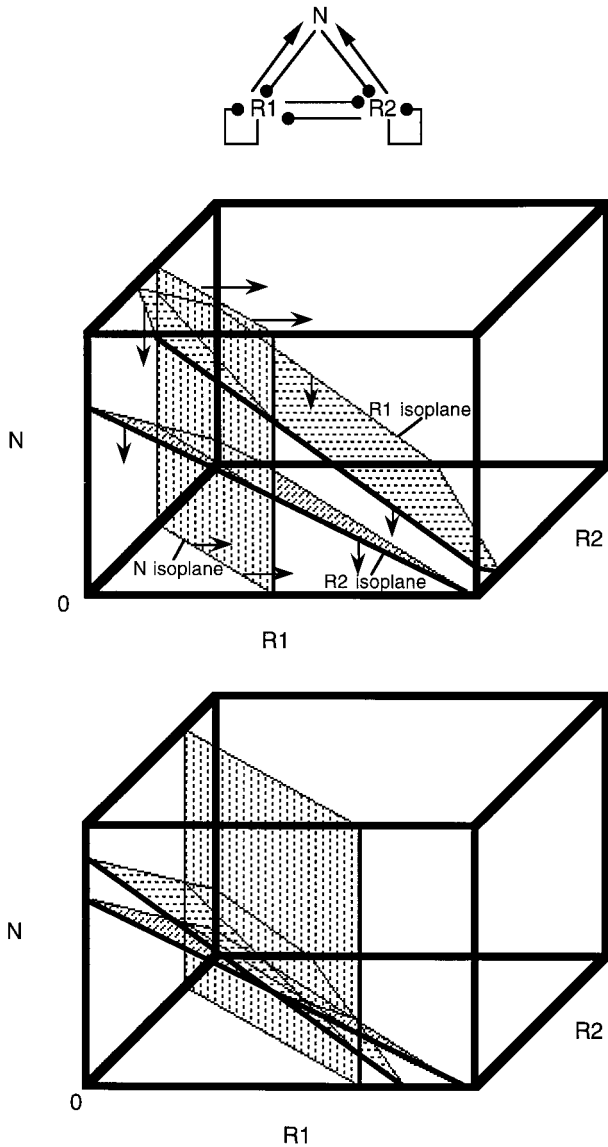
Figure 7: Isoplane analysis for a two trophic level model with competitors on the bottom level. Symbols in species interaction diagram at top of page, as in figure 2. Other graph symbols, as in figure 4. Lower graph shows effects of increasing disturbance on all trophic levels, with disturbance concentrated on competitive dominant.

and

for R_2: $\quad N = [r_2(1 - \alpha_{22}R_2/S - \alpha_{21}R_1/S) - \rho m]/c_{2n}$.

Increasing disturbance moves the resource isoplanes toward the origin. Given that R_1 is the competitive dominant (i.e., the R_1 isoplane starts above that of R_2), an intermediate level of disturbance can potentially promote coexistence if it concentrates on the competitive domi-

nant. In this circumstance, the R_1 isoplane catches the R_2 isoplane and then passes it. The effects of disturbance on the top trophic level complicate the picture in two ways. First, the resource isoplanes may drop below the consumer isoplane. Therefore, the consumer may drop out of the community because its food supply is too low as a result of disturbance. Second, disturbance induced mortality affecting the top trophic level causes its isoplane to move away from the origin (and consequently the resource isoplanes), reducing the chances of coexistence. In addition, loop analysis (Puccia and Levins 1985) indicates that stable coexistence requires the following relationships to hold:

$$\alpha_{11}\alpha_{22} + (b_{1n}c_{1n}^2 + b_{2n}c_{2n}^2)S^2 > \alpha_{12}\alpha_{21},$$

and $\hspace{6cm}$ (15)

$$b_{1n}c_{1n}(\alpha_{22} - c_{2n}\alpha_{12}) > b_{2n}c_{2n}(c_{1n}\alpha_{21} - \alpha_{11}).$$

These criteria are more likely if the per capita effect of intraspecific competition is greater than interspecific competition, if competition is weak relative to consumer-resource interactions, and if consumers have a larger impact on the stronger interspecific competitor. If the relationships do not hold, coexistence is impossible regardless of disturbance. As a consequence, the intermediate disturbance hypothesis holds under limited circumstances in this case.

Case 7: Competitors on Two Trophic Levels. As mentioned previously, disturbance might affect the diversity of competitors at more than one trophic level. Are the predictions of the intermediate disturbance hypothesis altered in this circumstance? The simplest case would be when there are two resource species (R_1, R_2) competing with each other and two consumer species (N_1, N_2) competing for the resources. A simple model of this scenario would be

$$dN_1/dt = (b_{11}c_{11}R_1 + b_{12}c_{12}R_2 - \mu_1 - m)N_1,$$
$$dN_2/dt = (b_{21}c_{21}R_1 + b_{22}c_{22}R_2 - \mu_2 - \delta m)N_2,$$
$$dR_1/dt = (r_1 - \alpha_{11}R_1/S - \alpha_{12}R_2/S$$
$$\hspace{2cm} - \rho_1 m - c_{11}N_1 - c_{12}N_2)R_1, \hspace{1cm} (16)$$

and

$$dR_2/dt = (r_2 - \alpha_{22}R_2/S - \alpha_{21}R_1/S$$
$$\hspace{2cm} - \rho_2 m - c_{12}N_1 - c_{22}N_2)R_2,$$

where symbols follow those of competitors in equations (1) and (5), but with additional subscripts for parameters in resource equations to designate which resource is affected. For the purposes of this article, I will again as-
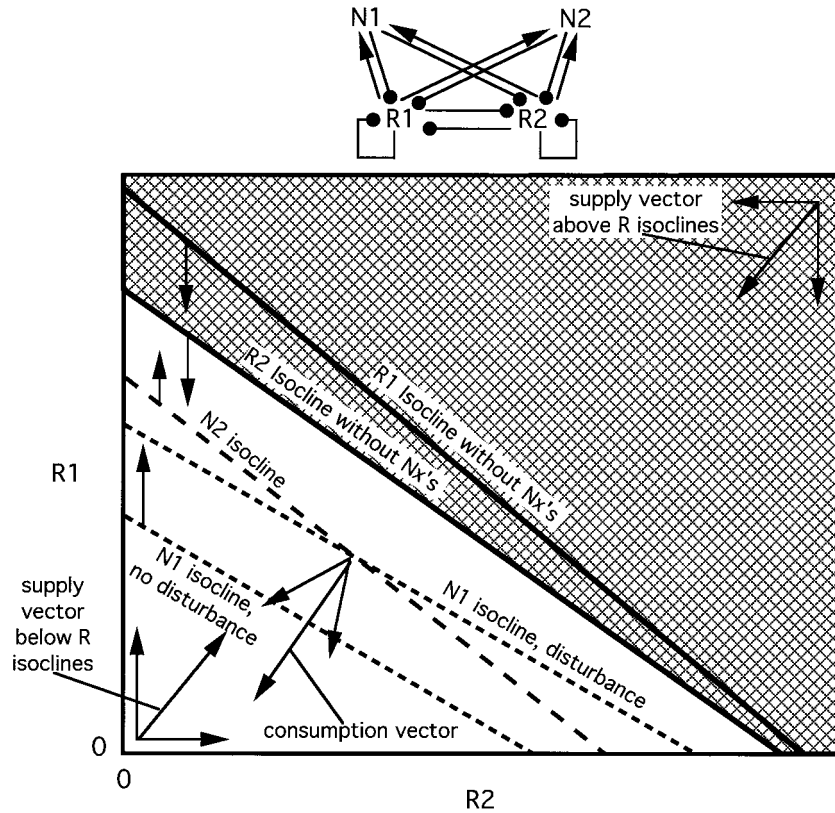
Figure 8: Zero net growth isocline analysis of a two trophic level model with competitors at both levels. Symbols in species interaction diagram at top of page, as in figure 2. Solid lines in graph indicate isoclines of the two basal resource species in the absence of consumers, sparsely dashed line indicates the isocline of N_2, and densely dashed lines indicate the isocline of N_1 under low disturbance (*lower line*) and higher disturbance (*higher line*). Single arrows extending from isoclines in the graph indicate the direction of movement of each isocline as disturbance increases, triple arrows in the lower-left and upper-right corners indicate the general direction of the supply vectors (changes in R_1 and R_2 in the absence of N_1 and N_2) in the unshaded and shaded regions of the graph, respectively, and the triple arrows coming from the isoclines indicate the general direction of a consumption vector (joint effects of N_1 or N_2 on R_1 and R_2).

sume that N_1 is competitively superior to N_2 and will also assume that R_1 is competitively superior to R_2 in the absence of consumers. Isoclines of the consumers can be expressed solely in terms of resources, so a modification of the ZNGI analysis of Tilman (1982) can be used (fig. 8). The consumer isoclines are

$$\text{for } N_1: \quad R_1 = (\mu_1 + m - b_{12}c_{12}R_2)/b_{11}c_{11}$$

and

$$\text{for } N_2: \quad R_1 = (\mu_2 + \delta m - b_{22}c_{22}R_2)/b_{21}c_{21}. \tag{17}$$

These form two negatively sloping curves with respect to the R_1 and R_2 axes, with the competitively superior species N_1 having the lower curve because it can survive on lower resource levels. Increasing disturbance acts to shift the Y-intercepts upward (offsetting increased mortality requires higher resources). Because the consumer isoclines must cross for feasible coexistence, intermediate

levels of disturbance can potentially promote coexistence by acting more strongly on the competitive dominant. The possibility of coexistence differs from the situation where consumers compete for a single dynamic resource and requires that consumers differentially exploit the resource species (i.e., the slopes of the isoclines must differ).

The conditions for stable coexistence also require consideration of the dynamics of the two resources and the impact that the consumers have on them. Both consumers reduce the abundance of both resources (at the per capita rate $-c_{ij}N_i$ for resource i and consumer j), so their net effects on R_1 and R_2 are described by consumption vectors that point down and left. To obtain an equilibrium, the production ("supply") of resources in the absence of consumers and disturbance (the $R_i(r_i - \alpha_{i1}R_1/S - \alpha_{i2}R_2/S)$ terms for resource i) must offset the consumption pressure by N_1 and N_2, or the resource species

will not persist. Therefore, the supply vector must point up and right to offset any combination of consumption vectors. The isoclines of R_1 and R_2 in the absence of consumers (here termed ''consumer-free resource isoclines'') delineate the general shape of the supply vectors (figs. 2, *top,* and 8). The supply vector points up and right only in the lower-left portion of the graph, so coexistence only occurs in the region below both consumer-free resource isoclines. Mechanistically, this means that resource populations can only withstand consumers in situations where they have surplus population growth in the face of competition and agents of mortality other than the consumers. As described in the one trophic level case, disturbance lowers the consumer-free resource isoclines. As a consequence, disturbance reduces the area of possible coexistence. Furthermore, because disturbance raises the isoclines of the consumers, the point at which they cross moves upward and may occur out of the region of potential coexistence.

Finally, the inverses of the per capita consumption vectors must bracket the supply vector at the point of potential coexistence. If the supply vector falls outside of the range of angles delineated by the inverse of the consumption vectors, no additive combination of consumption vectors (i.e., consumer densities) can offset the resource supply rate. In this circumstance, the consumers eat too much of one resource, driving it extinct. Furthermore, coexistence occurs only with differential consumption by the consumers on the different resources, which produces consumption vectors pointing at different angles. Two consumption vectors pointing at the same angle cannot bracket the supply vector. Disturbance can change the inclination of the supply vector, depending on its relative impact on the different resource species, and so may either shift it into an area of potential coexistence or make it too steep or too shallow for coexistence. In addition, loop analysis indicates that an equilibrium point will be unstable unless the following three conditions are met:

1. either

$$b_{21}c_{21}/b_{22}c_{22} > b_{11}c_{11}/b_{12}c_{12} \quad \text{and} \quad c_{12}/c_{11} > c_{22}/c_{21},$$

or

$$b_{11}c_{11}/b_{12}c_{12} > b_{21}c_{21}/b_{22}c_{22} \quad \text{and} \quad c_{22}/c_{21} > c_{12}/c_{11};$$

2. $b_{11}c_{11}^2 + b_{21}c_{21}^2 + b_{12}c_{12}^2 + b_{22}c_{22}^2 + \alpha_{11}\alpha_{22}/S^2$ (18)

$$> \alpha_{12}\alpha_{21}/S^2;$$

3. $(b_{11}c_{11}^2 + b_{21}c_{21}^2)\alpha_{22} + (b_{12}c_{12}^2 + b_{22}c_{22}^2)\,\alpha_{11}$

$$> (b_{12}c_{12}c_{11} + b_{22}c_{22}c_{21})\alpha_{21}$$

$$+ (b_{11}c_{11}c_{12} + b_{21}c_{21}c_{22})\alpha_{12}.$$

These conditions, independent of disturbance regime (m), will generally hold when consumers prey more heavily on different resources and intraspecific competition among resource species is stronger than interspecific competition between resource species.

In summary, the intermediate disturbance hypothesis is predicted under only a subset of two trophic level situations with both competing consumers and competing resource species. It is most likely to occur when disturbance targets the competitively dominant consumer species and when resource species can exist at far higher densities than those required to maintain individual consumer populations.

The special case where each of the competing resources has a specialized consumer (i.e., $c_{12} = c_{21} = 0$ or $c_{11} = c_{22} = 0$) is also worth considering; that is, the consumers are indirect mutualists (Paine 1980; Vandermeer 1980; Dethier and Duggins 1984; Wootton 1994*a*). In this case, the consumer isoclines are perpendicular to the resource species that they specialize on, insuring that the isoclines cross and the consumption vectors can offset any supply vector below both resource isoclines (pointing up and right). Therefore, disturbance never promotes coexistence of indirect mutualists; it only reduces overall diversity as it simultaneously lowers the resource isoclines and raises the consumer isoclines.

Case 8: Three Trophic Levels, Competitors in Middle. A three trophic level situation adds greater realism because both dynamic resources and dynamic predators affect the competitors. In addition, this framework disentangles the effects of keystone predation from physical disturbance. Following the two trophic level situation (eqq. [5]), a simple three trophic level model is

$$dR/dt = [r(1 - \alpha_{rr}R/S) - \rho m - c_{r1}N_1 - c_{r2}N_2]R,$$

$$dN_1/dt = (b_{r1}c_{r1}R - \mu_1 - m - c_{1p}P)N_1,$$

$$dN_2/dt = (b_{r2}c_{r2}R - \mu_2 - \delta m - c_{2p}P)N_2,$$ (19)

and

$$dP/dt = (b_{1p}c_{1p}N_1 + b_{2p}c_{2p}N_2 - \mu_p - \phi m)P,$$

where c_{ip} is the per capita consumption rate of species i by the predator, P; b_{ip} is the conversion rate of consumed individuals of species i into predator offspring; μ_p is the background mortality rate of the predator in the absence of disturbance; and ϕ is the effect of disturbance on the predator relative to the dominant competitor. This three trophic level system has been modeled graphically by Leibold (1996), using an extension of Tilman's (1982) ZNGI
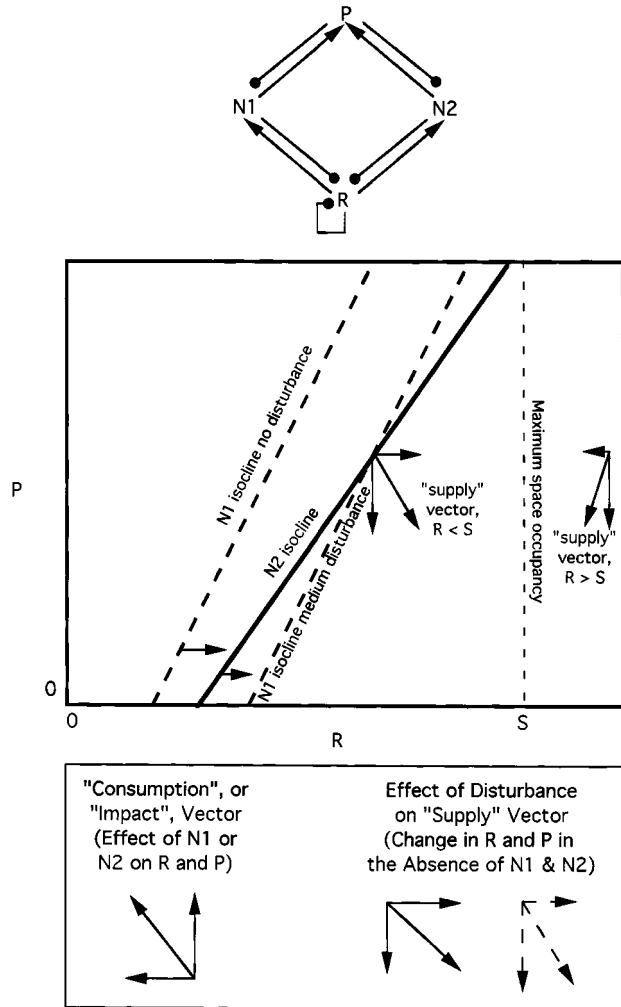
Figure 9: Zero net growth isocline analysis of a three trophic level model with competitors at the middle level. Symbols in species interaction diagram at top of page, as in figure 2. *Lines on graph: solid line* = isocline of N_2; *heavy dashed line* = isocline of N_1 at low disturbance (*left line*) and at higher disturbance (*right line*). Single arrows from isoclines indicate direction of movement with increasing disturbance, triple arrows indicate "supply vectors" (changes in resources and predators in the absence of the middle trophic level) on different sides of the lightly dashed line (maximum resource level). Direction of impact vector and effects of disturbance on supply vector shown below graph. Increasing disturbance shifts the supply vector from the solid to the dashed set of arrows.

technique. The competitor isoclines, which depend only on predator and resource abundance, are (fig. 9)

$$\text{for } N_1: \quad P = (b_{r1}c_{r1}R - \mu_1 - m)/c_{1p}$$

and   (20)

$$\text{for } N_2: \quad P = (b_{r2}c_{r2}R - \mu_2 - \delta m)/c_{2p}.$$

The isoclines must cross for coexistence. In addition, the vector describing the change of resources and predators in the absence of the competitors (analogous to the "supply vector" of Tilman 1982) must be compared with the vector describing the per capita effects of each competitor species on the predator and resource populations (the "impact vector" in Leibold 1996, analogous to the "consumption vectors" of Tilman 1982). In the absence of the competitors and disturbance, resources increase at the rate $[r(1 - \alpha_{rr}R/S)]R$, and predators decline at the rate $-\mu_p P$. This produces a vector that points down and right when $R < S/\alpha_{rr}$. The per capita effect of competitor species i is $b_{ip}c_{ip}P$ on predators and $-c_{ri}R$ on resources, producing vectors that point up and left. For coexistence of all species, some combination of impact vectors must add together to completely offset the supply vector. Graphically, the angle between the inverses of the two impact vectors must encompass the supply vector.

Patterns of coexistence depend on how disturbance affects different trophic levels. As disturbance on competitors increases, the competitor isoclines slide right along the R-axis. As a consequence, for the isoclines to eventually cross in a situation where N_1 dominates competitively, disturbance must act more strongly on N_1 such that $\delta/b_{r2}c_{r2} < 1/b_{r1}c_{r1}$). When this occurs, isoclines remain crossed (i.e., coexistence is possible) at all higher levels of disturbance, ignoring resource and predator considerations. But resource and predator considerations are important. First, as disturbance increases, the resource levels required to sustain coexistence eventually surpass the resource self-limitation term, and the supply vector points straight down or to the left. Under these circumstances, there is no linear combination of impact vectors that will offset the supply vector, and coexistence cannot be maintained. Hence high disturbance can drive one or both species out of the system, in accord with the intermediate disturbance hypothesis. Second, crossed competitor isoclines at resource levels below S/α_{rr} are insufficient to guarantee coexistence. When the isoclines eventually cross, impact vectors may have angles that cannot offset the supply vector, and disturbance will not affect coexistence.

Similar considerations obtain when disturbance acts on either predators, resources, or both. For predators, increasing disturbance increases their rate of decline in the absence of the competitors. For resources, increasing disturbance reduces the rate of growth in the absence of the competitors. Both effects rotate the supply vector clockwise, making it point downward more steeply. This rotation might take the supply vector from an angle too shallow for coexistence, to an angle where coexistence is possible, to an angle too steep for coexistence, consistent with the intermediate disturbance hypothesis. However,

the supply vector might already be too steep to permit coexistence, and disturbance would have no further effect.

Finally, keystone predation can permit coexistence without disturbance (Leibold 1996). Under these conditions, the isoclines start crossed, and the consumption vectors would bracket the supply vector. As a consequence, adding disturbance would never facilitate coexistence but might reduce coexistence by rotating the supply vector out of the feasible range. Finally, loop analysis shows that for any equilibrium to be stable, the following conditions must hold:

either

$$b_{r1}c_{r1}/b_{r2}c_{r2} < c_{1p}/c_{2p} \text{ and } b_{1p}c_{1p}/b_{2p}c_{1p} > c_{r1}/c_{r2}$$

or $\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ (21)

$$b_{r1}c_{r1}/b_{r2}c_{r2} > c_{1p}/c_{2p} \text{ and } b_{1p}c_{1p}/b_{2p}c_{2p} < c_{r1}/c_{r2}.$$

These conditions will generally hold when the predator feeds more heavily on the competitive dominant (see Leibold 1996 for a more detailed discussion). Otherwise, coexistence will not occur, regardless of disturbance level.

To summarize, in a three trophic level situation, increasing disturbance can lead to a range of outcomes including the intermediate disturbance hypothesis, no effects on coexistence, and reduced coexistence.

Case 9: Three Trophic Levels, Competitors on Bottom. This case can be examined by extending equations (13) to include a predator population feeding on species N.

$$dR_1/dt = [r_1(1 - \alpha_{11}R_1/S - \alpha_{12}R_2/S) - c_{r1}N - m]R_1,$$

$$dR_2/dt = [r_2(1 - \alpha_{22}R_2/S - \alpha_{21}R_1/S) - c_{r2}N - \rho m]R_2,$$

$$dN/dt = (b_{r1}c_{r1}R_1 + b_{r2}c_{r2}R_2 - c_{np}P - \mu - \delta m)N,$$

and $\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ (22)

$$dP/dt = (b_{np}c_{np}N - \mu_p - \phi m)P.$$

Solving for steady state yields the following relationships:

for R_1: $\quad R_1 = (S - \alpha_{12}R_2 - c_{r1}SN/r_1 - mS/r_1)/\alpha_{11},$

for R_2: $\quad R_1 = (S - \alpha_{22}R_2 - c_{r2}SN/r_2 - \rho mS/r_2)/\alpha_{21},$

for N: $\quad R_1 = (\mu_n + \delta m + c_{np}P - b_{r2}c_{r2}R_2)/b_{r1}c_{r1},$ $\quad$ (23)

and

for P: $\quad N = (\mu_p + \phi m)/b_{np}c_{np}.$

Analyzing this set of relationships graphically is not straightforward because it involves a four-dimensional system. The dimensionality can be reduced, however, by recognizing that the P steady-state relationship requires

that N is a positive constant whose value depends on the various predator birth and death parameters but not on the densities of other species. This result implies that changes in the disturbance regime will not affect the presence (but might affect the abundance) of N, as long as the three-level structure remains intact. We can use this result to simplify the analysis by substituting the constant from the predator solution into the N terms contained in the equations for R_1 and R_2, yielding the following isoplanes (fig. 10):

for R_1: $\quad R_1 = [S - \alpha_{12}R_2 - c_{r1}S(\mu_p - \phi m)/b_{np}c_{np}r_1$
$$- mS/r_1]/\alpha_{11}$$

and $\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ (24)

for R_2: $\quad R_1 = [S - \alpha_{22}R_2 - c_{r2}S(\mu_p + \phi m)/b_{np}c_{np}r_2$
$$- \rho mS/r_2]/\alpha_{21}.$$

Notice that these equations now match the form for the single trophic level case. As a consequence, if disturbance acts only on the basal level, disturbance at intermediate levels will facilitate coexistence at the basal level if disturbance acts preferentially on the competitive dominant. There is, however, an important difference: disturbance on the top trophic position can alter the outcome depending on the relative preferences of the middle trophic level on the bottom-level competitors. Specifically, if disturbance also acts on the top level, and if the middle-level consumer feeds preferentially on the competitive inferior, the predator disturbance term will slow down or possibly reverse the rate at which the isoplane of the dominant competitor moves toward the origin relative to the competitively inferior species, and coexistence may not be possible.

The effects of disturbance on the isoplane of the middle consumer must also be considered. Increasing disturbance on this level moves the isoplane of the middle consumer away from the origin (fig. 10) as the isoplanes of the basal species move toward the origin, reducing the chances of coexistence.

Finally, the stability of any feasible equilibrium point must be considered. Based on loop analysis (Puccia and Levins 1985), stable coexistence will occur only when

$$(r_1\alpha_{11} + r_2\alpha_{22})b_{np}c_{np}^2/S$$
$$> r_2\alpha_{21}b_{r2}c_{r2}c_{r1} + r_1\alpha_{12}b_{r1}c_{r1}c_{r2}. \qquad (25)$$

Obviously, disturbance would not affect long-term coexistence unless this condition is upheld. In summary, the intermediate disturbance hypothesis can work in some situations when competitors occur at the bottom level of a three-level system, but not in all situations.
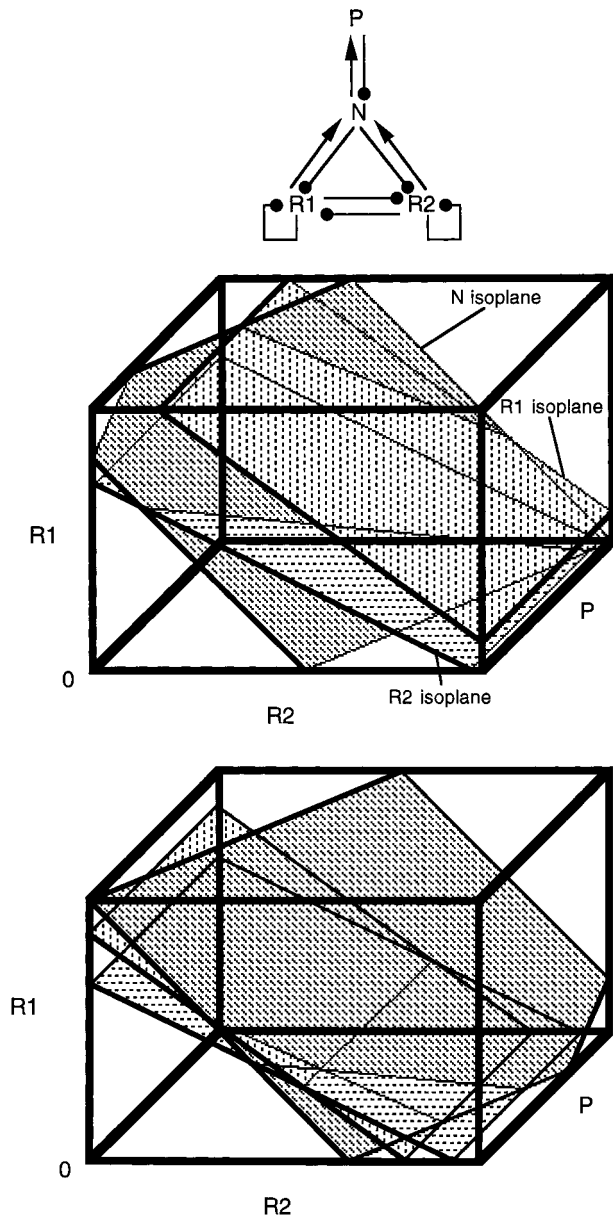
Figure 10: Isoplane analysis for a three trophic level model with competitors on the bottom level. Symbols in species interaction diagram at top of page, as in figure 2. Other graph symbols, as in figure 4, except isoplane for *N* designated by hatching that does not parallel any axis (*N*-axis not shown in this graph). Lower graph shows the result of increasing disturbance on all species, with largest effect on the competitive dominant.

Case 10: Three Trophic Levels, Competitors on Top. In the final case considered here, I examine the three trophic level situation with competitors at the top level. Following previous examples, the equations describing this situation are

$$dR/dt = [r(1 - \alpha_{rr}R/S) - \rho m - c_{rn}N]R,$$
$$dN/dt = (b_{rn}c_{rn}R - c_{n1}P_1 - c_{n2}P_2 - \mu_n - \delta m)N,$$
$$dP_1/dt = (b_{n1}c_{n1}N - \mu_1 - m)P_1, \tag{26}$$

and

$$dP_2/dt = (b_{n2}c_{n2}N - \mu_2 - \phi m)P_2.$$

Solved at steady state, these equations yield the following:

for *R*: $R = (r - \rho m - c_{rn}N)S/r\alpha_{rr},$

for *N*: $R = (c_{n1}P_1 + c_{n2}P_2 + \mu_n + \delta m)/b_{rn}c_{rn},$

for P_1: $N = (\mu_1 + m)/b_{n1}c_{n1}, \tag{27}$

and

for P_2: $N = (\mu_2 + \phi m)/b_{n2}c_{n2}.$

As in the two trophic level case with competitors at the top level, the predator isoclines involve the shared resource expressed as a constant determined by different parameters. As a consequence, the steady-state solutions run parallel to each other in all dimensions and never cross regardless of the disturbance regime. Therefore, disturbance does not promote coexistence, and the intermediate disturbance hypothesis does not hold.

Discussion

The Intermediate Disturbance Hypothesis in Multitrophic Systems

Analysis of the models presented here demonstrates that the effects of disturbance on species diversity in multitrophic systems may deviate from the intermediate disturbance hypothesis. In many situations, disturbance either has no effect on coexistence or causes monotonic declines in diversity. This result arises for several general reasons. First, other mechanisms may facilitate coexistence, in which case disturbance can only act to disrupt coexistence. Second, disturbance may act directly or indirectly on higher and lower trophic levels, changing coexistence criteria in complex ways. Therefore, management strategies for complex multitrophic systems need to carefully consider the effects of varying the disturbance regime.

Although the intermediate disturbance hypothesis does not always work in multitrophic situations, it does hold under many circumstances. Within my analysis, several patterns are associated with increased coexistence at in-

termediate levels of disturbance. Specifically, basal species in the food web competing for nondynamic resources often exhibit maximal coexistence at intermediate levels of disturbance, whereas disturbance did not facilitate coexistence of competitors at the top of the food web. Species embedded within the food web in more complex ways could follow the intermediate disturbance hypothesis, but under relatively restricted conditions. Therefore, the effects of disturbance may be somewhat predictable depending on the ecology of the study species. Furthermore, intermediate disturbance hypothesis–type patterns more commonly arose when the disturbance focused on a single trophic level of competitors. This result raises the question of how disturbances impact species at different trophic levels in real communities. Since most disturbance-related studies have concentrated on single trophic levels, we currently do not know the extent to which disturbance directly impacts multiple trophic levels.

Interaction of Disturbance with Density

Another interesting pattern the analysis reveals concerns the nature of disturbance within a trophic level. In two-level systems, density-independent disturbance did not facilitate coexistence, but density-dependent disturbance promoted coexistence. This result raises the question of whether density-dependent disturbance occurs under natural circumstances. The local biota generally does not affect the extreme climatic events that usually cause disturbance. As a consequence, disturbance is often considered a density-independent event.

Disturbance can be characterized both by its cause and effects, however, and although causes of disturbance are generally density independent, the effects may not be. For example, wave disturbance events that impact intertidal mussel beds permit coexistence of other sessile species (Dayton 1971; Paine and Levin 1981; Sousa 1984). While the mussels do not affect the wave-regime impacting the shore, the probability that waves rip mussels from the shore is density dependent, because the ratio of mussel mass per unit area to attachment area on the rocks increases with population size (Harger and Landenberger 1971; Paine and Levin 1981; Wootton 1993). Similar mechanisms arise in other ecological systems. High fuel loads increase the chances of fire affecting a large number of individuals; high tree densities increase the chances of wind-induced disturbance, as falling trees are likely to knock down neighboring trees; and individual plants and animals can often escape disturbance by inhabiting limited numbers of safe sites in the face of severe water movement or temperatures (Andewartha and Birch 1954; Sousa 1984). In all of these examples, however, density-dependent disturbance impacts either sessile

species competing for space or space-associated resources (e.g., light) or mobile species competing for a limited spatial resource (safe sites). In contrast, density-dependent disturbance most profoundly affected coexistence when competition arose via shared dynamic resources, rather than a static resource such as space, so the importance of density dependence in causing patterns expected under the intermediate disturbance hypothesis remains unclear. The density-dependent or density-independent nature of disturbance therefore requires further study.

The Role of Disturbance in Open Systems

The analyses also illuminate the role of immigration in mediating the effects of disturbance on coexistence. Previous work (Reice 1985; Doeg et al. 1989; Frid and Townsend 1989; Townsend 1989; Lake 1990) suggested that immigration obscures the effects of disturbance on coexistence. My analysis suggests a more complex picture in which the effects of immigration interact with trophic structure to control the effects of disturbance. In contrast to previous suggestions, immigration enhances, rather than minimizes, the effects of disturbance in a one trophic level situation. However, in a two trophic level model, immigration eliminates the effects of disturbance, facilitating the coexistence of competitors directly. As a consequence, trophic structure appears at least as important as immigration characteristics of species in determining the effects of disturbance. The surprisingly different effects of immigration in my different models suggest that its effects on more complex situations also merit further exploration.

My theoretical results match the general pattern of empirical results to date. Strong evidence for the intermediate disturbance hypothesis comes from work on sessile plant and animal communities (e.g., Platt 1975; Sousa 1979, 1984; Keeley et al. 1981; Sprugel and Bormann 1981; Hemphill and Cooper 1983; McAuliffe 1984; Denslow 1985), generally in situations with outside immigration to the site (seed dispersal or planktonic larvae). This situation matches the predictions of case 2, modeling competition for space in an open system with outside immigration. In contrast, little support comes from experimental work on mobile aquatic invertebrates (Thorp and Bergey 1981; Reice 1984, 1985; Robinson and Minshall 1986; Resh et al. 1988; Doeg et al. 1989; Lake et al. 1989; Lake 1990; Death and Winterbourn 1995), where study populations again have outside immigration (drifting, swimming, or crawling individuals). This situation matches the predictions of case 5, modeling consumers at higher trophic levels in an open system. The qualitative agreement between the different scenarios my analyses explore and those examined

to date in natural communities is encouraging and suggests that the results of the multitrophic analyses may have some validity.

Comparing Disturbance and Physical Stress in Multitrophic Systems

The effects of disturbance can also be compared with the similar concept of physical stress. Although the effects of disturbance on species coexistence have generally been considered in a single trophic level context, the effects of nonlethal physical stress have been explored in a multitrophic context using a verbal model (Menge and Sutherland 1976, 1987). Nonlethal stress differs from disturbance by causing changes in performance as opposed to mortality. I have also used multitrophic models to explore the consequences of physical stress and compared the results with the verbal model of Menge and Sutherland (1976, 1987). In the Menge and Sutherland framework, predator abundance is fixed, and physical stress reduces predator performance by reducing the effectiveness of prey capture. This scenario corresponds to case 6, the model of competitors on the bottom trophic level with a shared predator but with constant predator density. This modification yields the following two-dimensional isoclines for the competitors:

$$R_1 = (S - \alpha_{12}R_2 - Sc_{1n}N/r_1 - mS/r_1)/\alpha_{11}$$

and (28)

$$R_2 = (S - \alpha_{22}R_2/S - Sc_{2n}N/r_2 - \rho mS/r_2)/\alpha_{21}.$$

Under the Menge and Sutherland scenario, increasing physical stress decreases the consumption rate of predators on the competitors (the c_{in} terms). This situation is similar to the isocline analysis for case 1, a single trophic level with competition for space (fig. 2, *top*), but the isoclines move in the reverse direction relative to the effects of disturbance as stress increases. Like disturbance, stress can maximize diversity at intermediate levels, as postulated by Menge and Sutherland (1976, 1987). The predictions diverge, however, when predators are dynamic and/or when physical stress manifests itself in other ways. For example, in addition to reducing consumption rates, stress could reduce conversion efficiency (reduce the b_{xn} or r_x terms) or increase metabolic costs (increase the μ_x terms). Whereas the latter would produce similar results to changing disturbance, the former effects on consumption rates and conversion efficiency could produce different types of effects both on the existence of feasible equilibria and on their stability. The myriad of possible consequences of changing physical stress are beyond the scope of this article but represent an interesting direction for further exploration in multitrophic models.

The Three Components of Disturbance

My analyses highlight three separate processes associated with disturbance: increasing average mortality, increasing temporal variability, and increasing spatial heterogeneity. To understand the effects of disturbance, distinguishing the separate effects of these processes is important. Here I have concentrated on the effects of increasing average mortality in multitrophic situations. The intermediate disturbance hypothesis can be derived from these analyses, and the analyses yield results consistent with the general results of empirical studies to date exploring the interplay of disturbance and species coexistence. This focus also successfully predicts the effects of disturbance on river food webs in northern California (Wootton et al. 1996). Therefore, considering the consequences of increasing mortality rates appears useful.

The production of temporal stochasticity is a second aspect of disturbance advanced as being important by preventing the system from reaching a fixed equilibrium point. Within the context of the effects of disturbance, temporal stochasticity has generally not been separated from the effects of overall changes in mortality, which act to change the location of equilibrium points. In my analysis, temporal stochasticity introduced by disturbance does not affect the general pattern of species coexistence when overall mortality remained constant, suggesting that nonequilibrium conditions introduced by temporal stochasticity do not necessarily promote coexistence. Similar conclusions fall out of the general analysis of temporal variability presented by Chesson (1990), Goldwasser et al. (1994), and Chesson and Huntley (1997).

These findings do not preclude temporal fluctuations from promoting coexistence in all situations. Armstrong and McGehee (1976, 1980), Levins (1979), and Chesson (1990) have demonstrated that temporal variability can permit species coexistence under some conditions. For example, in Chesson's (1990) framework, temporal fluctuations introduced by disturbance might facilitate coexistence if disturbance disproportionally reduces the intensity of competition when the competitive dominant is at high density and would otherwise drive the inferior species out of the system. In general, the exact mechanism by which disturbance would modify competitive intensity beyond increasing mortality is not obvious. The effects of disturbance also need to be density dependent for this situation to arise. As mentioned above, the introduction of density-dependent mortality can promote coexistence regardless of temporal stochasticity. In any case,

further investigation is required for multitrophic models. In particular, the results of Armstrong and McGehee (1976, 1980) raise the possibility that adding disturbance-induced environmental stochasticity to a nonlinear model may produce quite different results. Coexistence in Armstrong and McGehee's (1976, 1980) models, however, arises through internally produced nonequilibrium conditions (i.e., from nonlinear interactions between species) rather than from exogenous features (i.e., from environmentally driven mortality fluctuations).

My analysis has not considered the third consequence of disturbance: spatial heterogeneity. Spatial structure can promote coexistence between pairs of species through a variety of mechanisms, including clumping of populations, spatial variation in habitat quality, and temporal escapes from interspecific interactions (e.g., Huffaker 1958; Levin 1976; Ives 1991; McLaughlin and Roughgarden 1993; Tilman 1994). At present, whether disturbance produces some of the spatial aspects that promote coexistence, such as differential clumping of populations, remains unclear. In addition, previous analyses of spatial structure have either concentrated on interactions between pairs of species or have been restricted to a single trophic level of competitors.

Whether conclusions based on previous analyses of spatially structured models apply to a multitrophic setting remains unexplored. For example, Tilman (1994) investigated the consequences of spatial structure and limited dispersal for coexistence of competitors on a nondynamic resource by extending metapopulation models (Levins 1969) to a metacommunity context. He found that a single nondynamic resource could permit the coexistence of an indefinite number of species if all species both experienced some level of disturbance and exhibited trade-offs between competitive ability and dispersal ability. Recasting this analysis with respect to variation in disturbance can lead to the intermediate disturbance hypothesis (J. T. Wootton, unpublished analysis). I applied this modeling approach to a two trophic level situation with competitors exploitatively competing for a dynamic resource (app. B). Again, my analysis indicates that a multitrophic perspective alters the conclusions. Like the nonspatial analyses presented previously, spatial structure introduced by disturbance coupled with dispersal limitation does not promote coexistence of exploitative competitors for a dynamic resource when analyzed from a metacommunity perspective (app. B). Plausible scenarios remain, however, in which intermediate levels of disturbance might promote coexistence of exploitative competitors. For example, if disturbance acts on sessile species comprising the habitat, and these sessile species differentially affect the consumer-resource relationships of consumers on a shared dynamic resource

such that each consumer is a superior competitor in one of the habitats, then it is easy to imagine that the resulting source-sink structure could permit coexistence. Clearly the links between disturbance, spatial structure, and coexistence in multitrophic situations merit further exploration.

Conclusions

Disturbance interacts with other ecological processes to affect patterns of species abundance and diversity. Our previous understanding of these phenomena was based on a single trophic level view of the world, yielding the intermediate disturbance hypothesis, but most real ecosystems contain more than one trophic level. My analysis of multitrophic models demonstrates that disturbance may yield different patterns of coexistence than those predicted by the intermediate disturbance hypothesis. Despite these deviations, several general trends emerge: basal species in food webs are likely to follow the intermediate disturbance hypothesis, whereas top consumers are not. The patterns predicted by the models successfully explain why the intermediate disturbance hypothesis has held in some empirical studies but not others. The model analyses also identifies the need for further empirical and theoretical study of the roles of immigration, the distribution of disturbance-induced mortality on different parts of the food web, and the relationship between disturbance-induced mortality and density. In addition, the implications of the three fundamental components of disturbance (mortality, nonequilibrial dynamics, and spatial heterogeneity) need to be distinguished and explored in more detail. Within the context of the models explored here, changes in mortality had the largest effect on model outcomes. Finally, my results illustrate the benefits of shifting from a single-trophic to a multitrophic perspective. By applying this approach to other questions posed in the context of competitive communities (e.g., physical stress, spatial processes, effects of dynamic consumers on the evolution of prey defense, the role of nutrients in community structure), similar insights may be gained, and conclusions will be more applicable to our understanding of real, multitrophic ecosystems.

Acknowledgments

APPENDIX A

Long-Term Effects of Disturbance-Induced Mortality on Herbivores in a Three-Level Food Chain

Suppose we have a three-level food chain consisting of vegetation (V), herbivores (H), and predators (P). A simple food chain model describing the dynamics of these three trophic levels is

$$dV/dt = [b_v R(1 - V/K) - c_{vh}H - m_v]V,$$
$$dH/dt = (b_{vh}c_{vh}V - c_{hp}P - m_h)H,$$

and

$$dP/dt = (b_{hp}c_{hp}H - m_p)P, \tag{A1}$$

where b_{xy} represents birth rates of species y per unit resource x consumed, R represents resources available to vegetation, K represents the strength of self-limitation by V, c_{xy} represents consumption rates of consumer y on its prey x, and m_x represents density-independent mortality, including mortality caused by disturbance. The steady-state solution to these equations is

$$V^\star = K[b_v - (c_{vh}m_p/b_{hp}c_{hp}) - m_v]/b_v,$$
$$H^\star = m_p/b_{hp}c_{hp},$$

and

$$P^\star = \{b_{vh}c_{vh}K[b_v - (c_{vh}m_p/b_{hp}c_{hp}) - m_v]/b_v\} - m_h. \tag{A2}$$

Notice that although increasing disturbance on herbivores (increasing m_h) reduces herbivore growth rate in the short term (eqq. [A1]), over the long term, increasing disturbance on herbivores reduces only predators (eqq. [A2]). Predators decline as a result of reduced production of prey. Herbivore populations are unaffected over the long term because reductions arising from increased disturbance are offset by increases resulting from lower predator abundance.

APPENDIX B

Analysis of a Two Trophic Level Model of Exploitative Competition with Spatial Structure

Tilman (1994) extended the metapopulation models of Levins (1969) to model a metacommunity of competitors at a single trophic level in a spatial context. This model predicted, given appropriate competition and dispersal trade-offs and unlimited space, that an unlimited number of species could coexist on a single space-associated, nondynamic resource. This modeling approach can be extended to a two-level situation (two competitors feeding on a common resource) to explore whether spatial structure can produce the same effect for exploitative competition involving a single dynamic resource (N_r) and two competitors (N_1 and N_2).

The model is expressed as the proportion (p_x) of sites occupied by species x. Within this model, a single site is either empty or occupied by a single individual of one of the species. I assume that competitors are unable to colonize a site without a resource individual and that they will consume the resource individual occupying any site that they colonize. Consumers may occupy a site for more than one time interval following colonization, living off of stored energy obtained from the consumed resource and any resource individuals that attempt to colonize the site. The model is

$$dp_r/dt = \gamma_r p_r(1 - p_r - p_1 - p_2) - \epsilon_r p_r$$
$$- \gamma_1 p_1 p_r - \gamma_2 p_2 p_r, \tag{B1a}$$
$$dp_1/dt = \gamma_1 p_1 p_r - \epsilon_1 p_1 + \gamma_r p_r p_1, \tag{B1b}$$

and

$$dp_2/dt = \gamma_2 p_2 p_r - \epsilon_2 p_2 + \gamma_r p_r p_2, \tag{B1c}$$

where γ_x is the rate at which an individual of species x or its offspring colonize a site (assumed constant for all sites, and <1 as a result of dispersal limitation), and ϵ_x is the rate at which an individual of species x is removed from a site as a result of dispersal, senescence, starvation, or disturbance. The first term in the equation of the resource species represents colonization of unoccupied plots, whereas the last two terms represent the loss of plots occupied by resources resulting from the colonization of consumers. The first term in the consumer equations represents successful colonization of sites with resources, whereas the last term represents resource colonization of sites already occupied by consumers. Solving for isoclines for these equations yields

$$p_r = 1 - \epsilon_r/\gamma_r - (1 + \gamma_1/\gamma_r)p_1 - (1 + \gamma_2/\gamma_r)p_2,$$
$$p_r = \epsilon_1/(\gamma_1 + \gamma_r),$$

and

$$p_r = \epsilon_2/(\gamma_2 + \gamma_r). \tag{B2}$$

Notice that the general form of equations (B2) is identical to those of case 3 (eqq. [6]), particularly in the existence of a singularity for the latter two equations (p_r is expressed as two different constants). As a consequence, the same conclusions hold as in the nonspatial case: there is no coexistence of exploitative competitors on a single resource with either changes in disturbance intensity (increasing ϵ_x) or spatial structure, at least for this model.

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