

COMPETITION–COLONIZATION TRADE-OFFS AND DISTURBANCE EFFECTS AT MULTIPLE SCALES

MARC WILLIAM CADOTTE¹

*Complex Systems Group, Department of Ecology and Evolutionary Biology, University of Tennessee,
Knoxville, Tennessee 37996 USA*

Abstract. The competition–colonization trade-off has long been a mechanism explaining patterns of species coexistence and diversity in nonequilibrium systems. It forms one explanation of the intermediate disturbance hypothesis (IDH) for local communities—specifically that diversity should be maximized at intermediate disturbance frequencies, yet only a fraction of empirical studies support IDH predictions. Similarly, this trade-off is also a powerful explanation of coexistence at larger spatial scales. I show, with a microbial experimental system, that the diversity–disturbance relationship is dependent on the relative distribution of species along this trade-off. Here I show that, when species are skewed toward late-successional habits, local diversity declines with disturbance. Yet, despite this trait skew, diversity at scales larger than the patch appears insensitive to the trade-off distribution. Intermediate disturbance frequencies produce the greatest diversity in patch successional stage, thus benefiting the maximum number of species at larger scales.

Key words: *intermediate disturbance hypothesis; metacommunity; microcosm; regional vs. local; spatial scale; species diversity; succession.*

INTRODUCTION

Disturbance has a long and recurring role as a potential explanation for the coexistence of species and the maintenance of patterns of species diversity (Levin and Paine 1974, Slatkin 1974, Petraitis et al. 1989, Tilman 1990, Chesson and Huntly 1997, Shea et al. 2004) often because disturbance resets local successional trajectories preventing early-successional species from going extinct at regional scales (Denslow 1980, Hastings 1980, Pickett and White 1985, Caswell and Cohen 1991, Chesson and Huntly 1997, Ellner and Fussman 2003). A fundamental aspect of disturbance-mediated coexistence in local patches is the hypothesis that species diversity is maximal at intermediate disturbance frequencies (Connell 1978, Sousa 1979, 1984, Petraitis et al. 1989).

The classic explanation for this intermediate disturbance hypothesis (IDH) is that species show a trade-off between competitive and colonization abilities, such that soon after a disturbance, colonists dominate. It is important to note that “colonist” species could be better dispersers (e.g., Rees 1995) or have higher intrinsic growth rates (Bolker and Pacala 1999) or some combination of both (Warren et al. 2006). However, only a fraction of empirical tests have supported the IDH, with results from some systems showing distinctly differing patterns, such as monotonic increases and declines with increasing disturbance intensity or fre-

quency (Mackey and Currie 2001). These discouraging results have led researchers to look for concurrent ecological processes that may be obfuscating the IDH, such as variation in habitat productivity (Kondoh 2001, Scholes et al. 2005, Cardinale et al. 2006), including a broader array of potential coexistence mechanisms (Roxburgh et al. 2004, Shea et al. 2004), and characteristics of the disturbances themselves (McCabe and Gotelli 2000, Hastings 2003).

Yet the local community scale is but one scale at which species coexist and pertinent ecological processes operate (Kniel and Chase 2004, Holyoak et al. 2005), and one can parse diversity patterns and relevant processes into local, beta (or average among-patch differences), and regional (which contains the entire species pool) (Lande 1996, Loreau 2000). Other ecological processes have been shown to have differential effects at different spatial scales (Fukami 2004, Steiner and Leibold 2004) as has disturbance (Ostman et al. 2006). Denslow (1980) viewed disturbances as a coexistence mechanism at larger spatial scales, yet too high or too low a disturbance frequency should ultimately limit coexistence even at larger scales.

The competition–colonization trade-off is potentially an important mechanism promoting coexistence at larger spatial scales (Slatkin 1974, Hastings 1980, Tilman 1990, Caswell and Cohen 1991, Pacala and Rees 1998, Amarasekare 2003, Kneitel and Chase 2004). Therefore, given the role of competition–colonization trade-offs for spatial coexistence, is the IDH a functioning hypothesis for patterns of diversity at larger spatial extents? Specifically, at intermediate disturbance frequencies, variation in successional stage should be

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¹ Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA. E-mail: cadotte@lifesci.ucsb.edu

greatest, and thus should promote greater diversity at the beta and regional scales of observation.

At all scales, the competition–colonization trade-off provides one basis for predicting disturbance–diversity relationships (but see Amarasekare 2003, Calcagno et al. 2006 for other potential mechanisms). Using an aquatic microcosm species assemblage known to exhibit competition–colonization trade-offs (Cadotte et al. 2006b), I examine whether this trade-off can explain disturbance–diversity relationships.

MATERIALS AND METHODS

Local patches were 125 mL Nalgene narrow-mouth square bottles connected together by clear Nalgene 3/16" (4.8 mm) tubing. Tube clamps were placed on every tube exiting the local communities, and when closed, movement of fluid and organisms was blocked. Local patches were arranged into five-patch landscapes by connecting local patches via dispersal corridors. Patches were arranged in parallel, which represents a distance dispersal gradient among patches. See Cadotte (2006a) for greater detail of experimental design, including standard microcosm procedures.

I used a total of 13 protozoan and rotifer species: *Blepharisma americanum*, *Chilomonas* sp., *Coleps* sp., *Colpidium striatum*, *Euplotes* sp., *Lepadella* sp., *Paramecium aurelia*, *P. bursaria*, *Philodina* sp., *Spirostomum* sp., *Tetrahymena pyriformis*, *Uronema* sp., and an undetermined rotifer species. Three species (*Philodina*, *Lepadella*, and *Euplotes*) were cultured from ponds in and around Knoxville, Tennessee, USA, while the rest were obtained from other laboratories and periodically restocked with individuals ordered from Carolina Biological Supply (Burlington, North Carolina, USA). Initial number of individuals ranged from 25 to 100 individuals/100 mL to reduce any strong interactions during the initial phase of the experiment (see Cadotte 2006a for more detail).

Disturbance treatments

A disturbance was resetting the successional trajectory of a patch to an empty state by closing tube clamps and replacing a randomly selected patch with a new patch consisting of bacterialized medium only. Therefore, local post-disturbance occupancy is entirely dependent upon a species' colonization ability.

Disturbance treatments manipulated the number and timing of disturbances over the span of eight weeks (Appendix) and were replicated four times (i.e., four replicate metacommunities for each treatment). The current results only consider the outcome at the end of the experiment and use the number of disturbances per week as the independent variable, referred to as "disturbance frequency."

Statistical analyses

See Cadotte (2006a) for sampling procedure. Species richness was measured at three scales of observation:

local, where the presence and absence of each species was scored, and the mean of the five local communities was used to calculate beta richness; regional richness was simply the total number of unique species found in the five local patches; and beta richness was calculated as the difference between regional and mean local richness (see Lande [1996] for calculation including sample size correction factor).

Species richness at local (mean value), beta, and regional scales was individually regressed against the log-transformed number of disturbances per week, in both a linear and nonlinear (quadratic) models. The number of disturbances per week was transformed since the increase in the number of disturbances per week between successive treatments increased with higher disturbance rates. If both models revealed a significant relationship, they were compared using Akaike's Information Criterion (AIC). Confirmation of a unimodal relationship was done with the MOS test, which determines whether maximal richness was at intermediate disturbance frequencies by creating constrained regression models in which the null hypothesis is that the maximal dependent values are found at either the minimum or maximum values in the independent variable (Mitchell-Olds and Shaw 1987, Fukami and Morin 2003).

In order to determine how individual species respond to increasing disturbance frequency, individual species occupancies were examined using log-linear models. Species with increasing occupancies are the colonists, benefiting from increasing the number of open patches. Those decreasing were the competitors, or those that exclude colonists and need longer time spans to colonize but remain part of local communities for long time periods once established.

RESULTS

Microcosm experiment

The relationship between local community richness and disturbance frequency in the microcosm experiment was best described as a negative linear relationship ($F_{1,42} = 30.182$, $P < 0.001$, $R^2 = 0.42$, $AIC = -7.25$) compared to a unimodal or quadratic relationship ($F_{2,41} = 16.680$, $P < 0.001$, $R^2 = 0.45$, $AIC = -6.41$; Fig. 1a). I also employed the Mitchell-Olds and Shaw test (MOS) and maximal richness was found at a disturbance frequency of 0.0097 patches disturbed each week, which was indistinguishable from a disturbance frequency of 0 ($P > 0.05$).

However, at both the beta ($F_{1,41} = 3.330$, $P = 0.076$, $R^2 = 0.08$, $AIC = -4.95$ for the linear model, and $F_{2,40} = 10.345$, $P < 0.001$, $R^2 = 0.35$, $AIC = -17.48$ for the quadratic) and regional scales ($F_{1,41} = 27.634$, $P < 0.001$, $R^2 = 0.40$, $AIC = 21.88$ for the linear model, and $F_{2,40} = 30.936$, $P < 0.001$, $R^2 = 0.61$, $AIC = 5.83$ for the quadratic), the unimodal model better described the relationship between diversity and disturbance frequency (Fig. 1b, c). The MOS test indicated that maximal

beta richness was found at 1.28 disturbances per week, and was best described by a unimodal relationship ($P < 0.01$). Similarly, regional richness was maximized at 0.81 disturbances per week and best described by a unimodal relationship ($P < 0.01$). These results indicate that the IDH was a robust descriptor of diversity patterns at these scales, despite the lack of IDH support at the local scale.

From the control for this experiment and in previous experiments (e.g., Cadotte 2006a, Cadotte et al. 2006a), I have shown that an average of 5–7 of these species coexist over long timescales, and these same seven species showed significant declines in number of patches occupied with increasing disturbance frequency (Fig. 2c, e, f, h–j, m). These seven are members of competitively structured communities, and do not colonize empty patches rapidly. Further, only four species showed occupancy increases with increasing disturbance frequency (Fig. 2b, d, g, k). Here two of these relationships are nonsignificant, but the pattern exhibited by *Colpidium striatum* (Fig. 2d) shows significantly greater occupancy at all disturbance treatments compared to the no-disturbance control, and *Tetrahymena pyriformis* (Fig. 2k) is only found in extremely high disturbance treatments.

DISCUSSION

It is important to note that this experimental system explicitly attempts to maintain homogeneous local patches in terms of resources; thus population dynamics or local interactions should not vary across space. Otherwise, heterogeneity among patches would potentially introduce other coexistence mechanisms, which may reduce the importance of competition–colonization trade-offs (Amarasekare 2003). For example, modeling work has shown that species coexistence in spatially heterogeneous landscapes with source and sink habitats can actually necessitate dominant competitors having higher dispersal rates (Abrams and Wilson 2004), which is antithetical to the competition–colonization trade-off.

Competition–colonization trade-offs and local diversity–disturbance relationships

Cadotte et al. (2006b) used two experiments to show that these species exhibited a competition–colonization trade-off (Fig. 3). They quantified this relationship with two experiments. They first measured colonization ability as the amount of time needed for species to colonize four patches in a five patch system, where the fifth patch was where the initial population was inoculated. Second, they assessed competitive ability through pairwise competition trials, where competitive ability was measured as the number of extinctions caused by a species.

The four species that increased occupancy with increasing disturbance frequency in this study (Fig. 2) are better colonists and poorer competitors, while the seven species that declined (Fig. 2) are superior

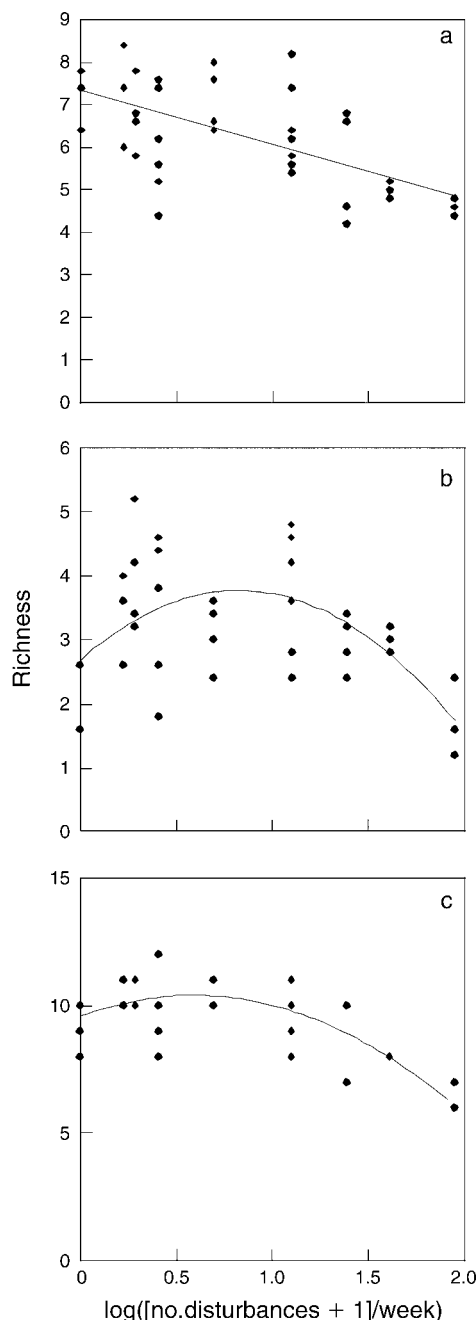


FIG. 1. Results of the microcosm experiment showing that (a) local richness linearly declines with increasing disturbance frequency, while richness at (b) beta and (c) regional scales conforms to the intermediate disturbance hypothesis (IDH). See *Materials and Methods* for estimation of species richness for each of the three scales.

competitors and generally inferior colonizers (Fig. 3). These results reveal that these species are skewed toward the competitive end of the competition–colonization trade-off. This skew means we should predict that increasing disturbance frequency should reduce local diversity.

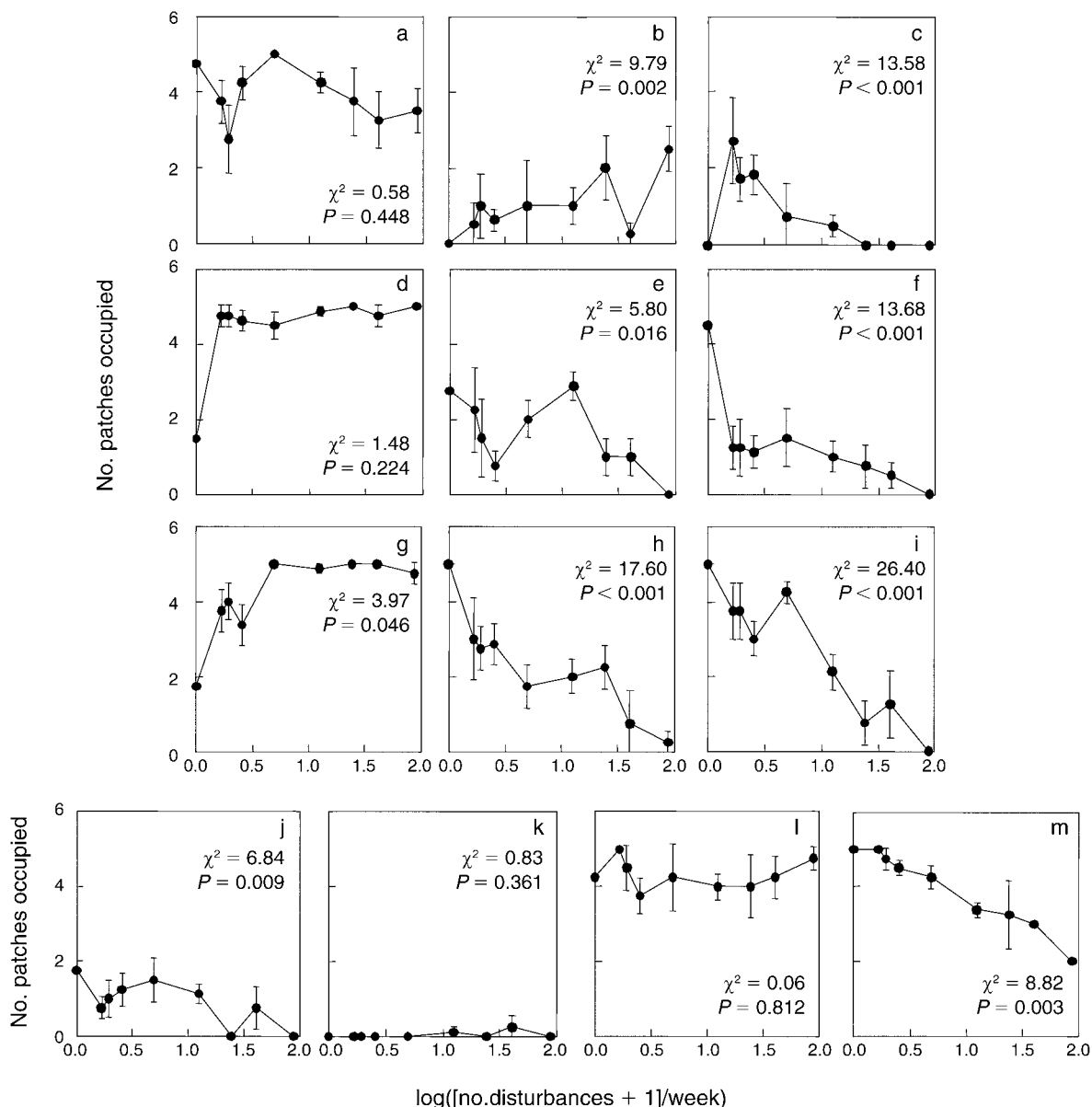


FIG. 2. Patch occupancy patterns for each of 13 species across increasing disturbance frequencies: (a) *Blepharisma americanum*, (b) *Chilomonas* sp., (c) *Coleps* sp., (d) *Colpidium striatum*, (e) *Euplotes* sp., (f) *Lepadella* sp., (g) *Paramecium aurelia*, (h) *P. bursaria*, (i) *Philodina* sp., (j) *Spirostomum* sp., (k) *Tetrahymena pyriformis*, (l) *Uronema* sp., and (m) unidentified rotifer. Results of log-linear models are indicated in each panel. Plotted points are means; error bars represent \pm SE.

The verbal model of the IDH assumes a uniform trade-off from the best colonists to the best competitors, such that very few species immediately invade newly opened patches, while very few species ultimately limit all others over long time scales (Connell 1978). However, the distribution of species along the competition-colonization trade-off continuum ought to depend upon evolutionary pressure from historical disturbance frequency. In frequently disturbed systems there should be a skew toward a greater number of colonists vs. competitors (Pianka 1970, Denslow 1980, Loehle

2000). Similarly, in low disturbance frequency systems, the trade-off continuum should be skewed toward species that exist in later successional stages (Pianka 1970, Denslow 1980, Loehle 2000). Thus, without knowing how species are distributed along a trade-off gradient beforehand, we should not necessarily expect the IDH to be true (e.g., Mackey and Currie 2001).

Several models examining patch occupancy and localized disturbances have found that the occupancy of late-successional species (or dominant competitors) declines with increasing disturbance frequency, while the

reverse is true for colonizing species (Hastings 1980, Caswell and Cohen 1991, Amarasekare and Possingham 2001). Further, in an examination of native vs. exotic plant responses to disturbances, Allcock and Hik (2003) showed that exotics, which tend to be weedy, increased with disturbance frequency. They also showed that the natives tend to decline with disturbances (Allcock and Hik 2003). Their explanation is an evolutionary one. Successful exotics tend to be adapted to ruderal, ephemeral habitats and thus exhibit traits often associated with “*r*-selected” species, while the majority of native plants tend to be adapted to habitats with low disturbance regimes (at least in a prehuman settlement regime) and thus exhibit relatively “*K*-selected” traits (Allcock and Hik 2003).

Studies assuming strict competition–colonization trade-offs usually show that maximal diversity results from intermediate disturbance rates (e.g., Caswell and Cohen 1991, Barradas et al. 1996). However, as mentioned previously, the majority of empirical studies actually fail to support the IDH (Mackey and Currie 2001). The present study is the first to show that local, non-unimodal diversity–disturbance relationships are possible, while still assuming competition–colonization trade-offs.

In another microcosm study, Warren (1996) found that disturbance did not enhance diversity, and that any disturbance effect was rather weak. His findings actually complement the current results because of the way his experiment was carried out. He manipulated dispersal by removing community samples and transferring them to other patches (Warren 1996), which is antithetical to the competition–colonization trade-off. Locally abundant species, which should be better competitors and relatively poor dispersers, were the most likely to disperse from the movement of a community sample. This type of dispersal experiment is not uncommon in microcosm studies (e.g., Cadotte and Fukami 2005, Cadotte et al. 2006a), but it is important to note that these types of studies manipulate dispersal in the absence of specific mechanisms such as competition–colonization trade-offs (Cadotte 2006b), and thus should require differing predictions. Further, Kadmon and Benjamini (2006) recently showed that neutral dynamics, in which a trade-off between competitive and colonization abilities was lacking, can lead to unimodal diversity–disturbance relationships, although coexistence in their model is assumed at the scale of the species pool, while metacommunity theory searches for large-scale coexistence mechanisms.

IDH at scales above the local patch

In order for diversity to recover from complete biomass removal, species must be able to disperse into new patches. Dispersal alone can be a process structuring local and regional diversity patterns (Cadotte 2006b), and differing dispersal rates can change how diversity responds to disturbance (Warren 1996). Dis-

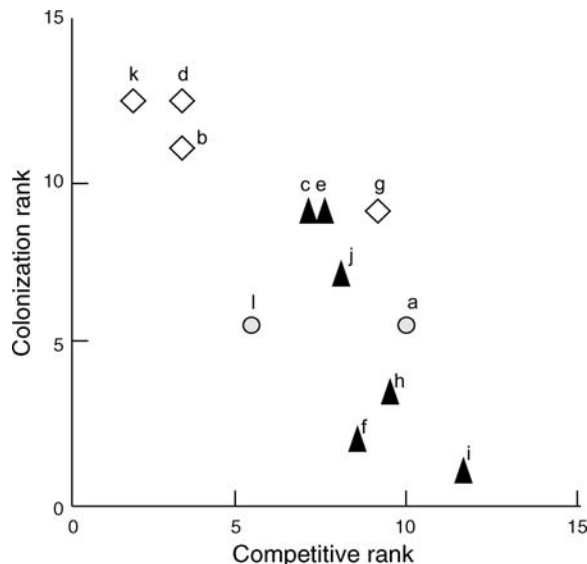


FIG. 3. The species used in this experiment reveal a general trade-off between relative competitive and colonization ability (from Cadotte et al. 2006b). Open diamonds are species that increased in occupancy with increasing disturbance frequency, black triangles are those that declined, and gray circles are species that showed no response to disturbance. Letters refer to species in Fig. 2.

persal is generally a homogenizing process, thus reducing beta, or among-patch, diversity (Cottenie and De Meester 2004, Cadotte 2006a, b), while disturbance, at least at low to intermediate frequencies, is a beta increasing process (Warren 1996, Ostman et al. 2006).

Traditional IDH studies examine patterns at the local scale in one of two ways: either as time since disturbance patterns within an individual patch; or as changes in average richness in multiple patches across a gradient of disturbance frequency. Here I examined changes in average richness, but also examined disturbance effects on regional coexistence and compositional changes in the form of beta richness.

In a modeling examination of the IDH at scales larger than local patches, Caswell and Cohen (1991), using a model that incorporates competition–colonization trade-offs, also show that beta diversity appears unimodally related to disturbance frequency, though they failed to discuss the biological reasons why. Warren (1996) showed that under low dispersal rates, disturbance increased beta diversity, even though the same treatment combination reduced regional diversity. In the current paper, the experimental results support the IDH at scales above the local patch.

The reason for the robustness of the IDH at the beta and regional scales is that local disturbances create a successional mosaic at a larger scale, and certain species are favored at certain successional stages (Denslow 1980, Chesson and Huntly 1997, Ellner and Fussman 2003). Large-scale species coexistence through a successional mosaic is the product of two potential mecha-

nisms, only one of which explicitly depends upon the competition–colonization trade-off (Amarasekare 2003). First is succession through facilitation (Connell and Slatyer 1977). Here, species adapted to differing temporal niches reach their greatest abundances at different times since the disturbance, and the invasion of late-successional species is dependent upon earlier colonists creating conditions more suitable for the late-successional species. Thus, too low a disturbance frequency favors late-successional species, and too high favors early-successional species across all patches. Facilitation is not likely to be important in this system because the results of Cadotte et al. (2006b) reveal that the dominant competitors colonize unoccupied patches without the assistance of early colonists. The second mechanism of coexistence is a purely transient process and likely explains the current results. Once patches are opened, colonizers have a much higher probability of colonization and exploit available resources faster than competitive species can either disperse into patches or increase in population size. With increasing time since disturbance, dominant competitors eventually invade and increase in population size, extirpating inferior competitors. Therefore at intermediate time scales, it appears as though coexistence is maximized.

Conclusions

It can be concluded then, that local non-unimodal diversity–disturbance patterns can be produced by species having competition–colonization trade-offs. However, several authors have concluded that the relative position of species along this trade-off gradient is itself dependent upon evolution under historical disturbance regimes (Pianka 1970, Loehle 2000). When testing the IDH or any diversity–disturbance relationship in local communities, researchers need to estimate relative competitive and colonization abilities of species, in order to adequately predict the nature of this relationship. However, diversity–disturbance relationships at larger scales appear relatively insensitive to the distribution of species along this trade-off gradient, and maximal diversity is promoted by intermediate disturbance frequencies.

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APPENDIX

Disturbance treatments used in the microcosm experiment (*Ecological Archives* E088-051-A1).