The assembly of experimental wetland plant communities

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The ability to predict the composition of communities from environmental factors is a central goal of community ecology. We carefully selected a pool of species and subjected it to a range of environmental factors to determine which factors were able to filter out subsets of species. We began with a pool of 20 species and sowed them into 120 wetland microcosms representing 24 different habitat treatments and monitored them for 5 yr. The treatments were fertility, water depth, fluctuations in water depth, soil texture, leaf litter, length of the initial growing season, and invasion by *Typha*. After 5 yr 14 species persisted; no rare species survived. The experimental communities differed from random expectation and were assembled by rules that constrained their organization. There were strong and consistent effects of fertility, water level, and leaf litter on community composition. Community assembly was modeled as a series of environmental filters. Some aspects of assembly were deterministic: trajectories were constrained within two "pathway basins" and species rank abundances were significantly concordant within treatments. Other factors indicated that assembly has a strong stochastic component: 50% of species were present only occasionally and we cannot accurately predict species ranks. Community stochasticity did not show any clear patterns among treatments.

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The ability to predict the composition of communities is a fundamental goal of community ecology. Diamond (1975) invoked the term "assembly rules" when investigating how different communities come into existence from a common species pool. Clearly if different communities are repeatedly assembled from a common pool, then there are rules that constrain community composition.

Empirical studies of patterns and deviations from random expectation have dominated the literature on assembly rules (Connor and Simberloff 1979, Gilpin and Diamond 1984, Moulton and Pimm 1987, Wilson and Roxburgh 1994). An alternative method for exploring the constraints on community assembly has been to experimentally synthesize communities in microcosms. Some microcosm experiments have focused on historical effects, how the order of invasion can affect community structure (Wilbur and Alford 1985, Robinson and Edge-

mon 1988, Drake 1991). Other experiments involving community synthesis have focused on how gradients (in resource levels, disturbance, or biotic complexity) affect diversity (Grime et al. 1987), the role of competition and realized niches (Austin and Austin 1980, Parrish and Bazzaz 1982, Austin et al. 1985, Campbell and Grime 1992), or ecosystem function (Lawton et al. 1993). Microcosms have also been used to make inferences on how gradients affect community composition. Campbell and Grime (1992) found that with seven species of upland herbaceous plants, the best competitors in productive conditions tended to keep their place in the biomass hierarchy under low fertility. Highly advanced microcosms (ecotrons) have recently been developed (Lawton et al. 1993), and they represent a great step forward in experimental community ecology.

These studies of experimental communities emphasized gradients and environment. Environmental factors

Table 1. The species used in the microcosm experiment, guild association[1], seed viability as germination rate in the laboratory, and mean abundances (number of contacts per 0.25 m^2) in year five.

Species name[2]	Guild[1]	Seed viability (%)	Abundance
Acorus calamus	interstitial tussock	87	<0.01
Aster nemoralis	stress tolerator	50	0
Bidens cernua	obligate annual	95	3.48
Carex crinita	interstitial tussock	80	17.68
Eleocharis smallii	interstitial reed	5	18.70
Epilobium ciliatum	facultative annual	100	0.14
Eupatorium perfoliatum	facultative annual	80	0.19
Glyceria canadensis	clonal dominant/tussock	85	6.65
Gnaphalium uliginosum	obligate annual	50	0
Hypericum ellipticum	interstitial clonal	100	0
Juncus filiformis	interstitial reed	100	1.51
Lythrum salicaria	facultative annual	100	95.08
Myrica gale	shrub	80	0
Panicum longifolium	interstitial reed	35	0
Penthorum sedoides	interstitial clonal	70	0.06
Rumex verticillatus	interstitial tussock	67	<0.01
Scirpus acutus	matrix clonal dominant	83	12.19
Typha angustifolia	matrix clonal dominant	75	1.42
Verbena hastata	facultative annual	90	<0.01
Xyris difformis	stress tolerator	85	0

[1] Guild associations from Boutin and Keddy (1993).
[2] Nomenclature as in Gleason and Cronquist (1963) except *E. smallii* Britton and *X. difformis* Chapm.

may act as filters (either directly or indirectly), selecting subsets of species with appropriate traits for a habitat and driving community assembly processes (Keddy 1992). A set of predictive assembly rules was devised by van der Valk (1981) that employed the concept of environmental filters. A theoretical set of plant guilds was defined according to life-history traits that were predictive of how each guild of species would respond to variations in wetland water level. Changes in water level remove species from the species pool, thereby qualitatively defining community assembly. Another trait-based approach was used by Box (1981) in a model of world vegetation, where different environments filtered plant growth forms and then competitive ability was used to sort the remaining species.

We have adopted the filter concept and have employed an experimental approach to assembly rules. We put a standard species pool through a set of potential environmental filters in order to screen the potential filters for their ability to remove species from the species pool, alter community composition, and alter the successional trajectory of communities. The approach we have taken represents a limiting case where there are no dispersal effects, therefore we need only be concerned with the effects of the environment and biotic interactions on community structure. This represents a fundamental difference from many of the experimental community systems that tested for the effects of immigration history on community structure. For many communities (and especially for plant communities) dispersal may not be limiting, and may not be a predominant factor structuring communities. Wright and Reeves (1992) found that high-

ly non-nested community structure is associated with habitat islands that are usually structured by immigration events. In general, mainland habitat archipelagoes are neither strongly nested or immigration limited. Freshwater aquatic plants show a nested pattern (Weiher and Boylen 1994), and so there is no biogeographical evidence to suggest that temperate freshwater wetlands are immigration limited. Where immigration rates are of lesser importance, it is the ability of propagules to tolerate the specific environmental factors of a site that determines the presence or absence of a species. A large number of propagules may arrive, but only a few may be able to tolerate the conditions at the site. Given that all species have some ability for dispersal (Hamilton and May 1977), and that pools of propagules accumulate in soils (Leck et al. 1989), equal emphasis needs to be placed on the way in which the environment filters out small subsets of species and thereby affects community assembly. Similarly, the experiment parallels secondary succession from a standard and known seed bank, and allows for the consideration of interactions among species, thus incorporating autogenic succession which was not a part of van der Valk's model (1981).

We were primarily interested in the process by which environmental factors selected different subsets of the initial species pool. Beyond this we had these specific hypotheses: (1) At high fertility *Typha* would dominate and exclude the smaller species regardless of other treatment type. (Therefore the high fertility treatments should converge). (2) Species richness would therefore be greatest in the low fertility treatments. (3) At low fertility each separate treatment type would have a greater like-

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lihood of bringing about a distinct community. (4) Of the additional treatment types, changes in water level would have the strongest effects.

The model system

The herbaceous wetland plant community found in the temperate zone of eastern North America was used as the model system. We chose to consider a herbaceous community because the establishment of herbaceous communities is relatively quick in comparison to forest or shrub systems. Furthermore, wetlands are still threatened by various factors, such as eutrophication, modification of flooding regimes, and invasion by exotic species, and the relative importance of these factors is unclear.

The microcosms in our experiment were specifically designed on the basis of the riverine wetlands that are found near or along the Ottawa River in eastern Ontario, Canada (described by Day et al. 1988). Day et al. found two major gradients underlying the Ottawa River wetlands. The first gradient was elevation, and it was linked to a series of factors that included spring flooding, wave and ice scour, summer water depth, litter deposition, soil organic content, and length of the growing season. The second gradient was related to fertility and was measured in terms of standing crop and litter.

Methods
General

A standardized seed mixture of 20 wetland plant species was used as the species pool. Seeds from 91 candidate species were screened for viability in a laboratory incubator (12 h photoperiod, 25°C/15°C), and from this group 20 species were chosen. We wish to emphasize that this was not a haphazard collection of species. The pool was carefully selected to represent the range of morphologies, life histories, and adaptive strategies that are found in the species pool of temperate eastern North American wetlands. Table 1 lists the species, their guild association, and their viability measured as germination rate in the laboratory. Although the goal was to select only species with high viability, our records indicate that one species had only 5% viability (*Eleocharis smallii*). Low viability was overcome by sufficient numbers of seeds as *Eleocharis* was the second most abundant species at the end of the experiment. Species included large clonal dominants such as *Typha angustifolia*, diminutive species such as *Xyris difformis*, common annual species such as *Bidens cernua*, common reeds such as *Scirpus acutus* and an invasive exotic, *Lythrum salicaria*. The field distributions and ecology of these species have been documented in a series of studies (Day et al. 1988, Moore et al. 1989, and Boutin and Keddy 1993).

The seed mixture was sown onto 120 microcosm containers on 11–13 June 1987 and they were grown for five yr. Each container (internal dimensions: 63 (length) ×42 (width) ×26 (height) cm) held 13 cm of 002 grade washed concrete sand. The size of the container corresponds to the quadrat size used to study wetland community patterns along the Ottawa River (Day et al. 1988). Sand was used because of the logistic problems associated with obtaining, autoclaving, and mixing approximately 4 m³ of wetland soil, and because Day et al. (1988) found that Ottawa River wetland soils are on average about 80% sand and only 5.5% organic. The containers were watered twice daily or constantly with Ottawa city tap water so that water levels were consistently at the soil surface. The experiment was located in an outdoor compound at Carleton Univ., Ottawa, Ontario, Canada (45°25'N, 75°45'W). The containers were annually flooded to a depth of 10 cm for overwintering (Moore 1990).

Habitat variables

The experimental design included 12 general wetland treatments, with each treatment replicated at two fertility levels ("infertile" and "fertile"). The 24 groups were replicated in five blocks yielding a total of 120 containers.

Six habitat variables were manipulated. Each was known to be important in determining the field distribution of species in North American wetlands:

1. Water depth (and availability) is of major importance in determining both the biomass and the community composition of a site (Hutchinson 1975, Spense 1982). Water depth was raised to a constant +5 cm or lowered to a constant −5 cm from the control level set at the soil surface (0 cm). The small amount of variation in water levels was due in part to the constraints imposed by the containers, and also because we were attempting to create a subtle gradient that mirrored small-scale changes in elevation.

2. The timing and duration of flooding events are also known to be of great predictive value in wetlands, e.g., prairie potholes (van der Valk 1981), the Great Lakes (Keddy and Reznicek 1986), and hydrologically linked lakeshores (Hill and Keddy 1992). Water depths were changed over the course of each growing season in order to represent long spring floods with summer drawdown. Depth was kept at +5 cm until mid-July when it was lowered to 0 cm (i.e. the soil surface). In a second treatment, depth was further lowered to 10 cm below the soil surface in August.

3. Leaf litter alters seed recruitment in wetlands (van der Valk 1981) and leaf litter gradients are associated with different wetland community types (Day et al. 1988). Leaf litter was added to the substrate at either a low application rate (50 g container⁻¹, 0.5 cm in depth) or a high application rate (150 g, 1.5 cm). Leaf litter in
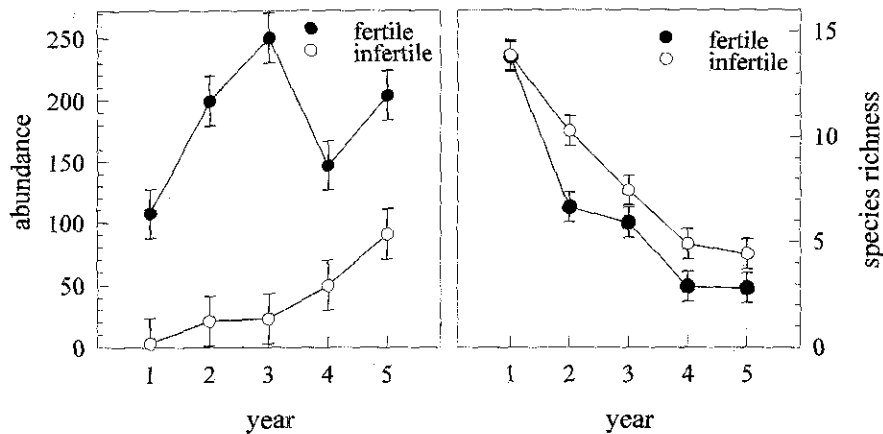
Fig. 1. Total relative abundance (above ground) and species richness in the mesocosms over five yr (means ±95% confidence intervals).

Ottawa River wetlands varies from 0 to 320 g per 0.25 m², with a mean of about 40 g per 0.25 m² (Day et al. 1988). The leaf litter was collected just before the experiment and consisted of *Scirpus fluviatilis*, with minor amounts of *S. americanus, Eleocharis smallii*, and *Typha angustifolia*.

4. Soil surface textures can affect germination rates in wetland plant species (Keddy and Constabel 1986), and the occurrence of rare plant species is often associated with gravel or cobble shorelines (Keddy and Wisheu 1989, Moore et al. 1989). Soil surface texture was altered by the addition of small pebbles (0.5 to 1.25 cm in diameter, applied to a uniform depth of 1.25 cm) or rounded cobblestones (single layer of rocks 2.5 to 7.5 cm in diameter).

5. In spite of the importance of water level fluctuation in wetlands (van der Valk 1981, Keddy and Reznicek 1986), little is known about the effects of timing of events on the establishment and maintenance of plant communities. It is conceivable that small differences in timing could have a major effect on germination and therefore greatly affect resulting species composition. Length of the initial growing season was altered by delaying the start of the experiment by 14 or 28 d. Day et al. (1988) found that growing season length was a part of a major complex gradient along the Ottawa River.

6. Ramets of *Typha* were added to one set of treatments at the beginning of year 2 in order to simulate the invasion by a highly competitive species that is known to dominate wetlands (Grace and Wetzel 1981, Grace 1987, Day et al. 1988).

In each of the above treatments two fertility levels were created. Fertilization provided an initial P loading of 1.32 g P container⁻¹ in the fertile treatments (N:P ratio of 2:1). This corresponds to an initial soil P concentration of about 19 μg P g⁻¹ soil. This value is about twice the mean soil P in fertile wetlands found by Day et al. (1988), but it is less than the maximum level found. Fertilization occurred every three weeks during the growing season to give an annual P loading of 8.21 g P yr⁻¹. The infertile treatments initially received 0.041 g P, which corresponds to less than 1 μg P g⁻¹ soil. Two hydroponic fertilizers were used in equal proportions, the first mixture (15–0–0) contained, by weight, Ca (19.0%), N (as nitrate 15.0%), and Mg (3.98%). The second fertilizer (7–11–27) contained N (7.0%), Mg (3.75%), P (11.0%), K (27.0%), S (4.8%), Fe (0.1%), Mn (0.085%), Zn (0.03%), B (0.027%), Cu (0.0041%), and Mb (0.009%).

Data collection and analysis

A non-destructive point sampling technique was used to survey the plant community of each microcosm. A 0.25-m² gridded quadrat was placed over each microcosm; at each intersection point in the grid (n = 50), a small rod was dropped into the soil and the total number of contacts for each species and total sum of contacts for all species in each container were used as measures of relative above ground biomass. The containers were sampled yearly, in August or early September.

Detrended correspondence analysis (DCA, Hill and Gauch 1980) was used to ordinate the community data; we included the data from all five years of the experiment. We performed two-way ANOVA on the axis 1 and 2 scores in order to test for effects of treatment level (e.g. water depth) and fertility on the final community composition (year five). For ANOVA we used a common control treatment – constant water depth at the soil surface (this treatment was repeated at both fertility levels but it did not undergo fluctuations, litter addition, substrate modification, timing alteration, or *Typha* addition). A series of three-way repeated measures ANOVA were used to test for effects of treatment level, fertility, and time (year) on species richness. Concordance in species rank abundances was calculated as Kendall's W following Siegal (1956) to quantify within-treatment correlation in species abundances.

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Table 2. Repeated measures three-way ANOVA of species richness, main effects and two-way interaction terms (F-values, *p < 0.05, **p < 0.01, ***p < 0.001).

	Treatment	Fertility	Treatment × fertility	Year	Trmt. × year	Fert. × year
Depth[1]	195.6***	47.48***	9.67***	153.66***	46.11***	9.36***
Fluctuation[1]	73.75***	46.76***	5.28*	99.13***	48.44***	5.41**
Litter[1]	0.89	220.4***	8.65**	169.00***	4.98**	6.47**
Texture[2]	0.50	77.63***	0.35	296.58***	1.88	12.14***
Start[1]	5.88**	56.96***	7.87**	268.52***	0.95	6.54**
Typha[3]	0.05	81.87***	2.55	84.58***	3.52*	4.06*

[1] The main treatment effects had 2 d.f., fertility d.f. = 1, interaction d.f. = 2, and error d.f. = 24, with repeated measures for 5 years;
[2] error d.f. = 23, otherwise same as 1;
[3] treatment d.f. = 1, fertility d.f. = 1, interaction d.f. = 1, error d.f. = 16. Adjusted p-values were used throughout as the tests generally did not meet assumptions of sphericity.

Results

Effects on vegetation properties

As the communities developed total plant abundance increased while species richness declined (Fig. 1). The fertile treatments had consistently higher biomass and lower richness than did the infertile treatments. Species richness was strongly affected by fertility level and year for all treatments (Table 2), but only two of the environmental variables were strongly significant: water depth and fluctuation in water depth, where high water level or fluctuations in water level were associated with lower species richness. The microcosms that were started 28 d after the others had greater richness than did the control treatments, and in year five the difference was about one extra species.

Key environmental factors and the resulting community types

The results consisted of a matrix of the abundance of 20 species by 24 treatments for 5 yr, with each treatment replicated 5 times. Table 1 shows species mean abundances for year five. To determine which environmental factors had greatest impact in producing different communities, we ordinated the entire five-yr data using DCA to produce an ordination space in which the final year-five communities could be compared and the pathways or trajectories could also be plotted. DCA scores, which measure the relative abundance of species in n-dimensional space, became the dependent variables for further analysis. Two-way ANOVAs of the year-five DCA scores showed that water depth, fluctuation in water depth, and in some cases, fertility significantly affected axis-one scores, while fluctuation or fertility significantly affected axis-two scores (Table 3). Litter, soil surface texture, initial starting date, and the addition of Typha had no

Table 3. Two-way ANOVA of DCA axis one and two loadings, data from year 5 (F-values, *p < 0.05, **p < 0.01, ***p < 0.001).

		Treatment		Fertility		Interaction	
		F	p	F	p	F	p
DCA1	depth[1]	14.83***	<0.001	0.44	0.520	10.81***	<0.001
DCA2	depth[1]	6.81***	0.009	32.12***	<0.001	0.39	0.683
DCA1	fluctuation[1,4] vs high	0.08	0.922	38.67***	<0.001	0.61	0.551
	vs zero	17.76***	<0.001	10.32***	<0.001	9.28**	0.001
DCA2	fluctuation[1,4] vs high	8.27**	0.002	1.00	0.327	1.50	0.243
	vs zero	10.12***	<0.001	1.02	0.322	1.58	0.227
DCA1	litter[1]	1.84	0.181	3.77	0.064	1.17	0.327
DCA2	litter[1]	0.23	0.797	4.90*	0.037	1.26	0.301
DCA1	texture[2]	0.91	0.415	3.27	0.084	0.631	0.541
DCA2	texture[2]	2.71	0.088	61.31***	<0.001	0.18	0.833
DCA1	start[1]	0.99	0.385	5.13*	0.033	0.19	0.832
DCA2	start[1]	0.36	0.702	45.91***	<0.001	0.78	0.468
DCA1	Typha[3]	0.13	0.723	3.94	0.065	0.11	0.753
DCA2	Typha[1]	2.00	0.176	41.80***	<0.001	4.48*	0.050

[1] The main treatment effects had 2 d.f., fertility d.f. = 1, interaction d.f. = 2, error d.f. = 29;
[2] total d.f. = 28;
[3] treatment d.f. = 1, fertility d.f. = 1, interaction d.f. = 1, error d.f. = 19;
[4] the two fluctuation treatments were compared to both constant high water depth and constant zero water depth.
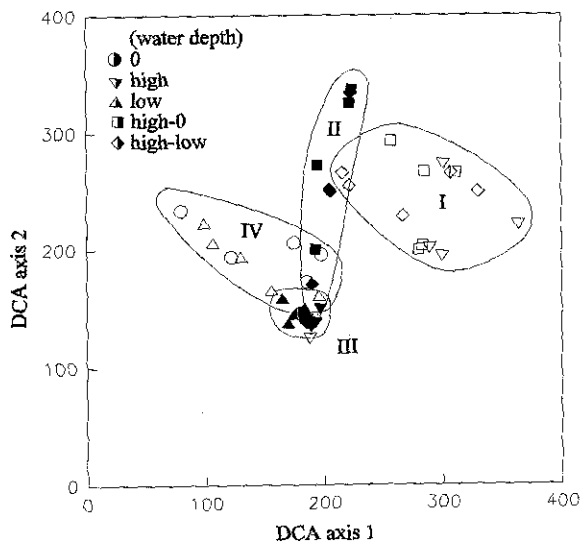
Fig. 2. DCA ordination of microcosm plant community data. Symbols represent water depth/fluctuation treatments, filled symbols represent high fertility, open symbols represent low fertility. Note that the other treatments (litter, soil texture, starting date, and additional *Typha*) were not significantly different from communities III and IV. Note that one replicate from group I ordinated within group III.

significant effect on community structure in comparison to the standard, constant water level zero-treatment group.

The DCA plot shows four community types which are distinguished by fertility level (fertile or infertile) and by water level – either constant (high, zero, and low) or fluctuating (high to zero, high to low) (Fig. 2). Community type I includes infertile treatments that received either constant high water (constant flooding) or spring flooding with summer drawdown. This community type was primarily made up of *Bidens cernua* and *Eleocharis smallii*. High axis-1 scores correspond to large amounts of *Bidens*, while large axis-2 scores correspond to large amounts of *Eleocharis*. The second community type includes the fertile treatments that underwent fluctuations in water depth (spring flooding and summer drawdown). These treatments were primarily composed of *Eleocharis* or *Lythrum*. Lower axis-2 scores along the center of axis-1 correspond to increasing *Lythrum* domination. Community type III includes the fertile treatments that had constant water levels, even those that were flooded throughout the summer. This community type was dominated by *Lythrum*, with some *Scirpus acutus*. This was the typical high fertility community type; the other treatments (litter, texture, starting date, and *Typha* addition), when at high fertility, were not significantly different from community type III. The fourth community type also includes infertile sites, but these did not undergo flooding. They had constant water levels at or below the soil surface. These treatments were mainly

composed of *Lythrum salicaria* and *Carex crinita*, with only small amounts of *Eleocharis* and little if any *Bidens*. Low axis-1 scores correspond to increasing coverage by *Carex* and decreasing coverage by *Bidens*. This was the typical low fertility community type; the other treatments (litter, texture, starting date, and *Typha* addition), when at low fertility, were not significantly different from community type IV. The interactions between depth, fluctuation in depth, and fertility observed in the ANOVA (Table 3) are also shown in that the arrangement of the communities does not follow a simple response to fertility on one axis and to water depth/fluctuation on the other axis. Furthermore, there is an apparent inconsistency in that the constant high water treatment can, at low fertility level, be similar to fluctuation treatment groups, whereas at high fertility, constant high water is unlike the fluctuation in water depth treatments.

Community trajectories and "pathway basins"

Consideration of community trajectories showed that only two "pathway basins" existed within our data (Fig. 3). We would define a pathway basin as a region where successional trajectories are constrained and tend toward some subregion. The ordination space in Fig. 2 was based on the community data for all years, and this allowed us to plot the mean trajectory for each treatment group. All the pathways drifted to the left (toward low axis-1 scores), and this was due, in part, to a decline in diversity. Notably, high dicot diversity corresponded to high axis-1 scores. The treatments that received either constant high water or spring flooding (fluctuation) followed a different
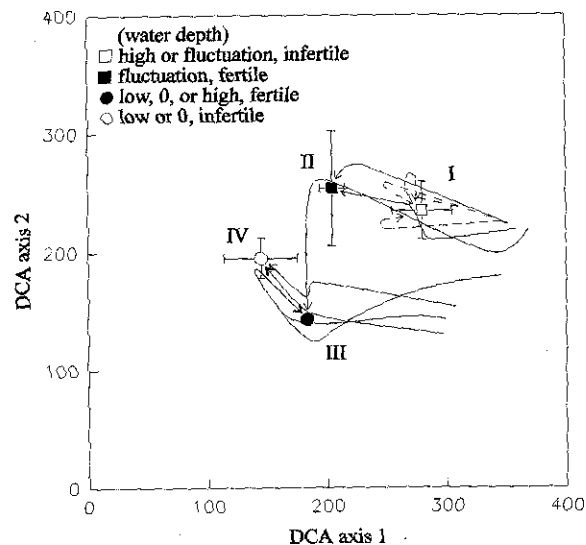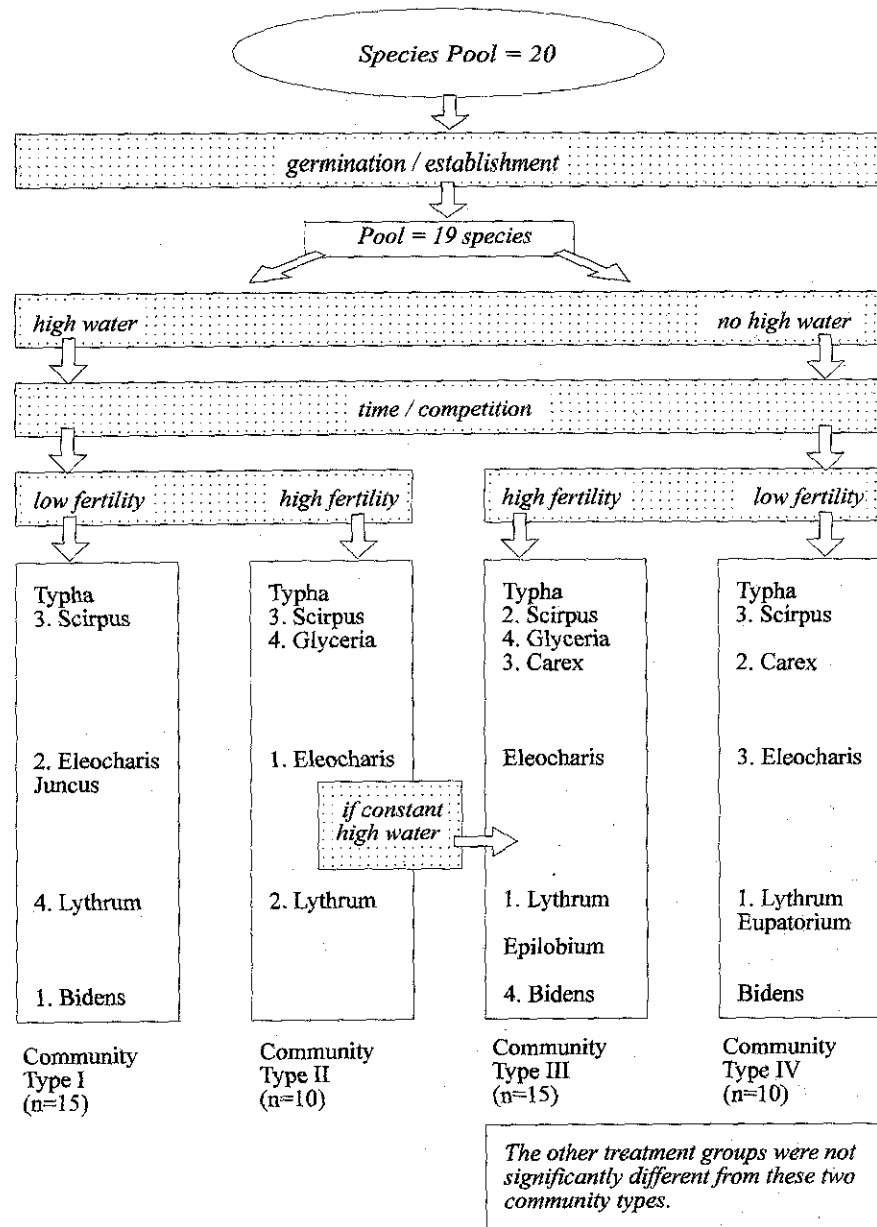

Fig. 3. Mean community trajectories in ordination space leading to the four community types (group means ±95% confidence intervals). Open symbols represent low fertility, filled symbols represent high fertility.

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Fig. 4. Community assembly model one (from the results of community ordination). Horizontal bands represent a series of "environmental filters". Numbers next to species in the final community types correspond to mean rank abundance. See text for further explanation.

Species Pool = 20

germination / establishment

Pool = 19 species

high water | no high water

time / competition

low fertility | high fertility | high fertility | low fertility

Typha 3. Scirpus	Typha 3. Scirpus 4. Glyceria	Typha 2. Scirpus 4. Glyceria 3. Carex	Typha 3. Scirpus 2. Carex
2. Eleocharis Juncus	1. Eleocharis	Eleocharis	3. Eleocharis
		if constant high water	
4. Lythrum	2. Lythrum	1. Lythrum Epilobium	1. Lythrum Eupatorium
1. Bidens		4. Bidens	Bidens
Community Type I (n=15)	Community Type II (n=10)	Community Type III (n=15)	Community Type IV (n=10)

The other treatment groups were not significantly different from these two community types.

general pathway than did the treatments that were not flooded. This first pathway had lower diversity and the communities were dominated by either *Bidens cernua* or *Eleocharis smallii* (community type I). The second pathway represents the development of a *Lythrum* dominated community where the most of the dicot species were quickly excluded leaving *Scirpus, Carex,* and *Glyceria* as species commonly found alongside *Lythrum* (community type III). The difference between the pathways was maintained regardless of fertility. The trajectories were therefore constrained by the different water level treatments. Fertility did not constrain the trajectory as both fertile and

infertile treatments followed similar pathways, within the limits set by water level effects.

The first pathway basin corresponds to community type I, and although there was a good deal of apparent variation around the mean, the community is distinct from the others at both year five and during the earlier years. Community type II followed a trajectory through this pathway basin to a point beyond, and indeed many of the replicates assigned to this community type are tending towards the second pathway basin at community type III (cf. Fig. 2). Community type II may be converging toward community type III, and this means that the con-
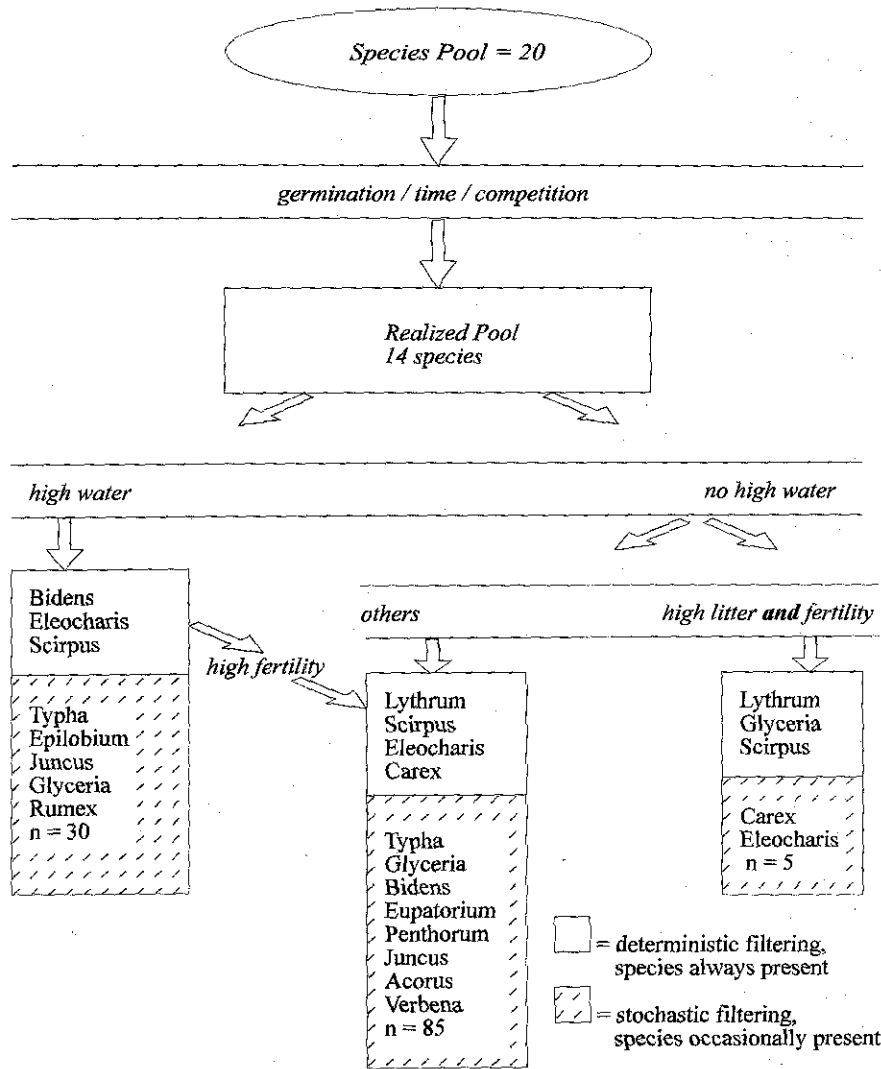
Fig. 5. Community assembly model two (from species presence data only). Horizontal bands represent a series of "environmental filters". Species in the final community types are ordered according to their mean rank abundances.

straints on trajectory that were imposed by water levels may be surpassed by increasing fertility.

Filters and the description of community assembly

Different environmental treatments can act much like filters by removing some species from the pool of available species, and allowing others to establish and spread (Keddy 1992). Species were considered to be filtered by a treatment if they were not found in any of the five replicate microcosms within a treatment group. Some of the treatments, i.e. "filters", had no novel effect on community structure, while others produced communities that were distinct.

We have developed two descriptive models of assembly for the experimental microcosms. One is based on species presence and absence only, while the other takes abundance into account and is based on DCA scores. Fig. 4 shows the process by which subsets of species were removed and abundances modified to give rise to the four community types described by DCA. Nineteen species became established during the first two years (i.e. had an abundance of at least one in one microcosm), therefore an unknown filter prevented the establishment of one species (*Panicum longifolium*). The second filter represents differences in establishment that were associated with water level, and were visualized in the community trajectories (Fig. 3). High water caused early separation in community type and many of these differences were maintained over time. The next filter represents the loss of species that were able to become established, but were

Table 4. Relative stochasticity of experimental communities expressed in terms of: a) species presence or absence (number of species occasionally present in a treatment group, with percent of the total number of species found in that group), b) species abundances (maximum variation in ordination space along DCA axis 1), and c) the ranking of species by their abundances (within-treatment concordance in abundance rankings, Kendall's W).

		a) Species occasionally present		b) Range along DCA axis 1		c) Concordance, Kendall's W	
		infertile	fertile	infertile	fertile	infertile	fertile
Water depth	low	5 (71%)	3 (60%)	97	21	0.586**	0.730**
	0 (control)	2 (33%)	1 (33%)	118	8	0.678**	1.000**
	high	3 (75%)	4 (80%)	176	11	0.348(n.s.)	0.598**
Fluctuation	high – 0	3 (50%)	5 (83%)	54	40	0.779**	0.432*
	high – low	4 (66%)	2 (50%)	114	33	0.533**	0.840**
Litter	low	0 (0%)	1 (33%)	79	19	0.668**	0.840**
	high	5 (63%)	2 (50%)	52	36	0.753**	0.720**
Texture	pebbles	3 (57%)	2 (50%)	23	74	0.744**	0.644*
	cobbles	6 (75%)	2 (50%)	96	66	0.654**	0.664**
Starting date	+14 d	3 (50%)	4 (80%)	74	76	0.729**	0.488*
	+28 d	4 (57%)	3 (60%)	82	19	0.703**	0.634**
Typha addition		4 (50%)	4 (67%)	170	12	0.672**	0.681**
Mean		3.5 (50%)	2.75 (57%)	95	35	0.654	0.689

** $p < 0.01$, * $p < 0.05$.

unable to maintain viable populations (e.g. *Hypericum*, *Xyris*). These species steadily declined in number until they were displaced from the microcosms, and only one was an annual (*Gnaphalium*). The remaining species pools were then modified by fertility level, and the four general community types are shown at the bottom of Fig. 5. The convergence of communities that underwent different courses in ordination space is shown as the horizontal "filter" linking communities II and III. Alternative pathways to the same endpoint were deterministically traveled by different treatment groups.

The species were ordered according to a trait-based functional grouping which we adapted from Boutin and Keddy (1993). Species with similar traits were located near each other, and gaps in the species pool may be interpreted as deletions of species with similar traits. At the top of the species pool are species with the ability to dominate sites with dense canopies (e.g. *Myrica gale*, a common wetland shrub, and *Typha angustifolia*, a cat-tail). The species gradate towards smaller species with less asexual reproduction to *Xyris difformis* which is a diminutive partially evergreen stress-tolerator (sensu Grime 1979, Murphy et al. 1990). The species below *Xyris* possess characteristics of ruderal species. The first subset are perennials that have high rates of sexual reproduction, and the remainder are obligate annuals. Sixteen of the species were assigned to guilds by Boutin and Keddy (1993); we inferred the relative positions of the remaining four species.

An alternative view of community assembly becomes evident when only species presence is noted (Fig. 5). Here we defined and utilized three possible categories under which a species was found: (1) not present in any of the five replicates of a treatment, (2) present in all five

replicates, and (3) present in some of the five, but not all of them. This distinction allows to consider how deterministic species presence/absence was within a treatment group. We have used the alternative term "stochastic" to encompass within treatment variation. Much of this variation may have deterministic causes, but those causes were outside our ability to control or measure. Therefore we call such noise "stochastic" as it appears as random error within the experiment.

Part of Fig. 5 follows from Fig. 4 – lack of establishment of one species and slow extirpation of five others led to a realized species pool of 14 species. Furthermore, this pool was primarily modified by effects associated with water depth. A new finding is that at high litter and high fertility *Glyceria* was always present (and in large numbers); this was not brought out by DCA. Here the convergence of communities is best viewed as a product of high fertility often filtering *Bidens* and allowing *Lythrum* entry into the community. Overall, only several species had constant membership within a treatment group, while a rather large number of species blinked in and out of replicate communities. We have interpreted this as stochastic filtering, a non-deterministic part of community assembly.

Assessing stochasticity

The preceding sections focused on among-treatment variation and the deterministic part of community assembly. In order to address the question of stochasticity in the experimental communities, we focused on three scales of within-treatment variation: presence/absence,

species abundances (in DCA space), and abundance rankings.

The number of species occasionally present in a replicate microcosm showed wide variation among the treatments, and there were no clear patterns (Table 4a). There was no effect of fertility level on the number of species occasionally present in a treatment group ($t = 1.28$, $p = 0.214$), nor were there any effects of treatment group (Kruskal-Wallis one-way ANOVA on ranks: $H = 3.949$, $p = 0.56$, d.f. = 5). Furthermore, the proportion of species blinking in and out did not differ between the two fertility levels ($t = -0.411$, $p = 0.69$) or treatment groups ($H = 6.392$, $p = 0.27$, d.f. = 5). The same proportion of species blinked in and out regardless of overall diversity. Higher diversity at low fertility comes from both constantly present species and transient species equally.

Most of the species that were present only occasionally had declining abundances over the last three years of the experiment. The timing of extirpation of a species is therefore stochastic when the time scale is only one year. Because there were no apparent effects of fertility or other treatment, the rate of extirpation of species is not significantly different among the treatments.

The infertile treatments had greater within-treatment absolute variation in species presence and abundance as measured by the range of scores along the primary DCA axis (Table 4b, $t = 4.02$, $p < 0.001$). In this case the fertile treatments can be thought of as having brought about a more deterministic outcome, as the communities were more constrained in ordination space. The other treatments did not affect the range along DCA axis-1 (one-way ANOVA $F = 0.228$, $p = 0.945$, d.f. = 5). When abundance information is added to the presence/absence data, the infertile treatments had greater apparent stochasticity than the fertile treatments.

A possible reason for this is that more nutrients brought about stronger dominance and a stricter competitive hierarchy, therefore we also considered concordance of species rankings among replicate microcosms. In many ways the experiment was a large competition experiment, and so we might expect that after five yr there would be consistent abundance rankings within each group of replicates. All except one of the treatment groups had significant concordance (Table 4c). Species tended to maintain their ranks within each treatment. Therefore, the abundances of species within the microcosms were constrained (i.e. the assembly rules also work on abundances). There was no effect of fertility level ($t = -0.626$, $p = 0.54$) or treatment type (Kruskal-Wallis test, $H = 3.954$, $p = 0.56$, d.f. = 5). There is no evidence to support the idea that/stricter hierarchies at high fertility led to the results described for the range in DCA scores.

Although the concordance values were almost always significant, the values do not indicate very tight controls on species rankings. The mean concordance value was about 0.67 which corresponds to a mean Spearman correlation of 0.59. Generally three of five replicates were strongly correlated ($r_s > 0.7$), while 2 were weakly corre-

lated ($0 < r_s < 0.5$). Negative correlations were rare. Although some species tended to be winners and others tended to be losers, we can only describe trends. We cannot supply deterministic species rankings; they must take the form of probabilities. An example: if there was high water level for any part of the growing season and low fertility, *Bidens cernua* has an expected probability of being the most abundant species of 0.67 (10 of 15 replicates), and a probability of 0.13 of being the second most abundant species. This reliance on probabilities reinforces the fact that species rankings had a significant stochastic component.

Discussion
Filters and community composition

In some community types differences in colonization, or founder effects, can be expected to control species composition if species are equally tolerant of abiotic conditions and if species are approximately equivalent in competitive ability (Yodzis 1986). In other cases, large pools of propagules are available to colonize sites, and the species may have vastly different competitive abilities and abiotic tolerances. We have shown that in the limiting case where all sites have identical species pools, different environmental conditions gave rise to different communities. There may be no need to invoke dispersal or colonization processes to account for differences among community types.

We found that some habitat variables strongly affected community composition while others had no significant effects. A proposed mechanism is that environments filter out species that do not possess the requisite traits for that habitat and the strength of competitive interactions subsequently modifies community composition. Ideally one would be able to order environmental filters in terms of importance. The first two filters (the filter that prevented germination and/or early establishment and competitive displacement over time) are clearly of primary importance – they removed one third of the pool. This emphasizes the importance of early germination and establishment in vegetation, and directs attention to the mechanisms underlying the filters operating at this stage (e.g. germination requirements, mycorrhizal infection, relative growth rates).

Although the experiment could be thought of as a long-term competition experiment, diversity was likely maintained by the seasonal dieback of above-ground biomass. Seasonal dieback may have slowed competitive exclusion of some species, and allowed for the coexistence of others. Many of the replicates were invaded by species that were not in the original species pool (e.g., *Juncus nodosus*); this means that gap creation was often sufficient for the recruitment of species after the initial phase of colonization. The implication of this is even when the herbaceous wetland is established, there may be

sufficient seasonal disturbance to make overriding historical effects very unlikely.

Fertility and water depth/fluctuation were clearly of greater importance than litter, surface texture, the addition of *Typha*, or starting date. Even though the microcosms that were started 28 d after the others maintained a slightly greater species richness, the filters brought about a community structure that was similar to the others. This observation, along with the convergence of replicates that followed alternative pathways indicates that community assembly has a strong deterministic component.

There is a continuing need for the comparative ecosystem synthesis advocated by Heal and Grime (1991). They suggest that we seek out the common themes of how a few environmental factors likely have consistent effects on certain functional groups of species in a wide range of ecosystems. In this experiment we had a common competitive dominant in 106 of 120 replicates, and a common group of extirpated species. Our results are in agreement with Campbell and Grime (1992): fertility had little influence on apparent relative competitive ability.

Traits and filters

As biologists we tend to think in terms of species rather than traits. Since the environmental factors presumably act on traits rather than species, we need to eventually explore how traits, rather than species, react to the treatments (Keddy 1992). In an experiment similar to this one, Stockey and Hunt (1994) used two seedling traits to predict the biomass of 15 wetland plant species grown in mixture for one season. Their community was relatively insensitive to their single environmental treatment: intermittent flooding.

In order to qualitatively assess how the different environmental factors may have filtered species according to traits, the species list in Fig. 4 was arranged according to guild associations. Species with similar traits were placed near each other and gaps in the species lists represent a deletion of a set of traits from the species pool. All the community types had at least two similar species grouped at the top of the list (*Typha* and *Scirpus*). These plants belong to the clonal dominant guild that makes up the matrix of many wetlands (Boutin and Keddy 1993). The species in this guild are generally tall clonal plants with deep rooting zone and rigorous asexual spread. These species also have high competitive abilities (Gaudet and Keddy 1995), but in no case were they most abundant. Those species that are found in interstitial areas in wetlands did quite poorly as seen by the gap between *Carex crinita* and *Eleocharis smallii*. These two species make up opposite ends of the interstitial guild, as the large tussocks of *Carex* are somewhat like a matrix species, while *Eleocharis* is more similar to the ruderals which are found at the bottom of the species lists. The nearly even spacing in the make-up of the final community types shows that most of the guilds persisted, and this supplies

qualitative evidence to support limiting similarity and guild proportionality (c.f. Fox and Brown 1993, Wilson and Roxburgh 1994).

Relationship with field conditions

Although the realism of any experiment is of course limited (Diamond 1986), the results and implications compare favorably to the natural wetlands we attempted to model in the microcosms. Along the Ottawa River, in areas of low fertility and low elevation (i.e. greater fluctuations in water level) there is a community type dominated by *Eleocharis smallii*, with modest amounts of *Scirpus acutus* and *Lythrum salicaria* (Day et al. 1988). This community type is similar to community types I and II. Day et al. described *Lythrum* as a gap colonizer, and found it to be abundant in areas where ice scour produces clearings. The development of communities in the microcosms paralleled secondary succession following a disturbance such as ice scour, and so the success of *Lythrum* was to be expected. Although Day et al. found that *Lythrum* domination was not a feature of any community type (they found *Typha* to be dominant in high fertility areas), *Lythrum* has since spread rapidly in many of their sites (pers. obs.). *Glyceria canadensis* persisted in the high fertility microcosms only, and it is often found in sheltered bays where there is rich organic soil (Keddy 1981, Day et al. 1988). *Eupatorium perfoliatum* is often found in sandy wet meadows along the Great Lakes (Keddy and Reznicek 1986), and on drying shorelines after drawdowns at beaverponds. In the microcosms it was found only in community type IV (low fertility and no flooding). *Carex crinita* grew in microcosms that were not flooded in the spring (types III and IV), but this apparent requirement was not known or expected. *Carex crinita* is often found at higher relative elevations in marshes along the Ottawa River (Day et al. 1988). Two species, *Xyris difformis* and *Panicum longifolium* (which is nationally rare, Argus and Pryer 1990), are found only in coastal plain wetlands (Keddy and Wisheu 1989). Their failure to persist is also consistent with the general inability to survive in most wetland types. This is in spite of the fact that we went out of our way to create infertile gravel shorelines with spring floods in this experiment.

On stochasticity

It is clear that the microcosm communities did not behave in an absolutely deterministic manner. The amount of stochasticity depends on the point of view of the observer and the time scale for which one is observing. On one hand only about 50% of species were consistently found within sets of replicates, while on the other hand this represented an average of 85% of the entire species pool. Our goal was to measure within-treatment variation in a number of ways in order to address stochasticity as a

factor. Any further discussion of the results in Table 4 would be burdened by confusion related to the notion of "half-empty versus half-full". The fairest statement is that although the experiment yielded generally consistent and apparently deterministic results, closer inspection reveals an inner lining of inconsistencies and apparently random behavior. An implication of this is that even when we attempt to construct replicate communities, we must rely on probabilities regarding species presences and relative abundances. Assembly rules for plant communities will most likely not be as rigid as the rules of Newtonian mechanics.

Conclusions

The experimental communities showed clear evidence that community composition was constrained by assembly rules. There were strong and consistent effects of fertility, water level, and leaf litter on community composition. The observation that community assembly can follow different pathways, but converge on a common endpoint supports the idea that assembly processes are highly constrained. Some of the rules could be deduced for our experimental system, and therefore some rules could be deduced for natural plant communities. Although largely deterministic and predictable, community assembly has a strong stochastic factor. Within our controlled experiment, we would still be forced to utilize probabilities to make predictions about some species. The ranking of species tended to be concordant, but the prediction of rank abundance would be rather poor. There was no apparent trend regarding assembly stochasticity (or uncertainty), as it was scattered throughout the treatments. Therefore, the assembly rules that constrain community composition may work equally well at different points along environmental gradients.

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