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Microtopographic heterogeneity and floristic diversity in experimental wetland communities

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Summary

1 Coexistence is thought to be facilitated in heterogeneous environments due to interspecific differences in habitat preference. Microtopographic heterogeneity is a major factor structuring natural freshwater wetland communities and is thought to influence diversity. I tested whether interspecific differences existed in habitat preference for different microtopographic positions and whether diversity was associated with small-scale spatial microtopographic heterogeneity in experimental wetland communities.

2 I manipulated microtopographic heterogeneity to produce 'homogeneous' (flat surface) and 'heterogeneous' (hummock-hollow) treatments. Three propagule source treatments (seed bank, seeds, seed bank + seeds) were incorporated to determine if responses to heterogeneity depended on the propagule source. Habitat preferences for microhabitats within heterogeneous treatments were determined for each species by recording the number of individuals located on 'hummocks' or in 'hollows'. Responses to heterogeneity and propagule source were quantified by measuring richness, evenness, species abundances and above-ground biomass.

3 Small-scale variability in microtopography, on the order of 1–3 cm, produced highly significant differences in plant community structure. Both components of floristic diversity, species richness and evenness, were consistently greater in communities with heterogeneous microtopography.

4 Community composition, abundance of individuals and above-ground biomass responded differentially to heterogeneity and propagule source. Most species reached greater abundances in heterogeneous environments than homogeneous environments; however, species that were similarly abundant in both included *Eleocharis ovata*, *Alisma triviale* and *Sparganium americanum*.

5 Most species growing within the heterogeneous environments showed distinct habitat preferences for hummock or hollow microhabitats, with many rarer species, particularly woody perennials, favouring hummocks.

Keywords: coexistence, ecological restoration, microsite, productivity, seedling establishment, seed bank, species richness

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Introduction

Spatial and temporal environmental heterogeneity are thought to significantly to influence both the dynamics and structure of ecological communities (Wiens 1976; Huston 1979; Pickett & White 1985; Karieva 1986; Shorrocks & Swingland 1990; Kolasa & Pickett 1991; Tilman 1994). Increased species diversity is often associated with greater environmental heterogeneity (MacArthur & MacArthur 1961; Tilman 1982; Huston 1994). Coexistence in spatially structured communities may be facilitated by interspecific differences in factors such as dispersal ability between patches, germination microsite preferences, resource requirements, environmental tolerances, and mortality (Grubb 1977; Tilman 1982; Silvertown & Wilken 1983; Keddy 1984). Such differences are thought to affect competitive interactions between species, leading to the disruption of competitive interactions in heterogeneous environments (Chesson & Huntly 1989; Pacala & Tilman 1994). Facilitation of coexistence in heterogeneous environments has been demon-

strated in many two species systems (Huffaker 1958; Horn & MacArthur 1972; Karieva 1987; Pacala *et al.* 1990), but rarely have these demonstrations been extended to more complex model communities or field studies (Fitter 1982; Grime *et al.* 1987; Tilman 1994).

The vegetation dynamics and species diversity of many plant communities are thought to be strongly influenced by soil nutrient heterogeneity, yet few experimental studies have investigated this (Fitter 1982; Grime *et al.* 1987). Microtopographic variation has been strongly correlated with plant distribution and performance, for individual plant species (Harper *et al.* 1965; Sheldon 1974; Hamrick & Lee 1987; Eldridge *et al.* 1991), and for plant communities in wetlands (Schlesinger 1978; Collins *et al.* 1982; Hardin & Wistendahl 1983; Huenneke & Sharitz 1986; Titus 1990; Ehrenfeld 1995a) and uplands (Collins & Pickett 1982; Beatty 1984; Sterling *et al.* 1984; Petersen & Campbell 1993). Explanations for such patterns include differential seed accumulation (Huenneke & Sharitz 1986), variation in species germination requirements (Harper *et al.* 1965); and differences in growth and mortality at different microtopographic positions (Hamrick & Lee 1987; Eldridge *et al.* 1991).

Studies of natural freshwater wetland communities have suggested that topography is a major factor structuring these communities and may significantly influence diversity (Hardin & Wistendahl 1983; Huenneke & Sharitz 1986; Titus 1990). Apart from water content, other factors which affect habitat quality are likely to vary between hummocks and hollows; these include redox potentials, patterns of litter accumulation, compaction levels, and drought incidence (Ehrenfeld 1995b). Sources of topographic heterogeneity in wetlands are frequently the result of disturbance (Ehrenfeld 1995a). Examples include tip-up mounds from tree fall, channel building of muskrats, differential patterns of litter accumulation and erosion after flooding, and animal and vehicle tracks. The resulting scale of heterogeneity can vary considerably from large (e.g. > 1 m differences resulting from tree fall) to very small-scale variation such as that chosen for this study (e.g. 1–5 cm resulting from animal and vehicle tracks). Even at this smaller scale differential recruitment patterns of wetland plant species in central New Jersey have been frequently observed (personal observation). Keddy & Ellis (1984) also record differential recruitment patterns of species along water level gradients at a similar scale.

Experimental communities are increasingly used as model systems to study theoretical questions (Grime *et al.* 1987; Naeem *et al.* 1994; Weiher & Keddy 1995; Lawton 1995), but they also have practical applications (Gilpin 1987; Stockey & Hunt 1994). In this study I used experimental wetland communities to explore the relationship between small-scale microtopographic heterogeneity and species diversity. This issue is of theoretical interest, but can also be applied to develop strategies to improve floristic diversity in restored or degraded wetlands. In this study, experimental communities were also considered advantageous because they reduced uncontrolled forms of spatial and temporal heterogeneity. However, it should be remembered that these communities also lack features of natural wetlands that can affect recruitment processes, for example the presence of herbivores or pre-existing vegetation.

Community responses to microtopographic heterogeneity may vary with propagule source; this may be of applied significance due to the increased use of imported seed banks and/or seed additions as a source of propagules in wetland restoration (van der Valk & Pederson 1989; Reinartz & Warne 1993; Vivian-Smith & Handel 1996). Three additional treatments were therefore incorporated to assess the effects of propagule source (seeds, seed bank and seeds + seed bank). Species diversity, numbers of individual plants, species abundance patterns and above-ground biomass were quantified in the experimental communities to examine whether coexistence was facilitated by small-scale environmental heterogeneity and if these responses were dependent on the propagule source.

I tested the following hypotheses: (1) Interspecific differences in habitat preferences exist for freshwater wetland species at the fine scale used in this experiment. This would be demonstrated by differences in species composition between homogeneous and heterogeneous environments and by differences in species occupying the different microhabitats within the heterogeneous treatment. (2) Coexistence is facilitated in heterogeneous environments (Grubb 1977; Tilman 1982; Silvertown & Wilken 1983; Keddy 1984). This would be evident by increases in one or both components of diversity: species richness and evenness. Facilitated coexistence in heterogeneous environments could also be quantified by increased numbers of individuals and/or greater productivity, due to greater scope for resource specialization in heterogeneous environments (Tilman 1982; Keddy 1984; Tilman *et al.* 1996). (3) Responses to heterogeneity should be consistent across all propagule source treatments. Facilitated coexistence in heterogeneous environments should be independent of the propagule source used.

Materials and methods

EXPERIMENTAL DESIGN

A completely randomized factorial design consisting of two microtopography × three propagule source treatments was used. Each treatment combination was replicated five times. Experimental units consisted of 38 litre plastic tanks [internal dimensions 52 (length) × 36 (width) × 22 (height) cm]. These were filled with peat (2 parts) and sand (1 part). A slow release fertilizer (6 g Once®, O.M. Scott, Chicago;

N:P:K ratio 19:10:10) was added to the mix, and supplemented twice during the growing season with 5 mL of liquid fertilizer (Hyponex®, O.M. Scott, Chicago). Experimental tanks were placed in a mowed field at the Hutcheson Memorial Forest Research Centre, New Jersey on 30–31 August 1993. Water levels were checked every 2 or 3 days and maintained at 9–12 cm depth with drainage holes to prevent water accumulation greater than 12 cm. Water was supplied by natural rainfall supplemented with water from the nearby Spooky Brook.

MICROTOPOGRAPHY TREATMENTS

Microtopography treatments included a *homogeneous* or flat treatment and a *heterogeneous* treatment consisting of five artificial peat pot hummocks raised 2.5 cm above the surrounding substrate and filled with the same peat + sand mix (Fig. 1). Both treatments contained the same volume of substrate. Homogeneous treatments had an initial mean substrate depth of 9 cm, heterogeneous treatments had an initial variable substrate depth ranging from a continuously flooded 8 cm in the 'hollows' to a periodically exposed 10.5 cm on the 'hummocks'. At the termination of the experiment, hummock elevations ranged from 1.5–2.5 cm, indicating that some subsidence had occurred during the experiment.

PROPAGULE SOURCE TREATMENTS

Propagule source treatments consisted of (1) *seeds*; (2) *seed bank* (3) both *seeds* + *seed bank*. These were added to the experimental tanks as they were placed in the field. Seed and seed bank samples were collected across a range of hydrologic and disturbance conditions from an inner coastal plain swamp in South Brunswick, New Jersey. This site had a distinctive hummock-hollow topography and dominant vegetation consisting of a shrub matrix (e.g. *Vaccinium* spp., *Clethra alnifolia*, *Chamaedaphne calyculata*, *Cephalanthus occidentalis*), interspersed with patches of trees at higher elevations (e.g. *Acer rubrum*, *Liquidambar styraciflua*, *Quercus palustris*) and open patches of rushes and sedges in wetter and more recently disturbed areas.

The *seed bank treatments* consisted of 160 g of soil (containing the seed bank) from a composite of 100 soil cores, 2.5 cm (diameter) × 7 cm (depth). Soil cores were collected during August 1993 and stored for one week at 5°C prior to initiation of the experiment. Soil samples were sieved through a 12 mm screen to enable adequate mixing of the samples and to remove larger pieces of woody debris which could interfere with heterogeneity treatments.

The *seeds* treatment received seeds, plus an additional 160 g of peat + sand mixture to ensure equivalent amounts of growing medium were added to all experimental units. Seeds used consisted of a standard mix of 19 locally abundant native freshwater wetland species. These were collected during November 1992 to August 1993 and stored at 5°C. Species were selected to represent a variety of life history and growth forms, and included both annuals and perennials, as well as herbaceous and woody species (see Table 1 for species list). Many of the species at the site, and most of those used in the seed addition treatments are wind and/or water dispersed, producing large quantities of very small seeds. To approximate natural conditions large numbers of

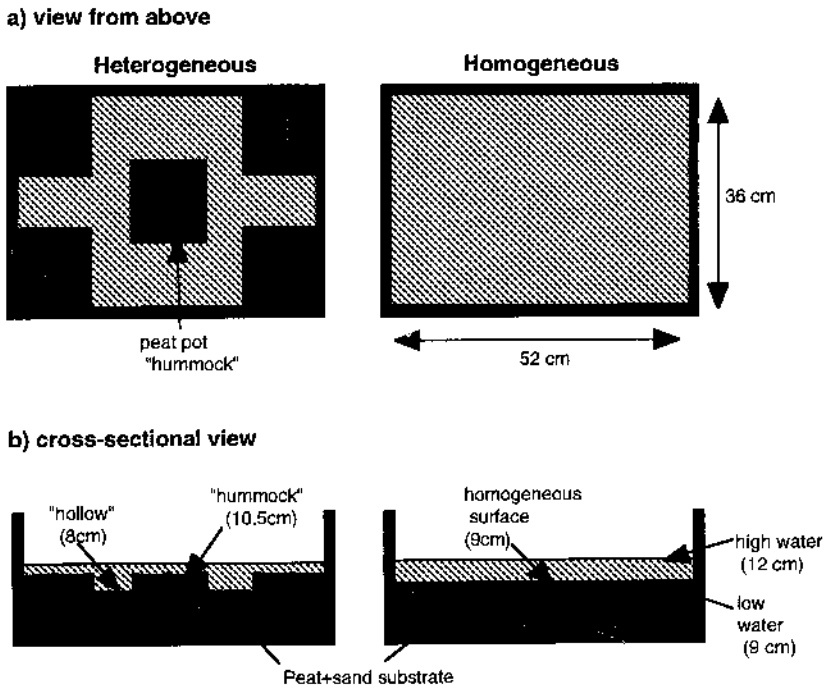

Fig. 1 Experimental community construction showing homogeneous and heterogeneous microtopography treatments.

Table 1 Species, life-form and approximate mass and number of seeds added in the treatments involving seed addition. Nomenclature follows that of Gleason & Chronquist (1991)

Species	Plant type	Mass of seeds added (mg)	Approximate number of seeds added
Alisma triviale	annual herb	150	500
Acer rubrum	woody perennial	*	50
Carex bullata	perennial sedge	800	250
Carex lurida	perennial sedge	530	250
Carex scoparia	perennial sedge	100	250
Carex stricta	perennial sedge	35	250
Chamaedaphne calyculata	woody perennial	60	1000
Cephalanthus occidentalis	woody perennial	*	50
Clethra alnifolia	woody perennial	60	1000
Eleocharis ovata	annual rush	850	500
Eleocharis palustris	perennial rush	100	250
Gratiola neglecta	annual herb	8	1000
Juncus acuminatus	annual rush	8	1000
Juncus effusus	perennial rush	8	1000
Juncus marginatus	annual rush	8	1000
Lindernia dubia	annual herb	6	1000
Scirpus atrovirens	perennial sedge	50	1000
Sparganium americanum	perennial rush	1000	500
Spiraea tomentosa	woody perennial	30	1000

* The seeds of these species were large enough to count accurately, quantities of all other species were measured by weight.

seeds were added to experimental communities receiving seed addition treatments. The very small seeds of many species made it impossible to ensure that each treatment received the same number of seeds of each species, as a result seed addition was standardized by adding the same mass of seeds of each species to each replicate (Table 1). The *seeds + seed bank* treatment consisted of the same seed mix used in the seeds treatment (but without the additional 160 g of peat + sand mixture), this was added to 160 g of soil from the composited samples used in the seed bank treatment, thus ensuring that all three treatments received the same amount of substrate.

DATA COLLECTION

To aid in identification of seedlings, reference specimens of many species present at the site (including those used in the seed addition treatments) were generated from germination of seed samples. In addition to this, many species reached reproductive maturity, including all of the annual and several of the perennial species, enabling comparison with reference specimens held in the Chrysler Herbarium at Rutgers University. Identity and numbers of individuals of each species were monitored at monthly intervals from 1 June to 1 September 1994; prior to this seedlings were too small to identify accurately. On 1 September 1994, after a year, I terminated the experiment and recorded final species richness, the number of individuals of each species and above ground total biomass for each species and each replicate community. Above-ground biomass was determined by harvesting each plant at the soil level, drying for 48 h at 80°C and weighing. It was not possible to determine below-ground biomass due to the extremely dense root growth present. For heterogeneous treatments I also recorded plant location (hummock vs. hollow).

DATA ANALYSIS

Species richness, number of individuals and total above-ground biomass were analysed using multivariate analysis of variance (MANOVA). This method was chosen to reduce the risk of Type I errors associated with multiple ANOVAs. After testing for normality, univariate ANOVAs were performed on each untransformed variable to determine which contributed most to multivariate significance. Species richness was determined at monthly intervals throughout the growing season and analysed using repeated measures analysis of variance (RMANOVA) to determine whether these changes were dependent on heterogeneity and propagule source. Species richness and Shannon evenness (E) and diversity (H') indices were used to detect the effects of microtopographic heterogeneity on floristic diversity (Magurran 1988). Evenness (E) and diversity (H') were calculated for each replicate community using the final data collected for richness and abundance. Due to their non-normality these were analysed nonparametrically.

To detect which species were causing response patterns, PCA (Principal components analysis) decomposing a covariance matrix, and the matrix of Pearson correlation coefficients were used to reduce the dimensionality of the plant community responses to hetero-

Table 2 MANOVA and univariate ANOVAs for microtopographic heterogeneity and propagule source treatment effects on community level response variables (species richness, number of individuals and total biomass)

MANOVA Source of variation	Num. d.f.	Den. d.f.	Wilk's Lambda	*F*	*P*
Heterogeneity	3	22	0.2639	20.46	0.0001***
Propagule source	6	44	0.1361	12.54	0.0001***
Heterogeneity × Propagule source	6	44	0.3745	4.65	0.0010**
ANOVA **Source of variation**	**d.f.**	**Type I SS**		***F***	***P***
Species richness					
Heterogeneity	1	433.200		54.84	0.0001***
Propagule source	2	144.200		9.13	0.0011**
Heterogeneity × Propagule source	2	3.800		0.24	0.7881
Error	24	189.600			
Number of individuals					
Heterogeneity	1	76709.633		44.29	0.0001***
Propagule source	2	162998.467		47.06	0.0001***
Heterogeneity × Propagule source	2	31342.467		9.05	0.0012**
Error	24	41566.800			
Total biomass					
Heterogeneity	1	2373.862		18.16	0.0003***
Propagule source	2	5311.058		20.31	0.0001***
Heterogeneity × Propagule source	2	1184.496		4.53	0.0214*
Error	24	3137.597			

geneity and propagule source. Anderson's test (1963) determined that only the first principal component was significant. Due to the many species present, changes in community composition due to heterogeneity and propagule source were analysed using ANOVA on the first factor scores. This approach was selected to reduce the risk of Type 1 errors associated with ANOVAs testing for each species' response (Alford & Wilbur 1985; Morin 1987). To aid interpretation, the abundances of only those species significantly correlated with the first principal component axis were tested using univariate ANOVAs. I transformed abundances of *Carex lurida*, *Carex scoparia* and *Gratiola neglecta* as $(\text{individuals} + 1)^{1/2}$ to enhance their normality, all other variables remained untransformed. MANOVAs and ANOVAs were performed using the PROC GLM in Statistical Analysis System (SAS 1988) and nonparametric tests were performed using JMP (SAS 1995).

Results

COMMUNITY-LEVEL RESPONSES

Heterogeneity and propagule source had a highly significant effect on species richness, number of individuals and total above-ground biomass (MANOVA, $P < 0.0001$) (Table 2). Comparison of main effect treatment means using post-hoc pairwise tests indicate that heterogeneous treatments had significantly more species, individuals and biomass, and the seed bank treatment produced significantly lower values for these response variables than the other propagule source treatments ($P < 0.05$, Tukey's HSD). However, these pairwise tests provide no information regarding the significant heterogeneity × propagule-source interaction. Abundance and total biomass are the major contributing variables to the differential response (Table 2). The biomass component of the interaction is due to very low biomass in the homogeneous soil seed bank treatment, most likely a direct result of poor recruitment (Fig. 2). The abundance component of the interaction term is due mainly to differential responses of the seeds and seeds + seed bank treatments to heterogeneity (Fig. 2). In contrast to biomass and abundance, species richness responded consistently to heterogeneity, and was greater in all treatments with heterogeneous microtopography (Table 2, Fig. 2).

HETEROGENEITY AND FLORISTIC DIVERSITY

Heterogeneity significantly influenced temporal changes in species richness (RMANOVA, Table 3). Heterogeneous microtopography treatments had greater species richness early in the growing season, this increased with time relative to homogeneous treatments (Fig. 3). Diversity (H') and evenness (E) were also found to be significantly greater in heterogeneous (mean $H' = 1.714$, mean $E = 0.772$), than homogeneous treatments (mean $H' = 0.572$, $E = 0.414$) (Wilcoxon signed rank $P < 0.001$) (Table 4). Species abundance distributions illustrate this and indicate

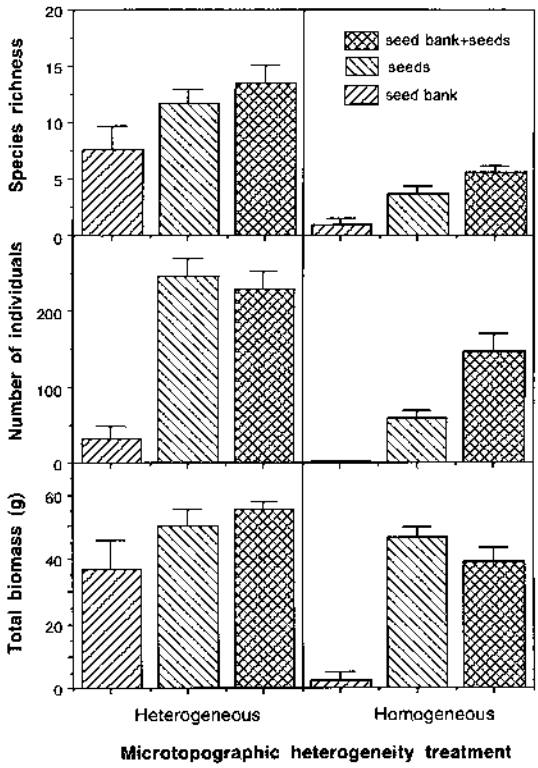

Fig. 2 Experimental plant community responses (species richness, number of individuals and total biomass) to heterogeneity and propagule source treatments (values shown are treatment means +1SE).

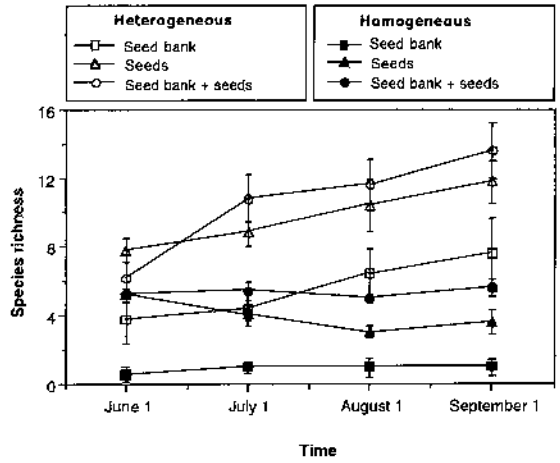

Fig. 3 Effect of heterogeneity and propagule source on species richness patterns over time for experimental wetland communities (values shown are treatment means +1SE).

Table 4 Mean diversity (H') and evenness (E) indices for each heterogeneity and propagule source treatment combination

	Propagule source		
Microtopography	seed bank	seeds	seeds + seed bank
Homogeneous			
H'	0.113	0.554	1.050
E	0.162	0.446	0.639
Heterogeneous			
H'	1.440	1.709	1.993
E	0.838	0.705	0.776

that more 'rare' species were present in heterogeneous treatments (Fig. 4).

COMMUNITY COMPOSITION

Differential responses to heterogeneity and propagule source

Community composition analysed using PCA provided a good representation of the original data matrix, with the first eigenvalue of 2501.13 accounting for 78.78% of the variance. *Alisma triviale*, *Carex lurida*, *Carex stricta*, *Eleocharis ovata*, *Gratiola neglecta*, *Juncus acuminatus* and *Sparganium americanum* were all significantly correlated with the first axis ($P < 0.001$) (Table 5).

ANOVA on the first factor scores indicated that both heterogeneity and propagule source differentially influenced community composition ($P = 0.0003$) (Table 6a). Individual ANOVAs indicate that the differential responses can be attributed to both the first and second principal component axes. Differential species responses were detected using univariate ANOVAs on species abundances (Table 6b); however, the seed bank treatment was dropped from this analysis due to very low numbers of individuals present (Table 7, Fig. 5). All species responded to heterogeneity, except *Sparganium americanum*, which was the only species responding to propagule source. Only *Eleocharis ovata*, and to a lesser extent *Sparganium americanum* and *Alisma triviale*, showed differential responses to heterogeneity and propagule source (Fig. 5). In homogeneous environments abundance of

Table 3 RMANOVA for microtopographic heterogeneity and propagule source treatment effects on species richness over time (measured 1 June, 1 July, 1 August and 1 September 1993)

MANOVA Source of variation	Wilk's Lambda	F	Num. d.f.	Den. d.f.	P
Time	0.4247	9.934	3	22	0.0002
Time × Heterogeneity	0.3640	12.811	3	22	<0.0001
Time × Propagule source	0.6659	1.653	6	44	0.1554
Time × Heterogeneity × Propagule source	0.8239	0.746	6	44	0.6159

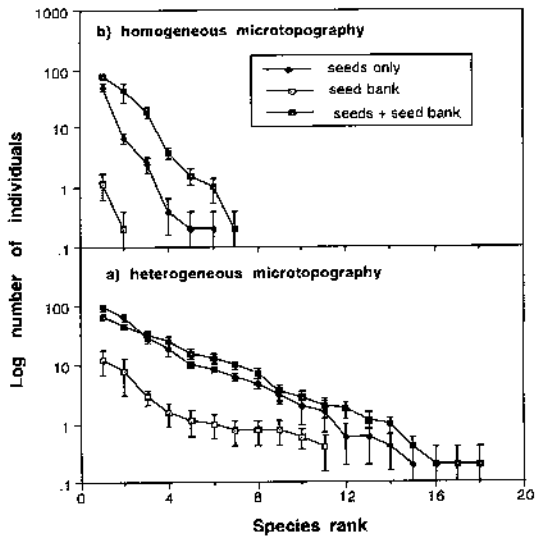

Fig. 4 Rank abundance plots showing species abundance distributions in homogeneous and heterogeneous experimental wetland communities (values represent treatment means +1SE).

these three species was greatest with seeds + seed bank addition, but in heterogeneous environments it was equal or greater with seeds only (Fig. 5). It is interesting to note that mean total biomass of *Eleocharis* was greater in homogeneous environments (mean ± SE 35.0 ± 3.27) than heterogeneous environments (21.5 ± 2.06). This indicates that, on average, plants were smaller in heterogeneous environments. Mean total biomass of *Alisma* and *Sparganium* did not show this response and remained approximately the same in homogeneous (5.9 ± 1.29 and 1.39 ± 0.70, respectively) and heterogeneous environments (6.89 ± 1.15 and 0.59 ± 0.11, respectively).

Habitat preferences within heterogeneous treatments: hummocks vs. hollows

Within heterogeneous treatments differences in abundance frequencies of species located on hummocks and hollows were assessed after adjusting for differences in area occupied by both microhabitats (*G*-tests, Sokal & Rohlf 1995). After making this adjustment the total number of individuals on hummocks ($n = 1573$) was similar to that of hollows ($n = 1523$), but the species abundance distributions comprising these totals differed between hummocks and hollows (*G*-test, $P < 0.0001$). More species showed distinct habitat preferences for hummocks (*Carex lurida*, *Carex scoparia*, *Juncus acuminatus*, *Juncus effusus*, *Lindernia dubia*, and *Ludwigia palustris*) than for hollows (*Alisma triviale and Sparganium americanum*) (Table 7). However, some species were found in approximately equal proportions on both hummocks and in hollows (*Eleocharis ovata*, *Gratiola neglecta* and *Panicum* sp.). No individuals of the five woody species were found in hollows.

Table 5 Factor loadings and Pearson correlation coefficients of species significantly correlated with the first principal component axis derived from PCA of individual species abundances

Species	Factor 1 loadings	Pearson correlation coefficient PC1
Alisma triviale	0.571	0.942**
Carex lurida	0.169	0.577*
Carex scoparia	0.187	0.601*
Eleocharis ovata	0.764	0.973**
Gratiola neglecta	0.063	0.579*
Juncus acuminatus	0.053	0.634*
Sparganium americanum	0.126	0.707**

*$P < 0.001$, **$P < 0.0001$.

Discussion

COMMUNITY COMPOSITION

Community composition and heterogeneity

Multivariate analysis of these experimental wetland communities indicates that heterogeneity significantly altered community composition. Heterogeneous environments were characterized by more species which reached greater abundances than homogeneous environments. However, there were some species that were abundant in both homogeneous and heterogeneous environments, particularly *Eleocharis ovata*, *Alisma triviale* and *Sparganium americanum*. Rarer species were mostly found in heterogeneous treatments.

Most species growing within heterogeneous environments showed distinct habitat preferences for either hummock or hollow microhabitats. More species, particularly the rarer species such as the woody perennials, favoured hummocks, indicating that this was the more generally preferred microhabitat. However, individuals of many of the most abundant species were found in both hummock and hollow microhabitats, indicating that variation existed within and between species for microhabitat preference. These results support the hypothesis that interspecific differences do exist in habitat preferences during establishment, a result also consistent with previous work (Keddy & Ellis 1984), but they also show that interspecific differences are not always well defined. Different species may share similar preferences for microtopographic positions (e.g. *Acer rubrum* and *Cephalanthus occidentalis*), and some species may be able to colonize a wider range of microhabitats than others due to intraspecific variation and plasticity in habitat preference (e.g. *Eleocharis ovata*).

Table 6 (a) ANOVA showing the effect of heterogeneity and propagule source on factor scores for the first principal component axis derived from principal component analysis of individual species abundances. (b) ANOVAs (seeds and seeds + seed bank treatments only) showing treatment effects on number of individuals measured for species significantly correlated with first principal components axis

(a)

ANOVA, Factor 1 Scores Source of variation	df	Type ISS	*F*	*P*
Heterogeneity	1	2.184	12.73	0.0016
Propagule	2	18.806	54.80	0.0001
Heterogeneity × Propagule source	2	3.892	11.34	0.0003
Error	24	4.118		

(b)

ANOVA Source	*Alisma triviale*	*Carex lurida*	*Carex scoparia*	*Eleoch. ovata*	*Gratiola neglecta*	*Juncus acumin.*	*Sparg. americ.*
Heterogeneity	0.0172	0.0001	0.0001	0.0247	0.0001	0.0001	0.9138
Propagule source	0.4832	0.8250	0.9050	0.9345	0.0939	0.0483	0.0010
Het. × Prop.	0.0271	0.8250	0.4659	0.0011	0.5031	0.4425	0.0123

Table 7 Total number of individuals present in experimental wetland communities for each propagule source and heterogeneity treatment combination, and proportion of individuals found on hummocks for each species. *G*tests were performed on all species with more than 5 individuals present on both hummocks and in hollows. These determined whether equal proportions of individuals were found on hummocks and hollows (adjusted for equal area). S, Seeds; SB, Seed bank; S + SB, Seeds + seed bank; Proportion, proportion of individuals on hummocks

	Homogeneous			Heterogeneous			
Species	SB	S	S + SB	SB	S	S + SB	Proportion
Alisma triviale	0	35	204	0	308	216	0.195***
Acer rubrum	0	0	0	0	5	3	1
Clethra alnifolia	0	0	0	0	9	0	1
Cephalanthus occidentalis	0	0	0	0	25	9	1
Carex lurida	0	0	0	8	121	133	0.648***
Carex scoparia	0	1	8	3	138	123	0.650***
Cyperus sp	0	0	0	0	0	1	1
Echinochloa crusgalli	0	0	1	3	0	4	0.8
Eleocharis ovata	0	251	391	7	483	337	0.441 NS
Festuca elatior	0	0	0	1	0	0	0
Gratiola neglecta	0	3	8	0	35	60	0.538 NS
Hieracium sp.	0	0	0	3	1	2	1
Hypericum canadense	0	0	0	2	3	2	0.889
Juncus acuminatus	1	2	15	13	43	49	0.762***
Juncus canadensis	0	0	0	1	0	0	1
Juncus effusus	0	0	0	9	0	13	0.845**
Juncus marginatus	0	0	0	2	0	2	1
Lindernia dubia	0	0	0	8	20	34	0.821***
Ludwigia palustris	3	0	0	57	0	47	0.856***
Myriophyllum sp.	1	0	0	0	0	0	0
Panicum sp.	0	0	0	37	0	13	0.653 NS
Rosa multiflora	0	0	0	0	1	0	1
Sparganium americanum	0	10	103	0	47	63	0.297**
Scirpus cyperinus	0	0	0	4	2	0	1
Solidago rugosa	0	0	0	0	1	1	1
Spiraea tomentosa	0	0	0	0	10	7	1
Triadenum virginicum	2	0	2	5	1	3	0.667
Typha latifolia	0	0	1	0	0	0	0

$^{**}P < 0.01$, $^{***}P < 0.001$, NS = not significant.

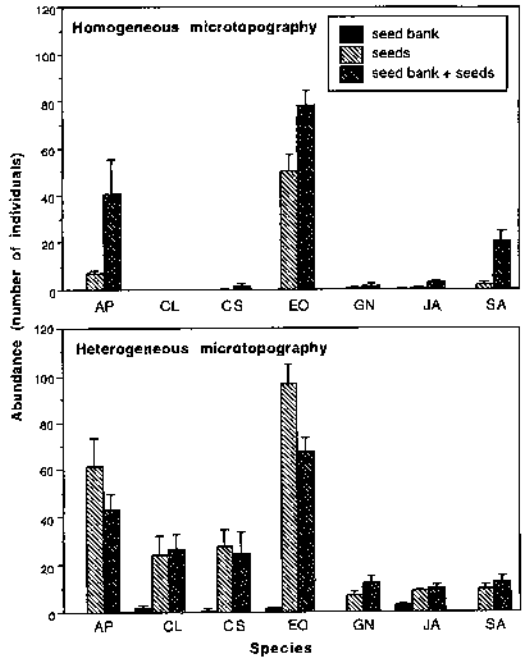

Fig. 5 Abundance of species significantly correlated with the first principal components axis for each treatment combination (values shown are treatment means + 1SE). Species codes are as follows: AT, *Alisma triviale*; CL, *Carex lurida*; CS, *Carex scoparia*; EO, *Eleocharis ovata*; GN, *Gratiola neglecta*; JA, *Juncus acuminatus*; SA, *Sparganium americanum*.

FACILITATED COEXISTENCE AND HETEROGENEITY

Diversity and heterogeneity: microsites and competition

The hypothesis of increased heterogeneity resulting in increased diversity was clearly supported by the greater overall diversity present in heterogeneous communities. This is consistent with theoretically based predictions of facilitated coexistence in heterogeneous communities (Grubb 1977; Tilman 1982; Silvertown & Wilken 1983; Keddy 1984; Huston 1994). Both components of diversity, richness and evenness, were greater in environments with greater microtopographic heterogeneity, a considerable contrast with the homogeneous environments which were characterized by few, dominant species.

Temporal patterns of species richness observed suggest how this may occur. The greater species richness of heterogeneous communities early in the growing season is most likely a result of the greater variety of available germination microsites thought to be present in these environments (Harper *et al.* 1965; Grubb 1977; Fowler 1988). Heterogeneous treatments increased in species richness throughout the experiment due mainly to later establishment of some rarer species such as *Cephalanthus occidentalis*, *Clethra alnifolia*, *Lindernia dubia*, *Spiraea tomentosa* and *Triadenum virginicum*. This contrasted greatly with the static or declining species richness observed in homogeneous communities. Such a trend is consistent with the explanation that homogeneous environments provide optimal conditions for few species, enabling these species to compete successfully with others which differ in their habitat requirements, thus leading to competitive exclusion and lower diversity (Pacala & Tilman 1994; Tilman 1994). These responses are also likely to be scale-dependent. Germination and establishment may be microscale dependent, with seed-soil contact and small differences in elevation being critical parameters (Harper *et al.* 1965; Harper 1977; Keddy & Ellis 1984; Keddy & Constable 1986). Competitive interactions are likely to be affected by larger scales of heterogeneity, which may correspond to factors such as root and shoot zones. In this experiment heterogeneity existed at a very small-scale, and was likely to affect mainly germination and establishment processes early in the growing season with competition becoming more important later in the growing season, when vegetation in the experimental tanks was dense.

Diversity and heterogeneity: spatial and temporal components

The consistently greater diversity in heterogeneous communities may not be due to spatial differences alone. Spatial and temporal heterogeneity are often closely linked (Grubb 1977; Platt & Weiss 1977; Denslow 1980, 1985; Pickett & White 1985). The interplay of these factors is thought to affect the diversity of many ecological communities because different species are favoured at different times and places due to variation in environmental and competitive conditions (Pickett 1980; Pickett & White 1985; Chesson & Huntly 1989). Microtopography in wetland communities affects more than simply spatial variation of water levels (Ehrenfeld 1995b), it may interact with temporal fluctuations in water levels to affect factors such as duration of flooding and soil nutrient dynamics. In these experimental communities, temporal variation in hydrologic conditions of all treatments existed due to small fluctuations in water levels (9–12 cm). As a result, hydrologic conditions present in the hummock–hollow microtopography of heterogeneous treatments were not only more variable at any given time, but also experienced much greater hydrologic extremes than homogeneous communities. The balance of anoxic and oxic conditions present in homogeneous and heterogeneous environments may also have differed, resulting in differing spatial and temporal patterns of soil nutrient availability. This interaction of both spatial and temporal components of heterogeneity may have magnified the variability experienced in the heterogeneous environments, differentially affecting the establishment of many species and, according to nonequilibrium models, leading to greater diversity (Pickett 1980; Pickett & White 1985; Chesson & Huntly 1989).

RESOURCE SPECIALIZATION AND HETEROGENEITY

There was mixed support for the hypothesis that coexistence is facilitated in heterogeneous environments due to increased resource specialization as measured by increased abundance and/or biomass. Pairwise post-hoc tests of main effect treatment means indicate that mean abundance and total above ground biomass were significantly greater in heterogeneous environments. However, abundance and biomass differed depending on the combination of heterogeneity and propagule source treatments suggesting that a more complex relationship exists between heterogeneity and these response variables, at least in experimental wetland communities such as this. Abundance was greater in all heterogeneous treatments than equivalent homogeneous treatments. Biomass only increased with heterogeneity in the seed bank treatments, these also had the lowest levels of species diversity. These results do not provide clear support for the hypothesis that facilitated coexistence in heterogeneous environments leads to increased numbers of individuals or productivity due to greater resource specialization by the more diverse array of species present. However, it is interesting to note that they are consistent with work in prairie communities that shows a direct link between productivity and diversity when there are fewer than 10 species present (Tilman *et al.* 1996).

HETEROGENEITY AND PROPAGULE SOURCE

Diversity increased consistently with heterogeneity regardless of the propagule source treatment. This supports the hypothesis that facilitated coexistence in heterogeneous environments should be independent of the propagule source used. The seeds only and seeds + seed bank treatments produced greatest species richness and plant densities. Large numbers of seeds were added in these treatments, which represented a system without dispersal limitation. The seed bank treatment resulted in lower species richness, highly variable numbers of individuals and great variability in plant size. This may be due to low propagule numbers present in the soil samples, which were only 160 g, or because conditions did not favour recruitment of the species which were present.

Inconsistent responses to heterogeneity across propagule source treatments for abundance and total biomass indicated that other aspects of community structure that respond to heterogeneity are dependent on the propagule source. This shows that for some species, in this case *Eleocharis*, *Alisma* and *Sparganium*, the addition of a small amount of soil is highly beneficial when situated in homogeneous microtopography which is inundated most of the time. Although the reasons for this are unclear, it may be that micro-organisms present in the soil samples containing the seed bank conferred some advantage to these species in a more microtopographically homogeneous environment. This result has implications for wetland restoration, indicating that if seeds are the sole propagule source, then soil inoculation may be useful, particularly when the substrate is relatively flat.

EXPERIMENTAL WETLAND COMMUNITIES: THEORY AND APPLICATION

Manipulation of the model wetland communities in this study showed that microtopography was an important determinant of floristic diversity and is significant in structuring these wetland plant communities. Future studies using similar model wetland communities would be of value in uncoupling the relationship between spatial and temporal heterogeneity, by separating the effects of topography and time period of flooding. Other theoretical issues which need further exploration, and are particularly suited to this approach include the role of heterogeneity as a determinant of diversity at multiple spatial scales and at differing fertility levels. Similarly, the role of heterogeneity in determining susceptibility to invasion by plant species, or pathogens could be investigated using systems such as this.

Results generated from studies of model communities, such as this one, can be applied to the restoration of degraded lands (Gilpin 1987). Increasingly in wetland restoration imported seed banks and/or seed additions are being used as the propagule sources for many projects (van der Valk & Pederson 1989; McKnight 1992; McDonald 1993; Reinartz & Warne 1993; Vivian-Smith & Handel 1996). The community responses to microtopographic heterogeneity in this study can be applied to restoration strategies which aim to increase floristic diversity in wetland communities. This may avoid problems of competitive exclusion experienced previously with seed addition treatments in model wetland communities which assumed equilibrium conditions and environmental homogeneity (Stockey & Hunt 1994). Creating heterogeneity also provides a variety of hydrologic conditions at any given time. This may reduce the need for management practices which aim to maintain species richness by mimicking nonequilibrium processes, such as fluctuating hydroperiods.

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