THE INTERMEDIATE DISTURBANCE HYPOTHESIS: PATCH DYNAMICS AND MECHANISMS OF SPECIES COEXISTENCE

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Abstract. The intermediate disturbance hypothesis (IDH) has been used for several decades as an explanation for the coexistence of species in ecological communities. It is intuitively simple, but deceptively so. We show, via discussion and examples, that the IDH is not one mechanism of coexistence, but rather summarizes a set of similar phenomena that can arise from the action of several different coexistence mechanisms. These underlying mechanisms are defined by the various ways in which species differ in their response to disturbance-induced spatial and temporal variability in resources and environmental conditions. As an example, the original specification of the IDH required patchy disturbances for coexistence. However, because the underlying mechanisms of coexistence can also operate at the within-patch scale, patchy disturbances are not a necessary requirement for coexistence under intermediate-disturbance regimes. These conclusions are illustrated through the analysis of three models: a spatial within-patch model, a spatial between-patch model, and a purely temporal model. All three generate similar patterns of coexistence under intermediate disturbance, yet underlying that coexistence lie at least two quite-distinct mechanisms of species coexistence: the storage effect and relative nonlinearity. The results from our analyses suggest that, as a promoter of species coexistence, the IDH is both broader in scope and richer in detail than has previously been recognized.

Key words: coexistence, mechanisms of; environmental variability; intermediate disturbance hypothesis; nonlinearity, relative; patch dynamics; reciprocal-yield law (RYL) model; species coexistence, storage effect.

INTRODUCTION

The intermediate-disturbance hypothesis (IDH) is one of the most frequently suggested nonequilibrium explanations for the maintenance of species diversity in ecological communities (Wilson 1990). Despite this, there remains considerable debate surrounding the IDH and its operation as a coexistence-promoting mechanism (Padisak 1994, Wilson 1994, Reynolds 1995, Bartha et al. 1997, Collins and Glenn 1997, Chesson and Huntly 1997, Dial and Roughgarden 1998, Buckling et al. 2000, Sheil and Burslem 2003). The term "intermediate-disturbance hypothesis" has also been used to mean that more species will be found at an instant in time under intermediate disturbance, irrespective of whether that diversity can be maintained over the long term. In this paper we use the term IDH solely to refer to a mechanism (or group of mechanisms) leading to long-term, stable species coexistence.

Two aspects of the IDH are addressed in this study. The first is whether the IDH is a simple mechanism in its own right, or whether it should be viewed as a complex of different coexistence-promoting mecha-

nisms. Sheil and Burslem (2003:24) suggest that the IDH is "an elegant but oversimplified representation of a complex knot of concepts: that many events can both augment and erode diversity through various linked processes at a range of scales." We attempt to untie this knot. Especially, we ask whether the differences constitute fundamentally different ways in which species coexistence is maintained, and we demonstrate for the first time that coexistence under the IDH can arise from at least two fundamentally different coexistence-promoting mechanisms: relative nonlinearity and the storage effect (Chesson 1994).

The second aspect we investigate is the role that spatial heterogeneity plays in promoting coexistence under intermediate disturbances. Discussions regarding the role of spatial heterogeneity have proved controversial, in particular whether spatially patchy disturbances are a requirement for coexistence (Wilson 1994, Bartha et al. 1997, Collins and Glenn 1997).

Our study is divided into two parts. First, we discuss in general the various ways in which disturbance can promote species diversity in ecological communities, and focus on the potential mechanisms of coexistence that might underlie the IDH. Especially, we ask whether the IDH requires spatially patchy disturbances to generate coexistence, or whether purely temporal mechanisms can also generate long-term, stable coexistence

under intermediate-disturbance regimes. We then illustrate these verbal arguments with three simple models that parallel these questions.

What Constitutes a Mechanism of Coexistence?

The term ''coexistence mechanism'' has been applied in a range of different ways in the literature, particularly in relation to coexistence under fluctuating environmental conditions. For example, Sheil and Burslem (2003) suggest that coexistence in ''within-patch'' and ''between-patch'' models constitutes two different coexistence-promoting mechanisms, both operating under the intermediate-disturbance hypothesis (IDH), whereas others have described the IDH as a mechanism in its own right (e.g., Wilson 1990). Here we define as the same coexistence mechanism those which have a fundamentally equivalent theoretical/mathematical basis, perhaps in spite of appearing to be different at the biological level. An example of this is discussed below (see *Empirical examples and models: Between-patch coexistence: Empirical examples*), whereby the empirical between-patch example of Sousa (1979*a, b*) and the within-patch example of Bonis et al. (1995) are both consistent with the operation of the same underlying ''mathematical mechanism''—the storage effect. Here we follow the terminology and classification of Chesson (2000*a*) in identifying three broad mechanisms that have at their basis distinct theoretical formulations. The first might be called *traditional niche partitioning*, which involves differences in behavior, resource acquisition, etc., that do not rely upon fluctuating environmental conditions. Examples include the avoidance of competition through the use of prey of different size, or utilization by different plant species of different light environments within a plant canopy. The other two mechanisms—the ''storage effect'' and ''relative nonlinearity''—are dependent upon environmental variability, such as disturbance, for their expression. Because these *fluctuation-dependent mechanisms* are integral to understanding coexistence under the IDH, they are discussed in greater detail below.

The IDH and Spatial Heterogeneity

Many definitions of disturbance have been suggested (van der Maarel 1993), but a common theme is the destruction of biomass (Grime et al. 1987), leading to the opening up of space and hence resources that can be utilized by new individuals. Central to the IDH is the notion of 'intermediate' disturbances. Most commonly this is interpreted as ''intermediate-timescale disturbances,'' i.e., coexistence is promoted when disturbances recur through time at intermediate frequencies. To provide a scale for comparison, and to give meaning to the word ''intermediate,'' the frequency of disturbance has to be seen in the context of the generation times of the organisms (Padisak 1994, Wilson 1994). The spatial extent of the disturbance and its intensity are also var-

iable in natural communities (van der Maarel 1993). However, for the sake of clarity only intermediate-time-scale disturbances are considered here, and the spatial extent and intensity are assumed constant.

One of the earliest discussions linking disturbance with species coexistence was provided by Hutchinson (1951, 1953), where he considered coexistence in a spatial context, i.e., some species occur in recently disturbed patches, other species in older patches. Although Hutchinson introduced the key concepts, it is important to note that he did not directly consider ''intermediate'' disturbances. This latter aspect was introduced by Horn (1975), and further amplified by Connell (1978, 1979) (see also Wilkinson 1999).

Within this spatial framework, coexistence requires: (1) spatially patchy disturbances and (2) a trade-off that causes species to perform best (e.g., grow, reproduce, and disperse) at different stages of the post-disturbance succession (Chesson and Huntly 1997). The IDH is commonly illustrated using a trade-off between competitive ability and dispersal; under high-frequency disturbances the better competitor but poorer disperser cannot persist, while under low-frequency disturbances the better competitor excludes the good disperser. At intermediate frequencies there is a parameter zone where both species coexist indefinitely, with the competitively inferior species occupying the recently disturbed sites. Chesson and Huntly (1997) suggest that this mechanism be renamed the ''successional mosaic hypothesis,'' while Wilson (1994) referred to this as a between-patch mechanism (both trying to convey a more detailed sense of how coexistence is maintained).

In the within-patch context, disturbances are assumed to be global in the sense that all organisms in the system are simultaneously affected by the disturbance, regardless of the spatial locations of those organisms. This means that there is no spatial component to the resulting disturbance-induced variability, hence spatial differences in colonizing ability cannot contribute to coexistence in this case. However, it is possible for species to differ in other ecologically meaningful ways that allow them to exploit the temporal variability. Such effects have been described as ''temporal niche differentiation'' (Wilson 1990). It therefore follows that coexistence is possible at the within-patch scale if mechanisms exist that allow the species to differentiate themselves in, for example, their use of resources that vary temporally because of repeated disturbance. This can be called a within-patch IDH, so long as it is recognized that it is a different mechanism from Hutchinson's original between-patch concept.

The IDH and Mechanisms of Species Coexistence

Despite the apparent conceptual clarity of the early verbal depictions of the IDH, there is still considerable confusion surrounding the role of disturbance in promoting species coexistence (Chesson and Huntly

1997). In this section we seek to clarify the means by which disturbance promotes species coexistence under the IDH.

Chesson (1991) has shown that, in general, for any pair or set of competing species to coexist they must differ in ecologically meaningful ways. However, the simple presence of ecological differences among the species does not guarantee coexistence. For coexistence to occur, additional requirements must be satisfied (Chesson and Huntly 1989, Chesson 1994). In the case of mechanisms of coexistence that rely upon environmental variability, these ecological differences define the various ways in which the species differ in their response to that variability.

Disturbances and their aftermath can be seen as environmental variability: immediate post-disturbance is one environment and the end of a recovery period is another. Because there are a large number of ways in which species can differ in their response to disturbance-generated spatial and temporal variability in resources and environmental conditions, it follows that there are potentially a large number of ways in which coexistence could be generated. Under such a postulate, the IDH is not a simple mechanism of coexistence in its own right, but rather a family of mechanisms unified by their outcome: coexistence under intermediate disturbance.

Although there are many kinds of biological difference between competitors that could lead to coexistence, Chesson (1994) has shown for pure temporal variation that coexistence can be attributed to the action of three broad categories of mechanisms: (1) the storage effect, (2) relative nonlinearity, and (3) a third category that incorporates all of those mechanisms that do not rely upon temporal variability.

Analogous mechanisms have also been shown to be operating to promote coexistence under spatial variation, which have been called the ''spatial storage effect,'' ''spatial relative nonlinearity,'' and a third category that incorporates all of those mechanisms that do not rely upon spatial variability (Chesson 2000*b*).

The *storage effect* operates when the species' attributes allow gains made during favorable growth periods to be 'stored' in the population for use during unfavorable periods, e.g., during periods of suboptimal environmental conditions, and/or periods when the impact of competition is increased. The concept of *relative nonlinearity* is conceptually and biologically distinct from the latter mechanism, and relates to differences in the responses of competitors to fluctuations in resource availability that are relatively nonlinear. In the analysis of the three models below we show that coexistence under the IDH can arise independently from both the storage effect and relative nonlinearity.

There are two important consequences of these insights. First, long-term, stable coexistence can occur only if the competitors differ in their response to disturbance. Therefore, disturbance cannot promote co-

existence among species that differ only in competitive rank. Even if disturbance changes the competitive ranks of the species so that each is the best competitor at different stages during the resulting succession, this is not sufficient for coexistence. Over time, one of the species will on average be better than the others, and hence, eventually, will win. The system may persist for a very long time if the average competitive abilities are very similar in the first place, but this is not stable coexistence as competitive exclusion will eventually occur, and, as Chesson and Huntly (1997) point out, slow competitive exclusion offers no insight or mechanism for the generation of species diversity in the first place. The model of Huston (1979) is of this type—it relies upon the delay of inevitable competitive exclusion, rather than the long-term, stable coexistence of competing species (Chesson and Huntly 1997).

Second, because disturbance can induce coexistence in a number of different ways, there is the potential for different mechanisms to be operating in different situations, or for many mechanisms to be operating simultaneously. The precise mechanisms present in a given situation will depend upon the particular characteristics of the competitors, and of the disturbance regime.

EMPIRICAL EXAMPLES AND MODELS OF COEXISTENCE UNDER INTERMEDIATE DISTURBANCE

We present results from three simulation models to demonstrate our conclusions that coexistence under the intermediate disturbance hypothesis (IDH) can arise in a number of fundamentally different ways.

In the first model, we illustrate coexistence as a between-patch mechanism, with a trade-off between competitive ability and dispersal ability. Many disturbances are likely to produce patchiness of this nature, e.g., tree fall in forests, animal disturbance resulting from foraging, and dislodgment of boulders in intertidal communities. In the second model, we illustrate how coexistence is achieved with intermediate-timescale disturbances at the within-patch scale, through a trade-off between competitive ability and seed longevity. This trade-off reflects the observation that many seed banks are dominated by early successional species that are absent or rare in the established vegetation (Kellman 1970, Thompson and Grime 1979). The final model we examine is based on Ellner's (1987) ''reciprocal-yield law'' (RYL) model, which describes the dynamics of annual plant species competing in a disturbed but spatially uniform habitat; thus it is a purely temporal model.

Between-patch coexistence

Empirical examples.—The most common interpretation of the IDH is that of a between-patch process, involving the recolonization of species by dispersal from distant areas. For example, Sousa (1979*a, b*) observed and experimentally manipulated a marine in-

a) Between-patch model

Disturbance   Disturbance

b) Within-patch model (aboveground only)

Disturbance   Germination   Disturbance   Germination
                  from   from
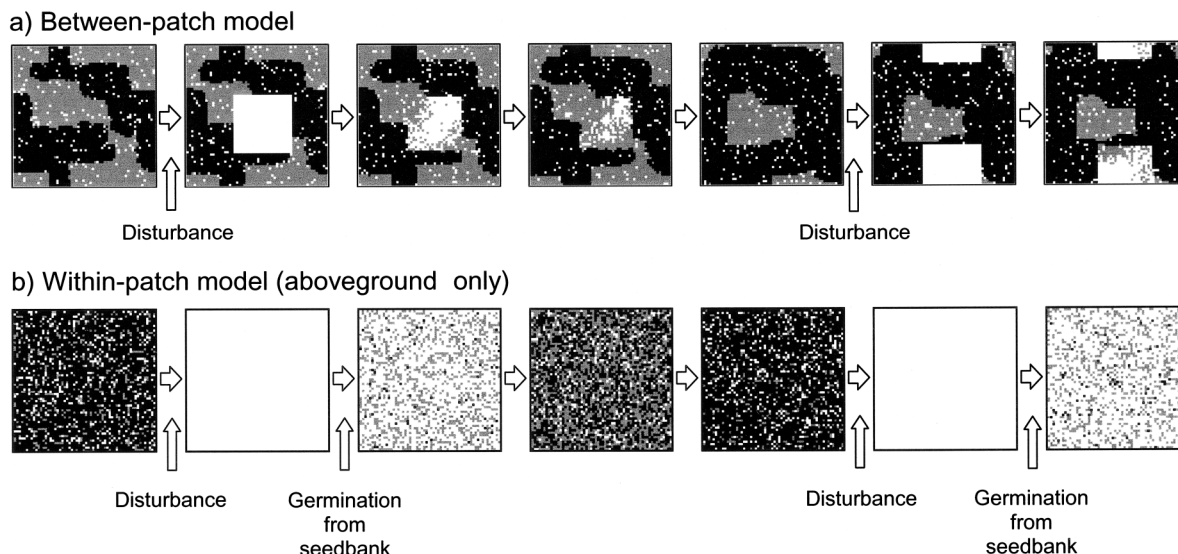   seedbank   seedbank

FIG. 1. Examples of "snapshots" from between-patch and within-patch simulation models illustrating how the coexistence is maintained in each. (a) In the between-patch model, the inferior competitor (gray species) is able to persist in the system due to its greater dispersal ability. Following disturbance (white area) it is able to quickly colonize the disturbance patch and reproduce before it is excluded by the superior competitor (black species). Repeated disturbance may allow the two species to coexist indefinitely. (b) In the within-patch model, over time the inferior species becomes numerically dominant in the seed bank due to its higher seed longevity (seed-bank dynamics not shown in the figure), while the superior competitor progressively assumes dominance aboveground through competitive exclusion of the inferior competitor. When disturbance occurs, recolonization comes predominantly from the inferior competitor via its greater seed pool, resulting in a post-disturbance succession with the inferior competitor dominating soon after disturbance, and the superior competitor later. Repeated disturbance continually resets the successional process, potentially allowing coexistence of the two species.

tertidal community to elucidate the successional processes and the potential coexistence-maintaining mechanisms. In that system the major disturbance was dislodgement of boulders by storms. In the absence of disturbance, a succession occurred from early pioneer species such as the green alga *Ulva* and barnacles, to communities dominated by the red alga *Gigartina*. Areas subject to intermediate-frequency disturbance were consistently more diverse than both undisturbed areas and those subject to frequent disturbance, and this diversity was maintained by (intermediate-frequency) disturbance opening the canopy and allowing recolonization from adjacent areas. The mechanism thus relies on the maintenance of a patchwork of boulders supporting communities at different seral stages of the successional process.

A second example can be seen in the work of Guo (1996) on bannertail kangaroo rat disturbance in plant communities of the Chihuahuan desert. Disturbance comprised mound construction and associated soil disturbance, and disturbance intensity was measured as the distance from a mound. In the most intensely disturbed areas (on the mounds), only annual plant species (r species) were able to germinate and establish, giving low species richness. In the least disturbed areas with minimal rodent activity (intermound areas), only competitive perennial species (K species) could survive, others being competitively excluded, resulting in low richness. In mid-intensity disturbance "ecotonal" areas

a mixture of r species and K species was found, giving maximal richness.

In both of these examples coexistence requires spatially patchy disturbance, with the inferior competitors but better dispersers and/or colonizers being able to persist through the maintenance of a patchwork of areas of different successional stages within the region.

A simulation model of between-patch coexistence.— The modeling approach is based on a cellular automaton, with a "landscape" of cells on a torus (Fig. 1). There are two "plant" species in the simulation, an inferior competitor and a superior competitor, and each cell can be occupied by only one individual of one species at a time. At the start of the simulation a small number of cells are initialized with individuals of each species. At each time step mature individuals reproduce and disperse their propagules (seeds) into the surrounding landscape. Seeds of the inferior competitor can successfully establish only in empty cells, whereas the superior competitor can both establish in empty cells and also competitively displace inferior competitors. A further life-history parameter, dispersal distance, defines the distance around the parent within which its seeds are capable of dispersing. This parameter can be manipulated to generate the appropriate trade-off.

The two species have identical life-history parameters in fecundity, longevity, and age to maturity. We examined the behavior of the model for two cases. In the first, the maximum dispersal distance from the par-
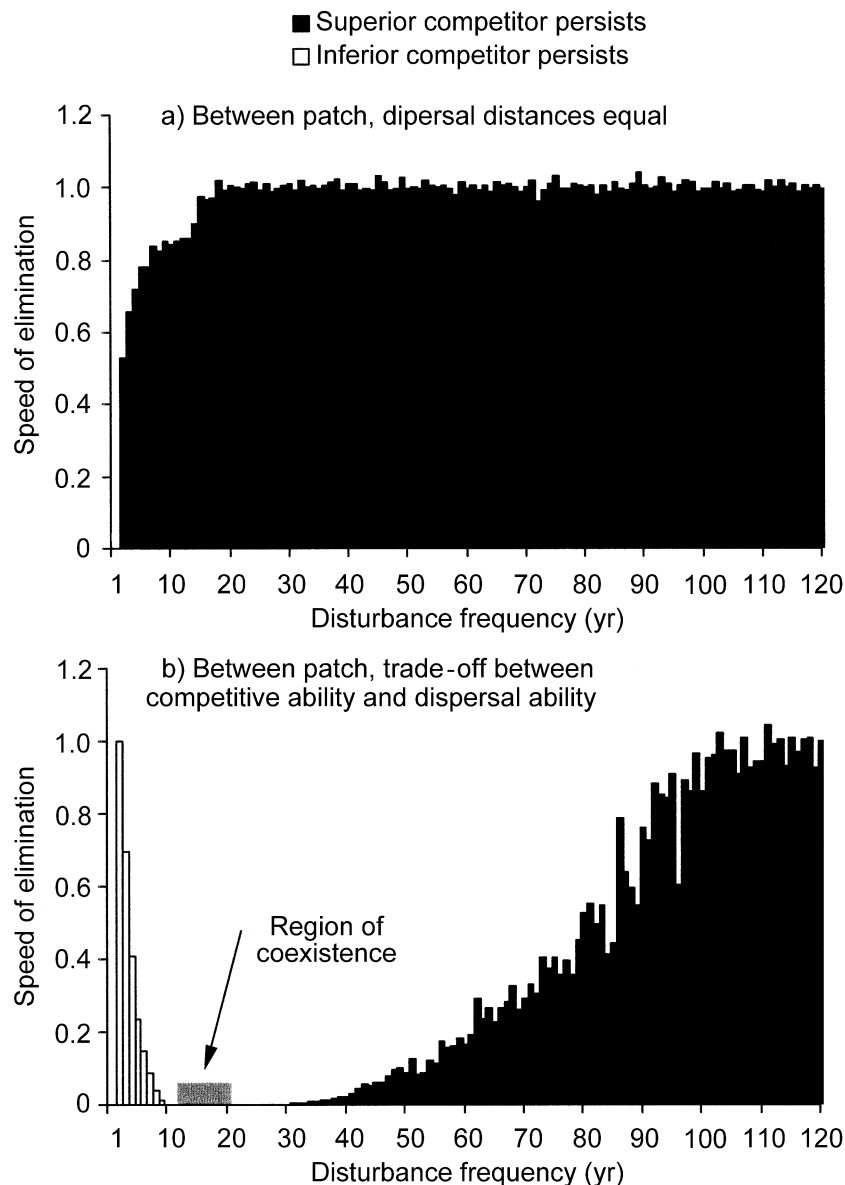
FIG. 2. Between-patch model results. Black bars indicate competitive exclusion of the inferior competitor by the superior competitor. White bars indicate persistence of the inferior competitor and loss of the superior competitor. The speed of elimination (y-axis) for disturbance frequencies where only the superior competitor persists is the inverse of the time taken for the inferior competitor to be eliminated, scaled relative to the time taken for exclusion to occur in the absence of disturbance. The speed of elimination for disturbance frequencies where only the inferior competitor persists is the inverse of the time taken for the superior competitor to be eliminated, scaled relative to the time taken for exclusion to occur at the lowest (i.e., most frequent) disturbance regime capable of maintaining a viable population. The values at each disturbance frequency are the average over 30 replicate runs of the model; although the y-axis units are arbitrary time steps in the model, for convenience we are calling them "years." (a) Without a trade-off and where the superior competitor is able to persist under the disturbance regime (disturbance frequencies >1), the inferior competitor is always excluded. (b) With a trade-off there is a region of coexistence where both species coexist indefinitely.

ent is the same for both species. In the second, the inferior competitor has a greater dispersal distance than the superior competitor, i.e., there is a trade-off between competitive ability and dispersal distance.

Disturbances are located at random within the landscape as discrete patches of a fixed size, with each

disturbance patch being ~17% of the total landscape area. All individuals within a disturbance patch are killed (Fig. 1a). In separate runs, disturbance frequencies are varied from 1, where disturbances occur at every time step, to a maximum of 120, which is the period within which competitive exclusion of the weak-

a) Components of species coexistence under fluctuating environments
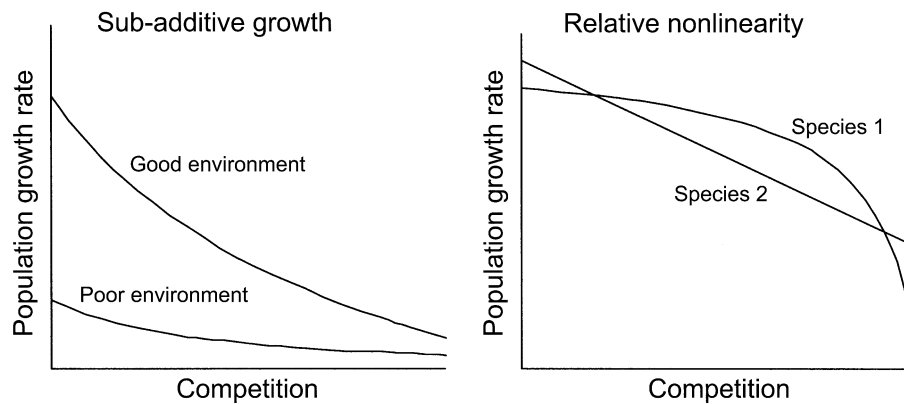
b) Species coexistence in the between-patch model
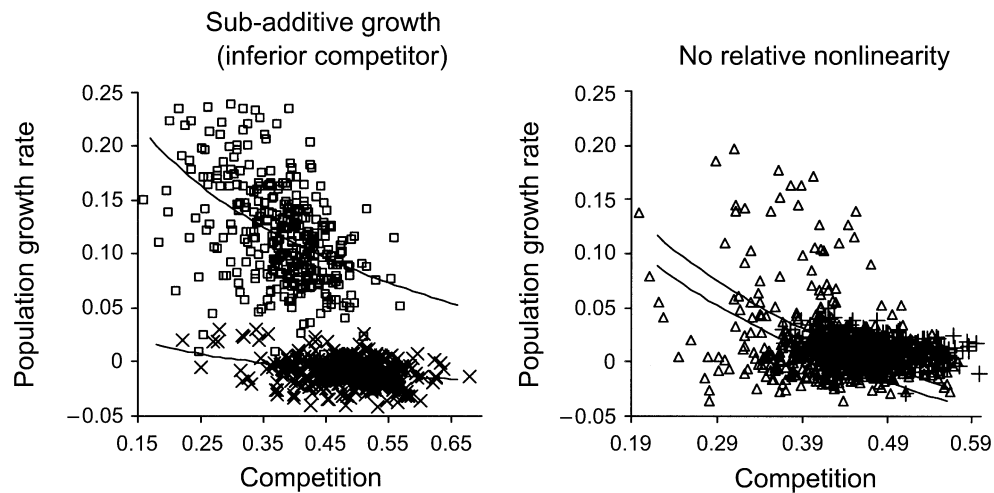
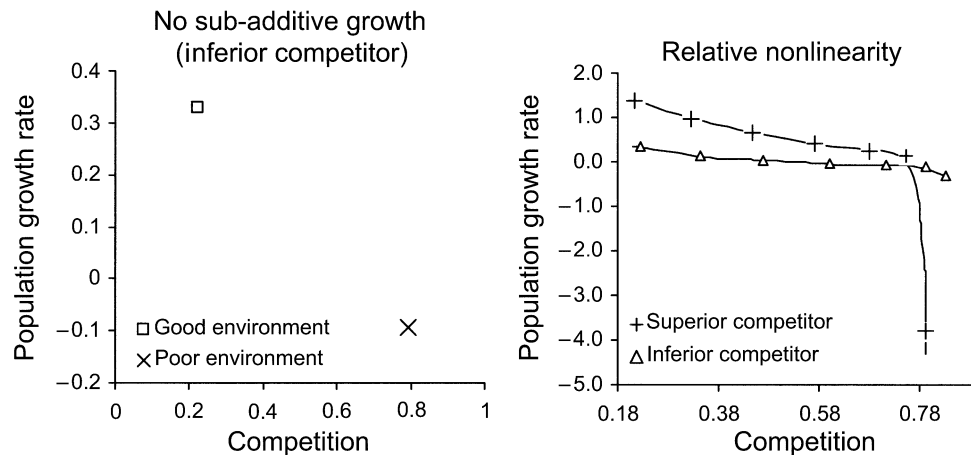## c) Species coexistence in the RYL model

Fig. 3. Illutration of two coexistence-promoting mechanisms operating under variable environments. (a) Characteristic "signatures" of two distinct mechanisms of species coexistence, redrawn from Chesson (1991). Sub-additive growth is a key component of the storage effect mechanism of coexistence and can be detected by plotting the population growth rate of a species against the degree of competition it experiences in two contrasting environments ("poor" and "good"). The curves in the right-hand panel show relative nonlinear responses of two competitors to competition and constitute a mechanism of coexistence that is distinct from the storage effect. (b) Signatures of the two coexistence mechanisms expressed in the between-patch model. The curves are best-fit regression lines ($y = a \times \ln(x) + c$), highlighting the general trends in the data. The figure clearly shows strong sub-additivity for the inferior competitor, confirming the importance of the storage

er competitor occurs. Disturbances occur at regular intervals through time.

For each disturbance frequency (1–120) and each case of the model (with and without trade-off), 30 replicate runs of the simulation are made. For each run there are three possible outcomes: (1) neither species can persist under the current disturbance regime, (2) one species persists indefinitely in the system and the other is eliminated, and (3) there is indefinite coexistence of the two species. When outcome (2) occurs, the average time taken for the species to disappear from the landscape is recorded. Each run was continued until one of these outcomes was reached, up to a maximum of 2 000 000 time steps (see Appendix A).

Results.—In the absence of a trade-off between competitive ability and dispersal distance, and when the disturbances occur at every time step (disturbance frequency = 1), neither species can maintain a positive population growth rate at low density, and the extinction of both occurs (Fig. 2a). At all other disturbance frequencies the superior competitor eventually excludes the inferior (Fig. 2a).

When the trade-off is added, and disturbances are frequent (disturbance frequencies from 2–11, Fig. 2b), the superior competitor is quickly eliminated. Poor dispersal means that the superior competitor tends to form clumps, and hence has a high chance of eventually being eliminated by frequent patchy disturbances. In contrast, the greater dispersal distance of the inferior competitor allows it to persist in the landscape. When disturbances are infrequent (disturbance frequencies >20), the superior competitor excludes the inferior competitor. At intermediate disturbance frequencies (12–20) there is a window within which both species coexist indefinitely. These results show that disturbance on its own does not necessarily result in coexistence (Fig. 2a); a trade-off in species biologies is also required (Fig. 2b).

Underlying mechanism of coexistence.—The underlying mechanism of coexistence in the between-patch model is illustrated in Fig. 3b, and shows graphically a key ingredient of the storage effect: sub-additive or buffered population growth. Soon after disturbance, and when competitive pressure is low, the inferior competitor is able to expand rapidly, as is reflected by the large population growth rates under these conditions.

Towards the end of the disturbance cycle, competition is near-uniformly intense and the population growth rate is lessened; however, it is not lessened to such an extent that the gains made during the most favorable periods for growth are negated. The ''storage'' aspect here refers to the ability of the weaker competitor to store members of its population in those parts of the post-disturbance landscape that are ''protected'' from the superior competitor as a direct result of the superior competitors low dispersal ability. Note that the relative nonlinearity mechanism is not operating in this model.

In Fig. 3b the population growth rate is the change in log-number of occupied cells from one time step to the next, and competition is the number of times a species within a cell was competitively eliminated over the same time step, divided by the total number of cells in the simulated landscape. In the sub-additivity panel the population growth of the inferior competitor is plotted for two time periods that reflect ''good'' and ''poor'' environments for this species—immediately post-disturbance (=good environment) and immediately prior to the next disturbance (=poor environment). In the relative nonlinearity panel, the population growth rates for both the superior and inferior competitor are shown for the whole disturbance–recovery cycle.

Within-patch coexistence

Empirical examples.—Unlike between-patch coexistence, there are fewer studies that have sought to either support or refute long-term species coexistence under intermediate disturbance regimes at within-patch scales, though at least two show the essential components (Bonis et al. 1995, Buckling et al. 2000).

In the study of Buckling et al. (2000) experimental microcosms were populated with three asexually reproducing populations of the bacterium *Pseudomonas fluorescens*. One population preferentially grew in the liquid phase within the microcosm, another on the bottom of the container, and another at the air–broth interface. Microcosms were subject to 'global' disturbance, which comprised regular mass-mortality events that comprised (following homogenization) the removal of 99.9% of the growth medium (i.e., 99.9% mortality) and replacement by the same volume of fresh medium. Additionally, microcosms were either contin-

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←

effect in this model. There is no evidence for relative nonlinearity. For the between-patch model the inter-disturbance interval = 15 years; population growth rate (*y*-axis) is the change in log number of occupied cells from one time step to the next; competition (*x*-axis) is the number of occupied cells that were competitively eliminated over the same time step, divided by the total number of cells. In the sub-additivity panel a ''good'' environment ($\square$) was defined as that occurring immediately after disturbance, and a ''poor'' environment ($\times$) as that immediately prior to the next disturbance event. In the relative nonlinearity panel the symbols delineate the inferior ($\triangle$) and superior ($+$) competitors. (c) Signatures of the two coexistence mechanisms expressed in the RYL model, showing the presence of strong relative nonlinearity, and an absence of the storage effect. ''Good'' and ''poor'' environments, and the symbols delineating inferior and superior competitors, are as in panel (b). For the RYL model the inter-disturbance interval = 7 yr; population growth rate (*y*-axis) is the change in log number of individuals from one time step to the next; competition (*x*-axis) is the $Y_i(t)$ term in the RYL model (see Eq. 2).

ually shaken, or were allowed to settle between disturbance events. A peak in diversity was observed in those microcosms left unshaken between intermediate-frequency disturbances. Coexistence at intermediate-frequency global disturbance in this system was apparently due to an interaction between disturbance frequency, the relative rates of competitive exclusion of the differing populations, and the existence of within-microcosm spatial niches.

The seed-bank dynamics of annuals in a Mediterranean marsh community provide a second empirical example of disturbance-mediated within-patch coexistence (Bonis et al. 1995). Global disturbance in this community consisted of regular drought, with all plants rapidly dying as the marsh dries out. There was also some evidence for animal disturbance. The plant species are predominantly annual, with a persistent seed bank. This study demonstrated all of the important components of the storage-effect mechanism of coexistence, with the seed bank acting as the means by which population gains made during favorable periods could be buffered during periods of drought. Investigation of the IDH was not a direct aim of this study, but expected losses of diversity at disturbances both more frequent (resulting in increased mortality) and more infrequent (resulting in competitive exclusion, as suggested by Bonis *et al.* [1995]), combined with the presence of a disturbance-mediated within-patch storage effect, provide the essential ingredients for the operation of the IDH.

Simulation model of within-patch coexistence.—

1. Global disturbance and spatially explicit within-patch dynamics.—In this within-patch model, a below ground seed bank for each cell is added to the between-patch model above, and three additional life-history parameters are included to link the seed bank with the aboveground dynamics. These are the probability of a seed being incorporated into the seed bank, the probability of a seed in the seed bank germinating, and the longevity of the seeds in the seed bank. Disturbance causes the death of all adults in the aboveground cells, i.e., the whole landscape is disturbed at a single time (Fig. 1b). The seed bank is not directly affected by the disturbance. Fire and drought are examples of a disturbance consistent with these dynamics.

In the periods between disturbances, mature individuals disperse their seeds at random across the landscape, with some of the seeds germinating immediately, and some being incorporated into the seed bank. Germination from the seed bank also occurs in these inter-disturbance periods. Immediately following disturbance, aboveground regeneration comes from the germination of seeds from the seed bank. In the model, when germination of a species occurs within a cell, all seeds that have accumulated within that cell germinate together, resulting in that cell's seed bank being emptied of that species.

In the first set of simulations, the life-history parameters for both species were set equal, i.e., there were no trade-offs. In the second set of simulations, the longevity of seeds in the seed bank for the superior competitor was less than that of the inferior competitor, thus introducing a trade-off between competitive ability and seed longevity.

Results.—The results for the within-patch model mirror those from the between-patch model (Fig. 4). Under very frequent disturbances (frequencies 10 or less) neither species can persist, because individuals do not reach maturity. With all life-history parameters equal, and for intermediate and high disturbance frequencies, the superior competitor always excludes the inferior (Fig. 4a). The inclusion of a trade-off between competitive ability and seed longevity results in a range of intermediate disturbance frequencies (35–44) within which both species coexist (Fig. 4b). Disturbance frequencies less than 35 result in the loss of the superior competitor due to its lower seed longevity, and disturbance frequencies >44 allow the superior competitor to exclude the inferior.

Underlying mechanisms of species coexistence.—Although the effects of disturbance are spatially homogenous in this model, the seed-bank dynamics generate within-patch spatio-temporal variation. This source of variation plays an important part in determining coexistence, particularly the seed-germination and seed-death dynamics, which vary both spatially and temporally within the landscape. In this context, disturbances reduce the advantage of germinating for both species, because only the aboveground life stages of each are affected. However, because the inferior competitor has enhanced seed-bank longevity, disturbance can indirectly benefit this species by decreasing the competitive asymmetry between the two competitors. With intermediate-frequency disturbances, the balance between these negative and positive effects is such that the spatio-temporal differences in germination biology promote coexistence. Disturbances in this within-patch model appear to play a role similar to that of harshness in the model described by Chesson and Huntly (1997). Note that the role of disturbance in promoting coexistence in this case is quite different from that described under the between-patch model, yet the basic mechanism is the same—the spatial storage effect—and the observation of coexistence at intermediate disturbance frequencies is identical.

2. Global disturbance and no spatially explicit component.—Coexistence under the previous two models was due to a combination of both spatial and temporal processes. However, we have argued that spatial variability is not a necessary requirement for disturbance-mediated coexistence, so long as the species are capable of differentiating themselves temporally in response to the variable conditions resulting from disturbance. Ellner (1987) referred to such temporal coexistence as ''time-sharing'' of a niche. Using a mod-

■ Superior competitor persists
□ Inferior competitor persists

a) Within-patch, seed longevities equal

b) Within-patch, trade-off between competitive ability and seed longevity
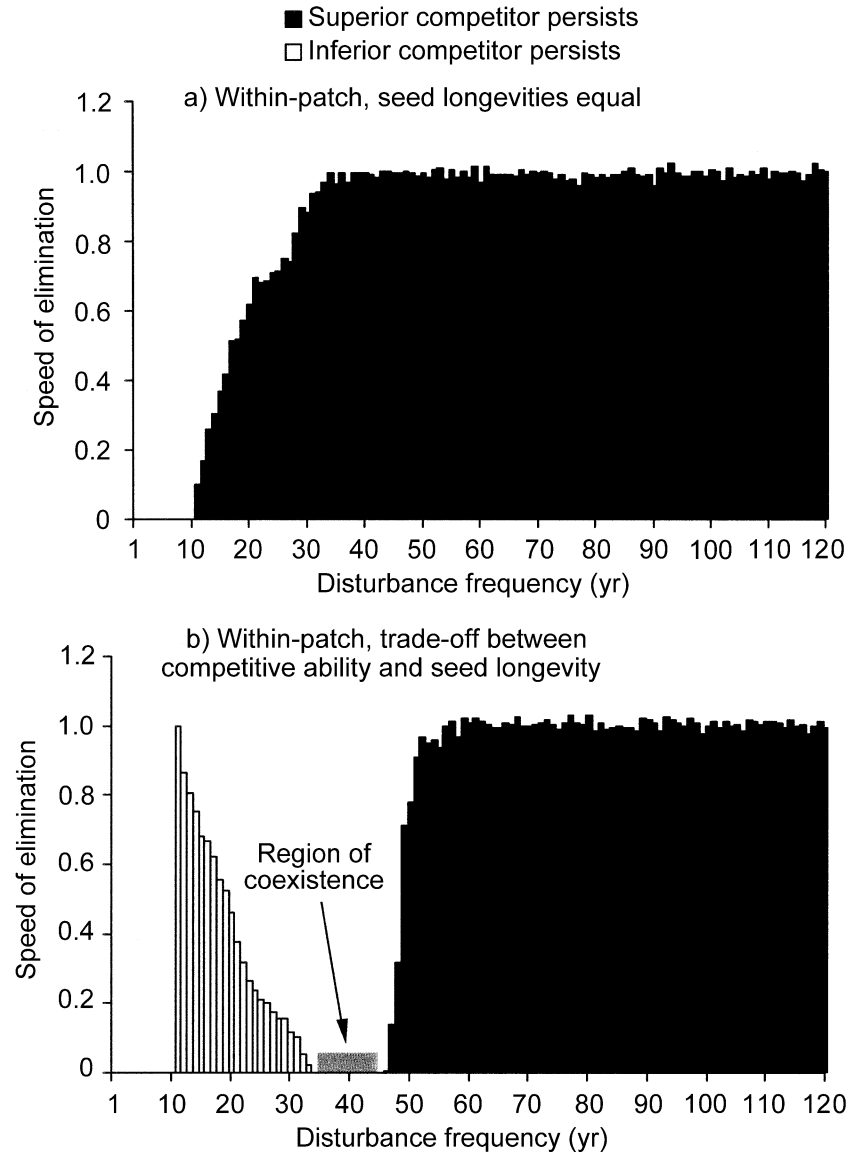
Region of coexistence

Fig. 4. Within-patch model results. The format is as in Fig. 2. (a) Without a trade-off, and where the species are able to persist under the disturbance regime (disturbance frequencies >11), the inferior competitor is always excluded by the superior. (b) With a trade-off there is a region of coexistence where both species persist indefinitely.

ification of Ellner's (1987) reciprocal-yield law (RYL) model, we demonstrate how purely temporal coexistence can arise under intermediate disturbance regimes. The term "reciprocal yield" in this model refers to the assumed inverse relationship between the population density of individuals and their per capita seed yield, i.e., competition (see also Ellner 1985).

The model assumes a spatially homogenous habitat, and is given by

$$N_i(t + 1) = N_i(t)\left[G_iK(t)\frac{1}{Y_i(t)} + (1 - G_i)s_i\right]. \quad (1)$$

Here N_i is the density of seedlings of species i, G_i is the germination fraction from the seed bank, and s_i is

the survivorship of seeds in the seed bank. The fraction of seedlings that survive beyond germination depends upon two factors, a density-independent parameter, K, which is used to model disturbance, and density-dependent within- and between-species competition, Y_i, which in this model takes the form

$$Y_i(t) = C_i + \sum_{j=1}^{n} \alpha_{ij}N_j(t). \quad (2)$$

In this expression C_i is a nonnegative constant, and the α_{ij}'s are competition coefficients quantifying the effect of species j on i. In Ellner's (1987) analysis K was allowed to vary randomly between years, however here we simplify the model and allow K to take only two

possible values: 0 for years in which a disturbance occurs, and 1 otherwise. As before, disturbances occur at regular intervals through time.

As for the within- and between-patch models, we assume a superior and an inferior competitor. Competitive superiority is achieved by setting the competition coefficients (α's) to be asymmetric. The coefficient defining the effect of the superior competitor on the inferior was set to 1.05, and the coefficient defining the effect of the inferior on the superior 0.95. Within-species competition coefficients were both set to 1.00.

Two cases of the model were again explored. In the first, both species have the same germination strategy, where $G_i = 0.85$, and $s_i = 0.15$ for both species. This can be interpreted as a ''high risk'' strategy for both species, because a high germination rate allows for rapid population growth, but leaves the species susceptible to disturbance due to limited seed-bank survivorship (Ellner 1987). In the second case of the model we allow the inferior competitor to have a ''low-risk'' germination strategy, where $G_i = 0.15$, and $s_i = 0.85$. This gives the inferior competitor an enhanced ability to cope with disturbance, but at the cost of a lower germination fraction. Because this is a purely deterministic model, only single runs at each disturbance frequency were required to determine coexistence or exclusion.

Results.—Despite spatial homogeneity, the results from the RYL model mirror those for the between- and within-patch models. When both species share the same germination strategy the superior competitor always wins, regardless of the frequency of disturbance (Fig. 5a). When the competitors have contrasting germination strategies, there is a range of disturbance frequencies (8–18) within which both species coexist (Fig. 5b). Disturbances more frequent than this result in the persistence of the inferior competitor only, and disturbances less frequent allow enough time for exclusion of the inferior competitor to occur.

Underlying mechanism of species coexistence.—The coexistence-promoting mechanism in the RYL model is demonstrated in Fig. 3c. In this model there is no stochastic variability, hence population growth rates and competitive pressures do not vary between years classified as either good (immediately post-disturbance, with resources freely available) or poor (six years following disturbance, as resources are becoming increasingly limiting), hence there is no opportunity for subadditivity to be expressed nor for the storage effect to be operating. There is, however, a very strong signal of relative nonlinearity, such that the response of the superior competitor to temporal variations in resource availability (and hence competition) is highly nonlinear relative to that for the inferior. The convex shape of this nonlinearity is such that the superior competitor's average population growth rate is significantly depressed as a result of the environmental fluctuations, allowing coexistence of the two competitors.

In Fig. 3c ''population growth-rate'' is the change in log-numbers from one time step to the next, and ''competition'' is the $Y_i(t)$ term in the RYL model described above. In the sub-additivity graph the population growth of the inferior competitor is plotted for two time periods; immediately post-disturbance and six years following disturbance, as described above. In the relative nonlinearity panel, the population growth rates for both the superior and inferior competitor are shown for the whole disturbance–recovery cycle.

Multi-species competition

The examples presented thus far have focused on competition between two competitors only. This was to focus attention on the underlying coexistence-promoting mechanisms, and to allow those mechanisms to be displayed graphically (Fig. 3). However, the results presented above are readily generalizable to the multi-species case. Appendix B presents an extension of the two-species RYL model to include multi-species competition (30 species). The results show the classic pattern consistent with the IDH (Fig. 6). At low frequency of disturbance (>15 years), the most competitive species has enough time to exclude all of the others, and a monoculture develops. Under the most frequent disturbance (every 2 years) many of the species towards the top of the competitive hierarchy cannot persist due to their poor germination fraction, and only 5 of the least competitive species persist. Diversity peaks at intermediate frequencies of disturbance, with a maximum of 25 coexisting species when disturbances recur every 7 years.

DISCUSSION

A number of researchers have investigated the role of disturbance in promoting species coexistence through mathematical models. Despite some appearances to the contrary, all share the common trait that, in order for an inferior competitor to coexist with a superior, there must exist ecological differences between the species, differentiating them in their response to disturbance.

Spatial models

In one class of spatial model the locations of the organisms are not explicitly included, but rather, the dynamics arise from the averaged properties of the spatial pattern. Caswell and Etter (1999) refer to this class of model as ''spatially averaged'' or ''mean field.'' A number of models of this type have been used to investigate the impacts of disturbance (e.g., Hastings 1980, Caswell and Cohen 1991, Nee and May 1992, Tilman 1994). The results obtained by Tilman (1994) are similar to our first cellular-automata simulations, in that coexistence is generated by a trade-off between competitive ability and dispersal ability.

The spatially averaged models of Caswell and Cohen (1991) were translated into spatially explicit cellular automata by Caswell and Etter (1999). It is interesting
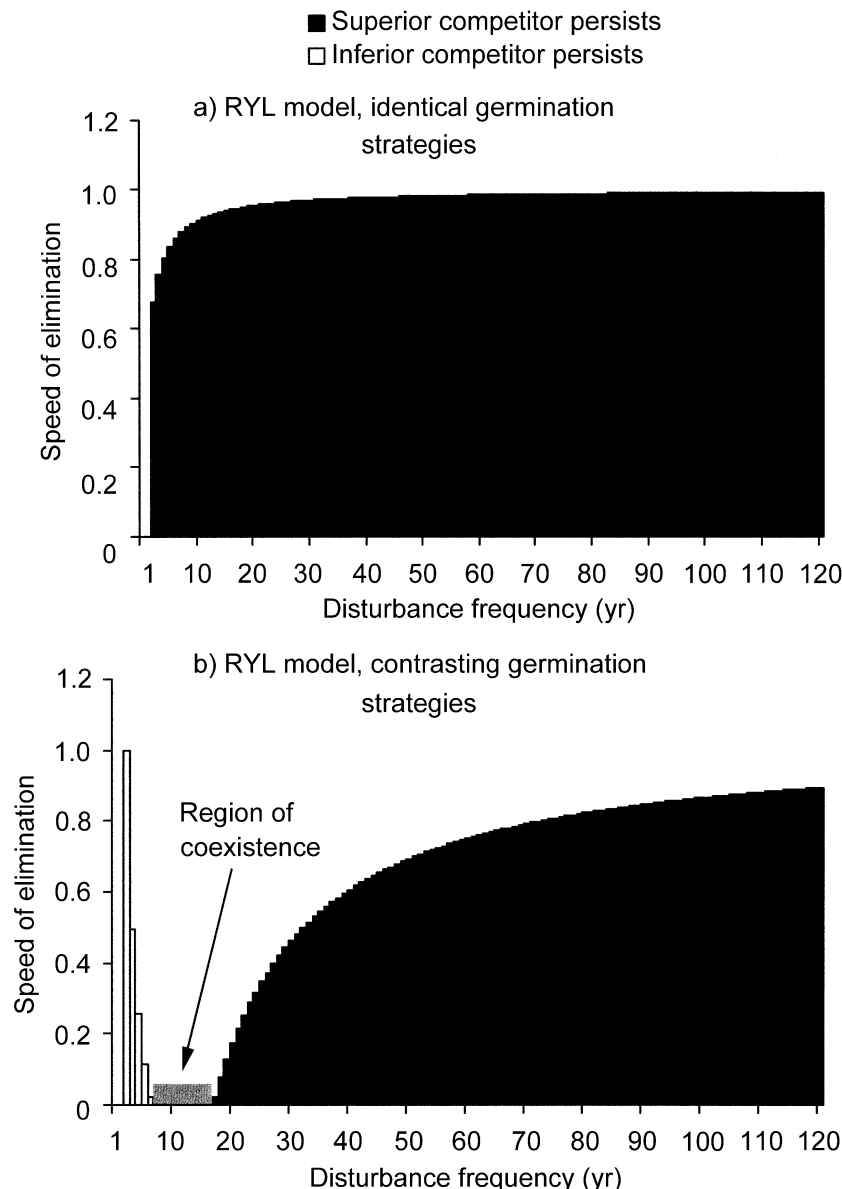
FIG. 5. Ellner's (1987) reciprocal-yield law (RYL) model. The format is as in Fig. 2. (a) When both species share a high-risk germination strategy, the inferior competitor is always excluded by the superior. (b) When the competitors have contrasting germination strategies, with the superior competitor having a high-risk strategy, and the inferior competitor a low-risk strategy, there is a region of coexistence where both species persist indefinitely.

to note that in the description of the input parameters the species appear equivalent, apart from competitive rank, yet coexistence is still observed. Although these results superficially give the impression that disturbance is promoting coexistence among equivalent competitors, contrary to our conclusions above, this is not actually the case, because the required differences in the species' responses to disturbance are implicitly included in the underlying structure of the models, rather than being explicitly defined as model parameters. Another important observation regarding the models of

Caswell and Etter (1999) is the presence of a lag between the onset of competition within a cell and the eventual exclusion of the weaker competitor. We argued above that such differences in the rates of competitive exclusion cannot play a role in promoting long-term stable coexistence, and this can be shown in the models of Caswell and Etter by forcing competitive exclusion to be instantaneous, and observing that the coexistence remains. This further highlights the fact that the basis of coexistence is the underlying differences in the species responses to disturbance.
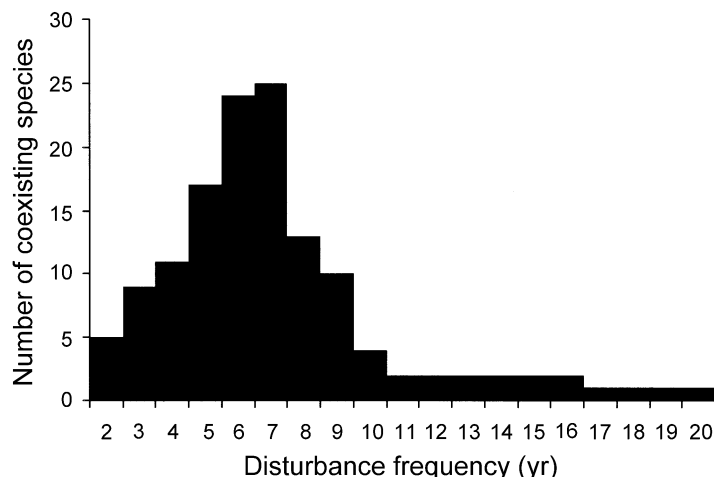
Fig. 6. Results from the multi-species reciprocal-yield law (RYL) model, showing a maximum number of coexisting species at intermediate disturbance frequencies.

Nonspatial (spatially homogenous) models

A number of authors have suggested that coexistence under the intermediate disturbance hypothesis (IDH) could apply in a within-patch or nonspatial context (e.g., Bartha et al. 1997, Collins and Glenn 1997). None of these authors has offered a mechanistic explanation of how this could arise, and as a simple generalization it is not true. A specific mechanism has to be present, of which two kinds, relative nonlinearity and sub-additivity (the storage effect), are currently known. Differences also have to be present in the biology of the species present, with a trade-off in attributes.

Bartha et al. (1997) attempted to illustrate within-patch coexistence in a series of simulations using Lotka-Volterra models. Bartha et al.'s (1997) analysis failed to demonstrate true coexistence, showing only a slowing down of the rate of competitive exclusion at intermediate disturbance frequencies. The reason lies in the linear additive structure of the Lotka-Volterra models on which their analyses were based (Chesson 1994). In this type of model, the mechanisms that allow species coexistence under fluctuating environmental conditions, e.g., relative nonlinearity and storage effects, are specifically excluded. Bartha et al. (1997) also analyzed a second set of simulations, but based on a model of between-patch dynamics (Czárán and Bartha 1989).

The early IDH concepts of Hutchinson (1951, 1953), Horn (1975) and Connell (1978, 1979) could operate only as "between-patch" mechanisms (cf. Fig. 3b). However, Chesson and Huntly (1997) suggested that coexistence in general can arise from a mixture of spatial and temporal effects, under specific conditions. Our models develop this for the IDH, and confirm that IDH coexistence can be due to spatial and/or temporal processes. In our between-patch model, the spatial differences were explicit as patches of different disturbance history within the area, giving an opportunity for the storage effect (sub-additivity) to enable coexistence. In our first within-patch model, the disturbance was ho-

mogenous over the area, but spatial patchiness developed, so that the storage effect could operate. In the second within-patch model (the modified RYL [reciprocal-yield law] model), the disturbances were spatially homogenous and there was no stochasticity, so no heterogeneity could develop. However, strong relative nonlinearity was present, which allowed coexistence (Fig. 3c).

Analysis of the underlying mechanisms for the three models highlights that not only can species differ in a large number of ways in their response to disturbance, but also coexistence under intermediate disturbance regimes can arise from fundamentally different coexistence-enabling mechanisms. Despite analysis of some of these mechanisms in the literature (Chesson 1994, Chesson and Huntly 1997) there is still considerable confusion about the role of disturbance in promoting coexistence in ecological communities (Dial and Roughgarden 1998). Not only is it insufficient to consider only disturbance in the absence of the underlying mechanisms, but the nature of the differentiation of species biology in the face of disturbance is also important.

The results presented here address only one subset of the mechanisms of coexistence that occur in natural communities. Other coexistence mechanisms that do not require environmental variability clearly do operate, for example, classical resource partitioning. Furthermore, natural disturbances are variable not only in their frequency, but also in spatial extent and intensity (van der Maarel 1993). All of these factors have the potential to provide further opportunities for species to differentiate themselves ecologically, and hence allow the coexistence of the plethora of species we see in natural communities.

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APPENDIX A

Additional details on the simulation models are available in ESA's Electronic Data Archives: *Ecological Archives* E085-007-A1.

APPENDIX B

Additional details on the methods underlying the multi-species coexistence presented in Fig. 6 are available in ESA's Electronic Data Archives: *Ecological Archives* E085-007-A2.