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Sequence effects of disturbance on community structure

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The sequence in which disturbance events occur has the potential to affect the structure of ecological communities, but its role has been generally overlooked. Most disturbance studies have focused on the frequency or intensity of disturbance, probably reflecting the influence of the intermediate disturbance hypothesis. To investigate the effects of disturbance sequence on community structure, I created laboratory microcosms of protists and small metazoans analogous to communities found in water-filled bamboo stumps. Using drought (disturbance D) and larval mosquito addition (disturbance M), I examined the following five treatments of disturbance sequence: D-M-D-M, D-D-M-M, M-D-M-D, M-M-D-D, and no disturbance as a control. The response of species to disturbance varied between disturbance types (D or M) as well as among species, and disturbance effects depended on previous disturbance events. As a result, disturbance sequence drove the microcosms onto different successional trajectories, sometimes leading to divergence in final community states in terms of species richness or species composition and relative abundance. This divergence occurred even under the same frequency and intensity of disturbance. These results suggest that historical information on disturbance sequence can be essential for explaining variation in community structure. The interaction of sequence with frequency and intensity likely enhances the role played by disturbance in ecological communities.

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Historical information is often essential at a variety of time scales for understanding patterns in ecological communities (Ricklefs and Schluter 1993). At ecological time scales, the history of species invasions has been shown in some circumstances to be a critical determinant of structure through field observations (Sutherland 1974, Barkai and McQuaid 1988, Thornton 1996), experiments (Morin 1984, Wilbur and Alford 1985, Gilpin et al. 1986, Robinson and Edgemon 1988, Drake 1991), and theory (Post and Pimm 1983, Drake 1990a, Law and Morton 1996). These studies have found that different sequences of invasion can create very different community structures at a local scale even with the same species pool and physical environment. Communities whose structure is strongly regulated by invasion history might not be so common in the real world, however. The role of invasion history largely derives from the strong influence of species interactions, but the importance and ubiquity of species interactions in natural communities remain a main focus of ecological research. This is partly because a variety of disturbance events frequently remove individuals from the community and thus interrupt the process of species interactions (e.g., Connell 1978, DeAngelis and Waterhouse 1987). Consequently, invasion history may be relatively unimportant under a regime of frequent disturbances.

However, not only species invasions but also physical and other disturbances may be another important element of history that influences community structure (e.g., Hughes 1989, Dublin et al. 1990, Tanner et al. 1996, Collins 2000). This is likely to be true especially when a community is being influenced by more than

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one type of disturbance, a common situation in nature. For example, many grassland communities are subjected to multiple disturbances including fire, grazing, and flooding (Collins and Barber 1985, Collins 1987, Coffin and Lauenroth 1988, Peart 1989, Dublin et al. 1990, Chaneton and Facelli 1991, Umbanhowar 1992). Many communities also experience both natural and anthropogenic disturbances (Sousa 1984, Hobbs and Huenneke 1992, Paine et al. 1998, Hughes and Connell 1999). In such cases involving multiple types of disturbance, the degree to which disturbance reduces population sizes and alters community organization may depend on disturbance type. Subsequent population dynamics may then follow different trajectories, and population declines caused by preceding disturbance events may influence the effect of the next disturbance (Hughes and Connell 1999). Consequently, the sequence of different disturbance events may determine whether populations will go extinct or persist within the community. Overall, community patterns can diverge when communities have experienced different disturbance sequences, even given the same frequency and intensity of disturbance.

Nonetheless, possible roles of disturbance sequence seem to have been generally overlooked. The mainstream of disturbance studies has focused on frequency and intensity rather than sequence (e.g., Sousa 1984, Pickett and White 1985, Petraitis et al. 1989, Wootton 1998, Collins 2000, Mackey and Currie 2000). This tendency is perhaps due to the influence of the "intermediate disturbance hypothesis" (Connell 1978, also see Horn 1975), which predicts that the species diversity of a community peaks under an intermediate frequency or intensity of disturbance. As Milchunas et al. (1988) pointed out, the hypothesis finds this pattern by lumping together numerous, very different types of disturbances on a single axis. This hypothesis and its theoretical (e.g., Huston 1979) and empirical (e.g., Sousa 1979, Paine and Levin 1981) testing are regarded as "one of the success stories of ecological science" (Rosenzweig 1995: 342) for its generality and simplicity. It is likely that this successful hypothesis has led most ecologists to direct their disturbance research toward frequency and intensity, leaving sequence largely unexplored (but see Dublin et al. 1990, Hughes and Connell 1999, Lesica and Cooper 1999).

In this paper, I investigate the successional trajectories that communities follow under different sequences of disturbance and test whether community patterns diverge after experiencing different sequences. For this purpose, I conducted a laboratory experiment using microcosms of protists and small metazoans, with drought and larval mosquito addition treated as two types of disturbance. I designed these microcosms as analogues to water-filled bamboo stumps found in the field. In the bamboo system, ecological processes occur at small temporal and spatial scales and can be easily simulated in the laboratory, making them useful for addressing questions of such historical factors as invasion and disturbance that require population monitoring over many generations of species involved (cf. Luckinbill and Fenton 1978, Lawler and Morin 1993, McGrady-Steed and Morin 1996, Warren 1996, Law et al. 2000). Moreover, bamboo stump systems are particularly suitable for studying disturbance sequence because two types of disturbance, drought and grazing by larval mosquitoes, exist under natural conditions (cf. Bradshaw and Holzapfel 1988, a similar system within a mosquito larvae community). Clearly, the results of a microcosm experiment should be treated with caution when they are applied to other systems of different scales and complexities (Grover and Lawton 1994, Carpenter 1996, Drake et al. 1996). Nevertheless, this study is aimed at providing a first piece of experimental evidence on disturbance sequence effects.

Materials and methods

Microcosm setup

To establish the microcosms, I collected dried leaf litter from bamboo stumps in a forest in Tokyo, Japan and brought them to the laboratory for experimental use. I then homogenized the leaf litter with a blender and placed 0.2 g of the homogenized leaf litter on the bottom of each of 50 plastic containers. The shape and size of these plastic containers (diameter 60 mm, depth 37 mm) were similar to those of the bamboo stumps. The containers had been sterilized with 70% ethyl alcohol before use. After placing the dried litter, I added 20 ml of deionized water to the plastic containers and housed them in an incubator with the temperature held constant at 25°C and the light condition 14:10 L:D. This setup procedure generated replicates of initially identical detritus-based microcosms that contained virtually the same source pool of microorganisms (i.e., organisms encysted in the homogenized dried leaf litter) under the same physical environment. With these microcosms, I monitored community dynamics with colonization of species from the leaf litter and with disturbance imposed by drought and mosquito larvae as described below.

Manipulating disturbances

I designed five treatments of the sequence of drought (disturbance D) and larval mosquito addition (disturbance M) to be imposed on the microcosms: (1) D-M-D-M, (2) D-D-M-M, (3) M-D-M-D, (4) M-M-D-D, and (5) no disturbance as a control. Each treatment had ten replicates. The first disturbance in each sequence was initiated on day 5, counted since the start of the experiment, and was terminated on day 6. Similarly, the second to fourth disturbances were initiated on days 11, 17, and 23 and terminated on days 12, 18, and 24, respectively. This disturbance protocol allowed me to investigate effects of disturbance sequence while maintaining both the same frequency (i.e., five-day interval) and intensity (i.e., the same time period of drought and mosquito addition; the same drying speed; the same number of larvae added; the same total number of disturbance events, namely two Ds and two Ms; see below for details) of disturbance across treatments.

Drought

Drought frequently occurs in bamboo stumps in the field as a function of rainfall events. When their habitat is dehydrated, microorganisms become inactive and some die but others form drought-resistant cysts. If the stump is refilled with water, the survivors become active again over a period of a few hours to ten days depending on species (McGrady-Steed and Morin 1996). Thus drought imposes a disturbance on aquatic microorganisms by severely altering population growth. Drying can affect the microbial community even before the habitat is completely dehydrated. For example, the encounter rate of organisms and the nutrient concentration change as the water level drops.

To simulate such drought, I stopped adding water until all water evaporated. For the whole course of the experiment, I daily added deionized water to the microcosms in order to compensate for evaporation from the containers and reset the water volume to 20 ml, except when I imposed drought on microcosms. Laboratory conditions were adjusted such that the complete drought periods started approximately five days (range 4.5–5.5 days) after the last day of water addition. This time period necessary for all water to evaporate was within the range of that observed in the field. The containers were refilled with 20 ml of deionized water on the day after drought. Thus, the complete drought periods lasted for 0.5 to 1.5 days. This dehydration-rehydration procedure was the same as that employed by McGrady-Steed and Morin (1996), except that I rehydrated microcosms with deionized water whereas McGrady-Steed and Morin used a bacterized medium.

Mosquito addition

The mosquito *Aedes albopictus* often lays eggs in water-filled bamboo stumps in the field. Their larvae inhabit bamboo stumps and graze on microorganisms. The presence of mosquito larvae can reduce species richness and abundance of microorganisms dramatically in small aquatic systems such as pitcher plants (Addicott 1974), banana bracts (Maguire et al. 1968), tree holes (Fish and Carpenter 1982, Eisenberg et al. 2000), and bamboo stumps (Kurihara 1954, 1983). Therefore, the presence of mosquito larvae can be considered another type of disturbance to the microorganism assemblage.

Mosquito predation may be better called a perturbation rather than a disturbance, since some ecologists draw a distinction between abiotic events (disturbances) and biotic ones like predation (perturbations). The marine literature tends to use these two synonymously because they have similar effects, i.e., clearing space. In other systems, the similarity can be more suspect. In this paper, I call both the drought and the mosquito addition disturbances merely for the sake of simplicity (see, e.g., White and Pickett 1985 and Karr and Freemark 1985 for more discussions on the usage of the terms).

To simulate mosquito presence, I added 40 last-instar larvae of *A. albopictus* into the microcosms using a pipette that had been sterilized with 70% ethyl alcohol and kept the larvae in the microcosms for 24 h. Although such a short duration of mosquito presence is certainly not realistic in nature, the duration was set this way in order to make the duration of disturbance M comparable to that of disturbance D. The larvae were obtained from the field and were maintained in deionized water for approximately 24 h before use to standardize their hunger level. The larvae were then carefully rinsed with deionized water before use in order to minimize possible contamination by additional microorganisms. To detect such contamination, it would have been helpful to include a transfer control (fluid without mosquitoes). However, contamination was most probably not a problem in this study, since no species was observed more frequently after the mosquito treatment (Table 1). I terminated mosquito presence by removing the introduced larvae with a sterilized pipette.

Sampling

Immediately after the daily water addition, I gently stirred each container to homogenize microorganisms in the water and removed a 0.05-ml sample to identify and count microorganisms present in the sample with the aid of a compound microscope (see Fig. 1 for sampling dates). Microorganisms counted included protists, rotifers, and nematodes. The leaf litter also contained bacteria, which were not monitored. On the days before drought, sampling was sometimes impossible owing to the insufficient amount of water.

Data analysis

To examine effects of disturbance on each species, I calculated the probability of occurrence for each species and compared the probability values before and after each disturbance. The probability of species occurrence describes the percentage of the replicates in which the focal species was present. During the drying periods, water volume decreased and the numbers of individuals counted were overestimated, compared to that of the other treatments that held 20 ml of water. Thus the direct measure of the number of species in such samples cannot be used for comparison. Accordingly, I calculated the standardized number of individuals of species i as $n_i = (v/20)m_i$, where m_i is the number of individuals of the focal species in the sample (i.e. the raw number) and v is the water volume of the drying replicate. This correction standardizes the proportion of the water volume of the sample to that of the whole microcosm. If a standardized population size was below one, I considered that the species was technically absent.

I further employed two indices of community structure, i.e., (1) species richness and (2) species composition and relative abundance. Species richness was defined as the number of species of active protists, rotifers, and nematodes recorded in the 0.05-ml sample. This sort of measurement is strictly termed species density and is a most commonly used measure of species richness (Magurran 1988). For the drying periods, I used the following correction formula based on the idea of rarefaction (Hurlbert 1971, Gotelli and Graves 1996):

Standardized species richness

$$= \sum_{i=1}^{S} \left[1 - \binom{N-m_i}{n} \Big/ \binom{N}{n} \right], \qquad n = (v/20)N,$$

where N is the number of individuals of all species counted in the sample; n is the number of individuals of all species expected if water volume was the same as control (i.e., 20 ml); S is the total number of species in the sample; and m_i and v are the same as defined above. Species composition and relative abundance were analyzed using detrended correspondence analysis (DCA). DCA is an ordination technique used to represent complicated data sets of species abundances in a low-dimensional space (Gauch 1982). For the drying replicates, I standardized population sizes using the same correction as above. I used data from days 5, 7, 11, 13, 17, 19, 23, 25, and 35, all of which were ordinated in a single DCA.

Using these two indices, I examined whether communities diverged because of the difference in disturbance sequence. Specifically, I compared the final states of the treatments that shared the last disturbance of the same

Table 1. List of the species observed, their response to disturbances, and their trophic status. Response to disturbance was determined by a Wilcoxon signed rank test performed on the difference between the probabilities of species occurrence (i.e., the proportions of the replicates in which the species was present) immediately before and one day after disturbance ($n = 8$ disturbance events). The plus sign indicates that the species was present in significantly more replicates after disturbance than before disturbance ($P < 0.05$). The minus sign indicates that the species was present in significantly fewer replicates after disturbance than before disturbance ($P < 0.05$, except * where $P = 0.068$). ns: the number of replicates in which the species was present was not significantly different between before and after disturbance ($P > 0.1$). na: the species were too rare to provide sufficient data for the Wilcoxon signed rank test. Pearson correlations between the first two DCA axes and species are also included.

Species	Response to disturbances		Trophic status	Pearson correlations	
	To mosquito	To drought		DCA axis 1	DCA axis 2
Ciliate #1	−	+	Bacterivore?	0.235	−0.026
Vorticella sp.	−	+	Bacterivore	0.569	0.118
Colpoda sp. #1	−*	+	Bacterivore	0.491	−0.310
Flagellate	ns	+	Bacterivore	0.568	0.158
Rotaria sp.	ns	−	Detritivore	−0.185	−0.300
Ciliate #2	−	ns	Bacterivore?	0.532	−0.231
Cyclidium sp.	−	ns	Bacterivore	0.001	−0.262
Crytolophosis sp.	−	ns	Bacterivore	−0.730	0.778
Hypotricha sp.	−	ns	Predator of bacteria/ciliates	0.207	−0.027
Leptopharynx sp.	−	ns	Bacterivore	0.354	−0.005
Pleurostomatida sp. #1	−	ns	Predator of ciliates	−0.275	−0.476
Spathidium sp.	−	ns	Predator of ciliates	0.045	0.003
Ciliate #3	ns	ns	Bacterivore?	−0.088	−0.040
Drepanomonas sp.	ns	ns	Bacterivore	−0.870	−0.032
Tetrahymena sp.	ns	ns	Bacterivore	−0.086	−0.099
Ciliate #4	na	ns	Bacterivore?	−0.060	−0.048
Pleurosotomatida sp. #2	na	ns	Predator of ciliates	−0.135	−0.067
Colpoda sp. #2	−	na	Bacterivore	0.053	−0.225
Ciliate #5	na	na	Bacterivore?	−0.051	−0.022
Ciliate #6	na	na	Bacterivore?	−0.087	−0.121
Ciliate #7	na	na	Bacterivore?	na	na
Nematode sp.	na	na	Bacterivore	na	na
Rotifer sp.	na	na	Detritivore?	−0.013	0.128
Suctoria sp.	na	na	Predator of ciliates	na	na

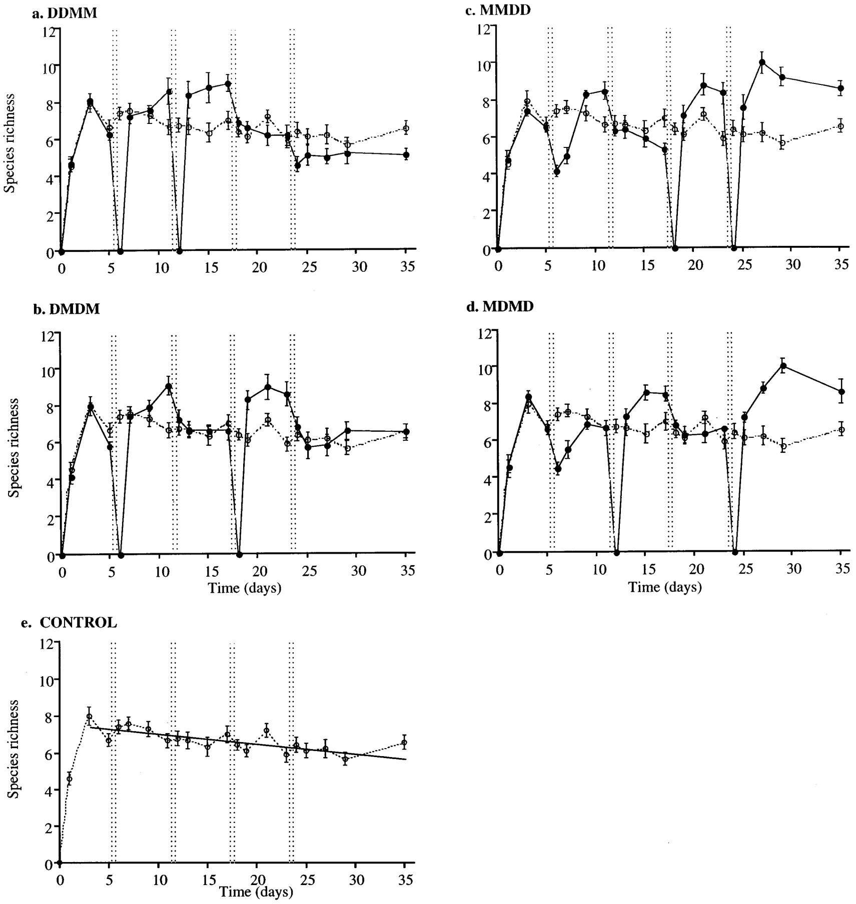

Fig. 1. Temporal change in species richness (mean ± 1 standard error). A short interval between two dotted lines indicates a period of disturbance. Species richness in the control community (e) shows a slight decline over time from day 3 to day 35 ($y = -0.048x + 7.50$, $\mathrm{df} = 1, 17$, $F = 17.26$, $P = 0.0007$, $R^2 = 0.50$).

type, namely treatments DDMM vs DMDM, and MMDD vs MDMD. If community structure significantly differed between DDMM and DMDM or between MMDD and MDMD or both, that would suggest that the information on the last disturbance is insufficient to explain variation in the structure. In such cases, the information on previous disturbances would need to be invoked.

Results

Response of species to each disturbance type

The response to disturbance varied between the disturbance types (i.e., D and M) as well as among the species (Table 1). Several species (i.e., Ciliate #1, *Vorticella* sp., *Colpoda* sp. #2, and Flagellate) were present in more replicates after disturbance D than before it. *Rotaria* sp. was present in fewer replicates after disturbance D, consistent with the result reported in McGrady-Steed and Morin (1996). The other species showed no significant trends in their response to D. On the other hand, after disturbance M, 10 species out of the 16 for which enough data were available for the statistical analysis were present in fewer replicates than before disturbance. The other species showed no significant response and none responded positively to M.

Species richness

Effect of each disturbance type

Species richness significantly decreased when microcosms experienced both types of disturbance: it decreased by 100% (i.e., reduced to zero) after disturbance D (this was because encysted protists did not yet have sufficient time to become active immediately after the refilling of water) and on average by 26% (range: 20 to 35%) after disturbance M. On the other hand, recovery patterns in species richness after disturbance differed between the two types. In most cases, species richness stayed at the same low level after disturbance M, whereas it quickly recovered after disturbance D and exceeded the level before disturbance within a day (Fig. 1). The recovery after disturbance D was through recolonization of species from the leaf litter into the newly added water.

Fig. 2a and b illustrate the difference between disturbances M and D. After disturbance M, species richness was always lower (Fig. 2a). The regression coefficient relating species richness before disturbance to species richness after disturbance was highly significant (df = 1, 7, $F = 113.53$, $P = 0.0001$, $R^2 = 0.960$). After disturbance D, species richness was higher in most cases (Fig. 2b). The value of the slope in the estimated regression line was lower (0.27) here than for disturbance M (0.97), and the regression coefficient was not significant (df = 1, 7, $F = 3.04$, $P = 0.1418$, $R^2 = 0.372$).

Temporal change

In all treatments, species richness increased during the first three days of the experiment and decreased on day 5 (Fig. 1). After day 5, species richness showed different trajectories as communities went through different sequences of disturbance. This behavior was due to different types and timings of disturbance. The effect of disturbance on species richness depended on the disturbance type as described above. Occasionally, disturbance effects also depended on the timing. For example, species richness increased after disturbance M when it was the first disturbance (Fig. 1c, d), but it stayed at relatively the same level otherwise (Fig. 1a–d). With no disturbance, species richness stayed fairly stable from day 5 through 35, with a slight but significant decline over time (Fig. 1e).

Final state

Species richness in each treatment remained relatively stable after communities had experienced all of the four disturbance events (Fig. 1a–d). Using data from this relatively stable state from day 27 to 35, I performed a repeated measures ANOVA to compare species richness among the treatments. The repeated measures ANOVA indicated that different disturbance sequences caused significant changes in species richness in this final period (df = 4, 43, $F = 29.31$, $P < 0.0001$). There was a significant difference in species richness in all pairs of treatments except between MMDD and MDMD. Treatments MMDD and MDMD held the highest number of species, DMDM and the control intermediate, and DDMM the lowest (Student-Newman-Keuls test, $P < 0.05$).

Species composition and relative abundance

Effect of each disturbance type

The results of the DCA suggest that both disturbance types affected species composition and relative abundance, but in a contrasting way (Fig. 3). In general, disturbance D moved the communities from a lower first-axis score to a higher score, while disturbance M moved them to the opposite direction (Fig. 4). The change in DCA scores before and after disturbance was significantly different for the first DCA axis (df = 12, $t = 4.31$, $P < 0.005$, with two M outliers excluded), although not significant for the second DCA axis (df = 12, $t = 0.69$, $P = 0.25$, with two M outliers excluded). Given these results together with the fact that the control communities moved from higher to lower first-axis scores over time (Fig. 3a), disturbance D appears to have brought communities back to an earlier successional stage, while disturbance M tended to "accelerate" succession. The magnitude of their effect greatly varied depending on the timing of the disturbance (Fig. 4). Particularly, disturbance M influenced the communities very differently in magnitude and even in sign on the two occasions when it was the first disturbance (mean changes in axis 1 score were + 112 and + 113, respectively). Table 1 includes Pearson correlations between DCA axes and species, showing which species loaded strongly on each axis.

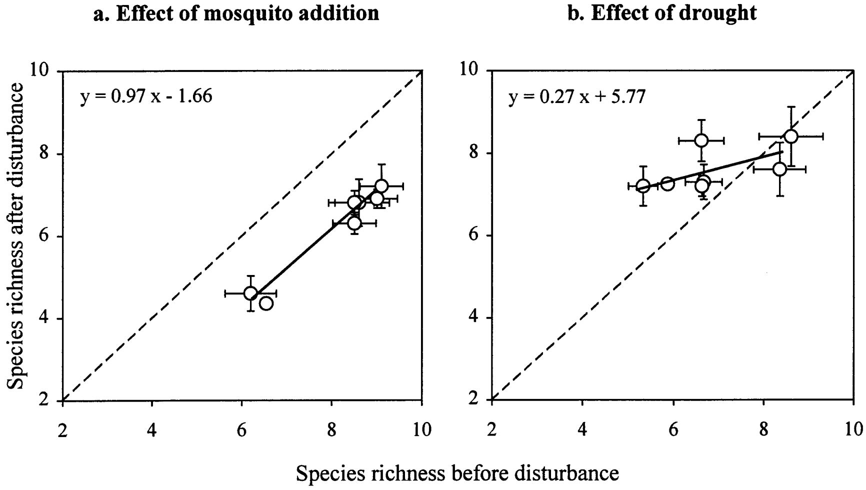

Fig. 2. Effect of disturbances on species richness. Each plot represents species richness (mean ± 1 standard error) before disturbance (x-axis) and after disturbance (y-axis). The mean values were obtained by averaging species richness across the replicates that shared the same disturbance history thus far. The data on the days immediately before, and immediately after (for M) or one day after (for D) disturbance, were used for x and y, respectively. Regression lines are estimated from mean species richness data points.

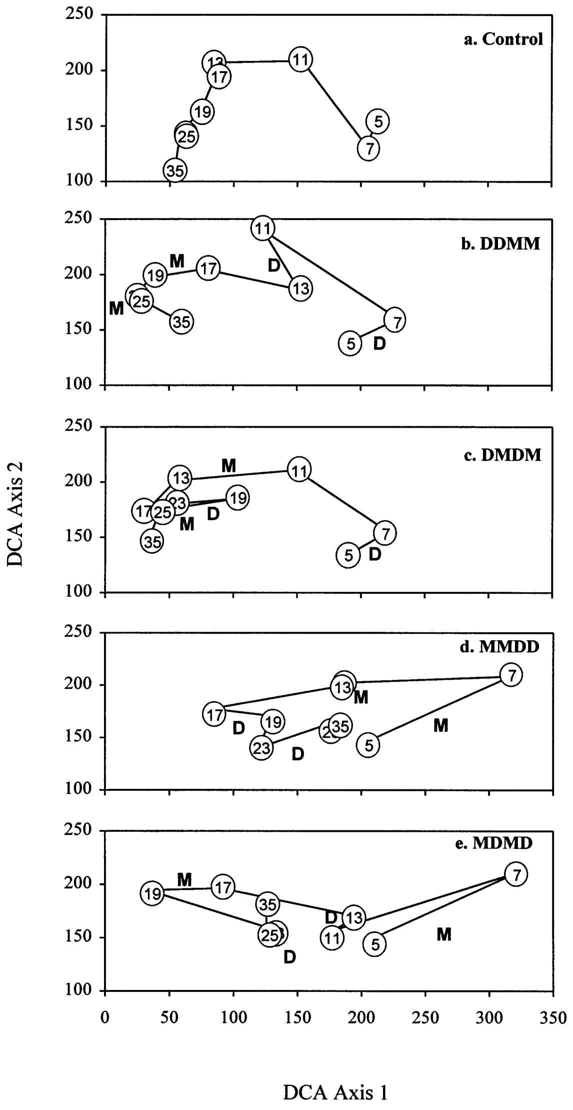

Fig. 3. Temporal change in species composition and relative abundance. The change is expressed in ordination plots from the detrended correspondence analysis (DCA) on composition and relative abundance. Data points are the mean ordination scores along the first two axes. The number in each data point represents the day of sampling. The letter D indicates the periods of drought disturbance, and the letter M mosquito disturbance. All samples were ordinated in the same DCA (see text), although separate graphs are shown for each treatment for clarity (as in Palmer et al. 1995).

Temporal change

Species composition and relative abundance changed over the whole course of the experiment even in the absence of disturbances (Fig. 3a). When disturbances are imposed (Fig. 3b–e), communities deviated from the control trajectory (Fig. 3a) after a disturbance. In treatments DDMM and DMDM, this deviation was only temporary in most cases, and the communities appeared to be resilient to the disturbances (Fig. 5a and b). On the other hand, in treatments MMDD and MDMD, such resilience was seen only in the first two disturbances (Fig. 5c and d). After the last two disturbances, the communities remained far from the control trajectory.

Final state

To examine final community states, I conducted two pair-wise comparisons, i.e., between DDMM and DMDM and between MMDD and MDMD. The first-axis score of the DCA on day 35 showed a significant difference between MMDD and MDMD ($P < 0.05$, Mann-Whitney U test), but no differences between treatments DDMM and DMDM ($P = 1.00$, Mann-Whitney U test).

Discussion

Disturbance sequence drove the experimental bamboo-stump communities onto different trajectories, sometimes leading to significant community divergence in final community states. This result implies that, in order to understand why a community exhibits its observed pattern, one may need historical information on disturbance sequence. Sequence as a historical factor may be important to community structuring not only in terms of species invasion as has previously been shown (reviewed in, e.g., Drake 1990b, Samuels and Drake 1997), but also in disturbance, a factor that could weaken the effects of invasion sequence. Furthermore, disturbance sequence caused community divergence even under the same frequency and total intensity of disturbance. This finding suggests that sequence can be an additional important descriptor of disturbance that explains variation in community structure after frequency and intensity are taken into consideration. Taken together, these results further provide experimental support to the

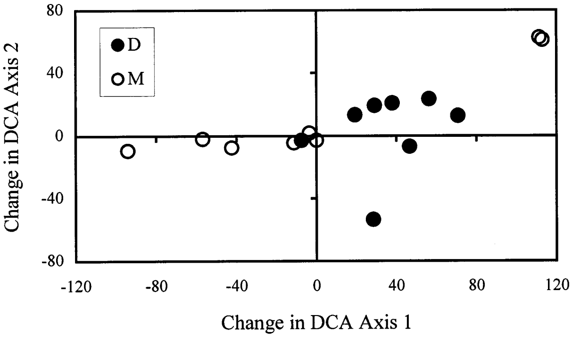

Fig. 4. Effect of disturbances on species composition and relative abundance. The effect is expressed as the magnitude of the change in the mean DCA scores that occurred between immediately before disturbance and one day after disturbance (i.e., days 5–7, 11–13, 17–19, and 23–25). The data are from the same DCA as in Fig. 3.

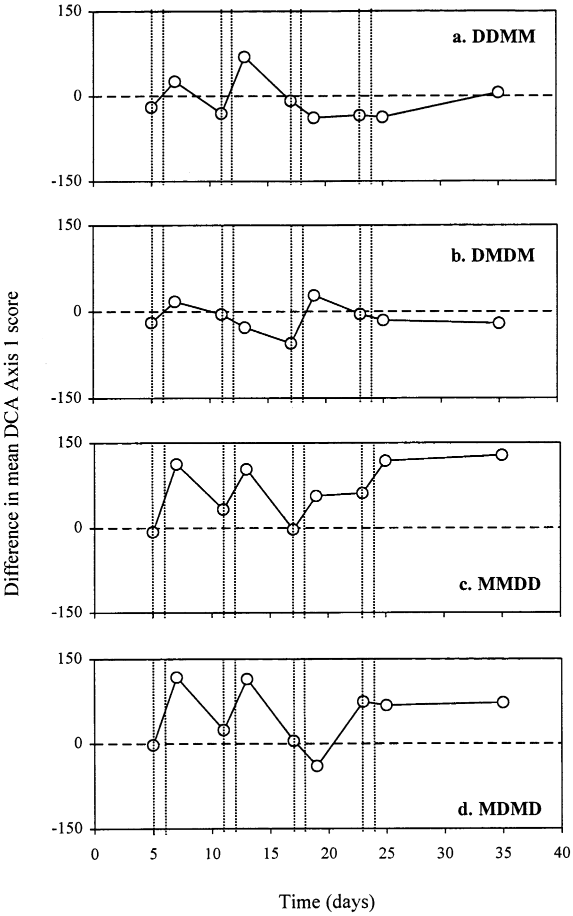

Fig. 5. Temporal change in the difference between the mean DCA Axis 1 score of the control (no disturbance) and of the disturbance treatments. The data are from the same DCA as in Fig. 3. A short interval between two dotted lines indicates a period of disturbance.

recent argument that examination of multiple disturbance types and their sequence is of great importance to the management and conservation of natural communities (Paine et al. 1998, Hughes and Connell 1999, Lesica and Cooper 1999).

Disturbance sequence and community divergence

Species richness differed significantly between treatments DDMM and DMDM, indicating that disturbance sequence did lead to community divergence. Since species richness level after the second D was similar between the treatments, the lower level in DDMM must have resulted from the occurrence of the last two successive Ms. The slope in Fig. 2a is statistically highly significant and is nearly one, indicating that disturbance M lowered species richness always by the same magnitude, approximately by 1.7. As a result, the number of disturbance Ms since the last disturbance D was responsible for the difference between the two treatments, one with two Ms and the other with only one M after the last D. On the other hand, species richness showed no significant difference between MMDD and MDMD. The slope in Fig. 2b is relatively close to zero and the regression was not statistically significant. This small value indicates that disturbance D was likely to cancel the effect of the preceding disturbances on species richness. Consequently, historical effects were not observed in this case. With the two comparisons taken together, it appears that species richness was determined by how many Ms occurred since the last D.

Theoretically, one could predict effects of disturbance sequence using a very simple model. In Fig. 2, I summarized the effects of the two disturbance types by linear regressions, though the regression for disturbance D was not significant. Disturbance in general may be expressed similarly. For example, disturbances A and B may be characterized by: A: $y = a\ x + b$, and B: $y = c\ x + d$, where x and y are species richness (or another index of community structure) before and after the disturbance and a, b, c, and d are constants. Then, species richness after a community has experienced two disturbance events in sequences AB and BA will be: $y_{AB} = ac\ x + bc + d$, and $y_{BA} = ac\ x + ad + b$, respectively. In order for y_{AB} and y_{BA} to be equal, the following equation has to be satisfied: $d(a - 1) = b\ (c - 1)$. Otherwise, the two different disturbance sequences always result in community divergence. The assumptions in this model, including the linearity of the response and the constant interval between disturbances, may not hold in nature, but relaxing these assumptions would not change the qualitative prediction that disturbance sequence easily causes community divergence.

Contrary to the results on species richness, species composition and relative abundance at the end of the experiment differed significantly between MMDD and MDMD, but not between DDMM and DMDM. The mechanisms responsible for these results are equivocal. It is at least clear that the variation in response to disturbance among species and between disturbance types (Table 1) caused the divergence. The effect of disturbances varied more and was less predictable on species composition and relative abundance (Fig. 4) than on species richness (Fig. 2), making it more difficult to generalize the pattern in changes in species composition and relative abundance. Nonetheless, these results in combination with the results on species richness show that the evaluation of community convergence and divergence can depend on the index of community structure under consideration.

One caveat should be mentioned concerning the interpretation of the differences in final measures of community structure. The apparent failure for the communities to converge may mean either of two possibilities: (1) communities were globally equilibrial in nature, but insufficient time elapsed after the last disturbance for convergence on an equilibrium composition; or (2) the communities did not have a single global equilibrium, and they either converged on multiple states or simply continued to change in composition through time (Drake et al. 1994, Grover and Lawton 1994). The experiment might not have run long enough to distinguish between these alternatives. Either way, however, the fact remains that the impact of disturbance sequence lasted for many generations after the last disturbance.

Disturbance and competition

The role of disturbance on community structure is often discussed in relation to competitive exclusion (e.g., Petraitis et al. 1989, Chesson and Huntly 1997). In the microcosms studied here, however, competition may have been unimportant. The five-day intervals between disturbance events were likely too short to allow competitive exclusion (cf. McGrady-Steed and Morin 1996). The slight decline in species richness in the control communities (Fig. 1e) might have been caused by competitive exclusion, but this hypothesis remains to be tested and it might be due to autecological causes. No significant competitive effects were detected among protist species under natural conditions as well (Taylor 1979), although the spatial and temporal scale differed between his system and this study's.

However, disturbance and species interactions do often occur together in natural communities. Disturbance frequency and intensity can regulate the importance of species interactions and consequently affect the importance of invasion history (Samuels and Drake 1997). Thus, the relative importance of invasion sequence and disturbance sequence is expected to vary depending on disturbance frequency and intensity. In this context, the interaction of disturbance sequence with disturbance frequency and intensity could greatly enhance the role played by disturbance in ecological communities. It seems worthwhile to explore such an interaction both theoretically and empirically in future research.

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