
Does Facilitation of Faunal Recruitment Benefit Ecosystem Restoration? An Experimental Study of Invertebrate Assemblages in Wetland Mesocosms

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Abstract

We used wetland mesocosms (1) to experimentally assess whether inoculating a restored wetland site with vegetation/sediment plugs from a natural wetland would alter the development of invertebrate communities relative to unaided controls and (2) to determine if stocking of a poor invertebrate colonizer could further modify community development beyond that due to simple inoculation. After filling mesocosms with soil from a drained and cultivated former wetland and restoring comparable hydrology, mesocosms were randomly assigned to one of three treatments: control (a reference for unaided community develop-

ment), inoculated (received three vegetation/sediment cores from a natural wetland), and stocked + inoculated (received three cores and were stocked with a poorly dispersing invertebrate group—gastropods). All mesocosms were placed 100 m from a natural wetland and allowed to colonize for 82 days. Facilitation of invertebrate colonization led to communities in inoculated and stocked + inoculated treatments that contrasted strongly with those in the unaided control treatment. Control mesocosms had the highest taxa richness but the lowest diversity due to high densities and dominance of *Tanytarsini* (Diptera: Chironomidae). Community structure in inoculated and stocked + inoculated mesocosms was more similar to that of a nearby natural wetland, with abundance more evenly distributed among taxa, leading to diversity that was higher than in the control treatment. Inoculated and stocked + inoculated communities were dominated by non-aerial invertebrates, whereas control mesocosms were dominated by aerial invertebrates. These results suggest that facilitation of invertebrate recruitment does indeed alter invertebrate community development and that facilitation may lead to a more natural community structure in less time under conditions simulating wetland restoration.

Key words: aquatic insects, colonization, Gastropoda, inoculation, macroinvertebrates, marsh, recruitment, restoration, stocking, wetland.

Introduction

Efforts to restore the community structure of degraded systems are often based on the untested assumption that providing the correct habitat structure will naturally lead to recovery of the appropriate community (i.e., the “If you build it, they will come” tenet, Palmer et al. 1997). However, recovery of a community may be limited by recruitment of organisms, and recruitment limitation can act as a control on local community structure (e.g., Ricklefs 1987; Palmer et al. 1996). Indeed, barriers to dispersal are now known to limit the success of many restoration efforts (e.g., Bradshaw 1996), especially when the restored system is isolated or has only limited connectivity to a functioning ecosystem.

Practices that enhance recruitment may increase the chances of restoration success. Establishment of direct connections between natural and restored areas are increasingly being used in restoration plans to facilitate ecosystem recovery (Keesing & Wratten 1998). But when degraded sites are isolated from a natural source of colonists and it is impractical to establish connectivity, how does one maximize the potential for normal community development? Two procedures, stocking and inocula-

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tion, have been used to facilitate the establishment of poorly dispersing taxa in restored areas. Direct stocking of target taxa has been successful and can allow restored areas to function like natural systems more quickly by facilitating the establishment of key species (Bradshaw 1996). However, stocking is often impractical because of (1) the difficulty of collecting all the fauna that should occur in an ecosystem; (2) the lack of knowledge about what species are most important to ecosystem recovery; (3) the lack of knowledge about the dispersal abilities of various species; and (4) the cost that direct stocking can entail. A second method for enhancing establishment of poor colonizers involves inoculating a site with small pieces of a similar natural ecosystem (Touart 1987; Bradshaw 1996; Brown et al. 1997). In many instances inoculation is more practical and cost effective than stocking because it has the potential to transplant many of the smaller and more ubiquitous members of a community in a single effort.

Stocking and inoculation through planting seeds and transplanting rhizomes and seedlings are common procedures in restoration of plant communities in wetlands (e.g., Reinartz & Warne 1993). Although some of these activities (e.g., use of plugs of rhizomes and soil) may also inoculate restoration areas with invertebrates, few studies have documented this inoculation. Stocking and inoculation of macroinvertebrates have recently been applied in wetland restoration projects in an effort to assist biological recovery (e.g., Brown et al. 1997). Although studies have assessed how these methods influence the recovery of target populations, there have been few rigorous tests to determine whether either method of facilitation (stocking or inoculation) has any effect on the development of entire communities. Because the functioning of a restored site will depend at least in part on community structure, it is important to determine whether these methods actually alter community development or are useful only in the recovery of individual target populations.

Attention is currently being focused on invertebrate communities during wetland restoration because invertebrates are known to have an important influence on the rates of nutrient cycling, primary productivity, decomposition, and the flux of energy between trophic levels in these ecosystems (Merritt et al. 1984; Murkin & Wrubleski 1988; Batzer & Wissinger 1996). Invertebrate communities similar to those found in natural wetlands develop rapidly in restored wetlands when restoration sites are adjacent to a remnant natural ecosystem (Paterson & Fernando 1969; Streever et al. 1996; Chovanec & Raab 1997). Restored wetlands that are more isolated, however, may develop invertebrate communities dominated by highly mobile taxa having aerial dispersal capabilities (Barnes 1983; Layton & Voshell 1991; Brown et al. 1997). Poorer dispersers, including most of

the non-insect invertebrates, are usually underrepresented in isolated restored wetlands (Barnes 1983; Brown et al. 1997). The lack of these taxa can lead to structural differences in the food web that may have important consequences for the recovery of ecosystem function (Palmer et al. 1997). A few pond and wetland projects have attempted inoculation with sediments from natural ponds and wetlands (Howick et al. 1992; Ferrington et al. 1994; Brown et al. 1997). The results of these studies, however, have been ambiguous because of experimental design constraints, including low replication and/or the inability to control sources of natural variation.

In the present study we used mesocosms to test whether inoculation only or inoculation plus stocking of a poorly dispersing taxa could alter the development of invertebrate communities in restored wetland sites. Our use of mesocosms allowed increased replication and reduced the number of confounding factors that have been associated with prior studies. The objectives of our study were (1) to determine whether inoculating a restored site with plugs of natural wetland vegetation and sediments would alter development of macroinvertebrate community structure relative to unassisted controls and (2) to determine whether inoculation plus deliberate stocking of a restored site with poorly dispersing taxa would modify invertebrate community development beyond that from simple inoculation.

Methods

The study site was located in southeastern Michigan just inland from Saginaw Bay, Lake Huron. Historically, this area was an extensive wetland complex characterized by wet prairies, coastal and inland emergent marshes, and forested swamps, bogs, and fens (Prince & Burton 1994). Over the past 150 years 70% of the inland wetlands have been diked, drained, and converted to farmland (Prince & Burton 1994). Because patches of natural wetlands remain as sources of colonists for restored areas, much of the area was being considered for wetland restoration by Michigan's Department of Natural Resources (Prince & Burton 1994). Thus, we chose this site for determining the influence of inoculation and stocking on the development of wetland invertebrate communities.

Plastic wading pools (1.5 m diameter \times 0.25 m deep) were used to create 15 wetland mesocosms alongside a corn field that was cultivated by local farmers through a cooperative agreement with the Michigan Department of Natural Resources Fish Point Wildlife Management Area (with parts of the crop left for waterfowl feeding during migration). The mesocosms were approximately 100 m from a remnant natural wetland. Topsoil from the corn field was used for soil in our mesocosms to

simulate wetland restoration of drained agricultural soils. The soil was contoured to form a water depth gradient that ranged from saturated soil with no overlying water to 15 cm water depth in each mesocosm. Mesocosms were filled with filtered water (approximately 150 μm mesh) from a nearby agricultural ditch and were refilled one to two times weekly during the experiment to replace evaporative losses.

Five replicate mesocosms were randomly assigned to one of three treatments: control, inoculated, or stocked + inoculated. Control mesocosms received only agricultural soils and filtered water to simulate the unaided development of invertebrate communities on a reflooded agricultural field. The only nearby sources of wetland invertebrate colonists for these mesocosms were a drainage ditch and the remnant wetland—a palustrine emergent marsh with wet meadow zones dominated by *Carex* spp. (sedges) and deeper water areas containing islands of *Typha latifolia* (broadleaf cattail). The inoculated mesocosms received agricultural soil and water as described for control mesocosms but were also inoculated with three vegetation/sediment cores (10 cm diameter \times 10 cm depth) taken from the wet meadow zone of the remnant natural wetland and embedded into the soil of the mesocosms. Our assumption was that these cores would contain a representation of the natural wetland fauna and/or their propagules and would facilitate the establishment of populations of poorly dispersing non-aerial taxa. Stocked + inoculated mesocosms received agricultural soil, water, and the vegetation/soil cores (as described for inoculated mesocosms) but in addition were stocked with 25 snails added according to their relative abundances in the remnant natural wetland (18 *Stagnicola* and/or *Fossaria*, 5 *Physa*, 2 *Helisoma*). Snails were selected as representative poor dispersers because they were the most abundant non-aerial invertebrates in the natural wetland. Thus, stocked + inoculated mesocosms were used to discern whether direct addition of a poorly dispersing invertebrate would alter community development relative to both unaided recovery (i.e., control mesocosms) and/or relative to mesocosms receiving an inoculum only (i.e., inoculated mesocosms).

The experiment began on 30 May 1995 and continued until 20 August 1995. Thus, invertebrates were allowed to naturally colonize all mesocosms for 82 days. Although this duration was probably sufficient to allow colonization and establishment of most strongly dispersing taxa (Williams 1987; de Moor 1992), our study did ignore those species having seasonal emergence in the fall or spring. Emergent and wet meadow macrophytes grew rapidly in all the mesocosms. We did not quantitatively sample the vegetation in this experiment due to time constraints; however, we could observe no qualitative differences in vegetation density or composition between treatments after only a few weeks.

On the final day of the experiment, basic chemical and physical parameters (dissolved oxygen, turbidity, conductivity, alkalinity, temperature, and pH) were measured to determine whether environmental conditions were similar among treatments, the natural wetland, and the source of water. Only turbidity differed among treatments, and conductivity was somewhat higher in mesocosms than in the ditch due to evaporation (V. Brady, unpublished data). We then sampled the invertebrate community in each mesocosm by sweeping 250- μm mesh nets through the water column, the submersed portion of the vegetation, and the top 5 mm of inundated sediment. Netting in each mesocosm continued until we could capture no additional animals. The invertebrate community in the natural wetland was also sampled with a 250- μm mesh dip net. Five 1-m sweeps were made through the water column, submersed vegetation, and surficial sediments in each of four shallow water habitats. The contents of all 20 sweeps were combined to form one composite sample from the natural wetland.

Invertebrates were subsampled (one sixth of each sample by volume) and identified to lowest operational taxonomic unit (Thorp & Covich 1991; Merritt & Cummins 1996). Chironomidae were subsampled again (one fifth of chironomids by volume) if there were more than 20 chironomid larvae and were identified to tribe. We tested for differences in the taxonomic composition of invertebrate communities among treatments with one-way analysis of variance (least-squares means procedure using SAS [SAS Institute 2000]). Dependent variables included the number of taxa, Simpson's diversity index, richness and abundance of non-aerial taxa, total invertebrate abundance, and abundances of individual taxa. Because abundance data were not normally distributed, densities were $\log(x + 1)$ transformed before testing. Taxa whose distributions were non-normal after transformation were tested non-parametrically (Kruskal-Wallis test). An alpha level of 0.05 was used for all analyses.

We used two similarity indices, the percent similarity index (PSI) and Morisita's index, to compare the communities in each of the mesocosms with the community in the natural wetland. Each of the two indices emphasizes a different aspect of community structure. The PSI compares the relative abundance of taxa shared between two communities. Morisita's index also compares community structure between two communities, but it is more sensitive than the PSI to differences in rare taxa and is relatively insensitive to differences in total abundance between samples (Brower et al. 1990). We calculated community similarity between each mesocosm and the composite natural wetland sample, resulting in five replicate measures of similarity for each treatment from each index. These five replicate measures were compared among treatments using analysis of variance (fol-

Table 1. Taxa collected from wetland mesocosms and a nearby natural wetland.

Taxon	Control	Inoculated	Stocked + Inoculated	p	Natural Wetland
Gastropoda (snails; total)	18.8 (0–64)a	213.1 (71–514)b	168.8 (75–382)b	0.0012	54
Lymnaeidae <i>Fossaria</i>	a	42.0 (0–71)b	7.5(0–30)a	0.022*	15
<i>Stagnicola</i>	0.8 (0–4)a	5.3 (0–19)a	51.0 (15–79)b	0.0002	15
Physidae <i>Physa</i>	18.0 (0–60)a	165.0 (23–424)b	102.0 (4–311)b	0.035	6
Planorbidae <i>Helisoma</i>	a	0.8 (0–4)a	8.3 (0–19)b	0.022*	18
Bivalvia (clams) Sphaeriidae					168
Annelidae (segmented worms)					
Oligochaeta Naididae	98 (0–480)		126.8 (0–555)		13
Hirudinea (leeches) Erpobdellidae		1.5 (0–8)	1.5 (0–8)		6
Hydracarina (mites)		1.5 (0–8)	1.5 (0–8)		3
Collembola (springtails)	1.5 (0–4)		0.8 (0–4)		
Ephemeroptera (mayflies)					
Baetidae	30.2 (0–64)	38.4 (8–90)	48.0 (4–98)		30
Caenidae <i>Caenis</i>					30
Odonata (dragonflies and damselflies; total)	297.0 (97–671)a	64.6 (15–142)b	30.8 (4–45)b	0.0012	18
Aeshnidae		0.8 (0–4)			
Libellulidae <i>Orthemis</i>	18.0 (0–49)	10.5 (0–23)	0.8 (0–4)		6
Coenagrionidae	279.0 (71–626)a	53.3 (11–124)b	30.0 (15–41)b	0.0022	12
Hemiptera (true bugs; total)	48.8 (19–117)a	7.6 (4–12)b	10.5 (4–22)b	0.003	25
Veliidae	18.8 (0–52.5)a	b	b	0.032*	
Corixidae	7.5 (0–11)	2.3 (0–8)	1.5 (0–4)		18
Notonectidae	9.0 (0–26)	1.5 (0–4)	3.0 (0–11)		6
Mesoveliidae <i>Mesovelia</i>	13.5 (4–30)	3.8 (0–11)	6.0 (0–11)		1
Trichoptera (caddisflies) Hydroptilidae					4
Coleoptera (beetles; total)	110.4 (41–187)a	21.3 (18–34)b	18.9 (4–45)b	0.0016	1
Halipilidae <i>Halipilus</i>	78.8 (11–143)a	11.3 (4–26)b	13.5 (4–34)b	0.007	
Dytiscidae <i>Hydroporus</i>	1.5 (0–8)		0.8 (0–4)		
<i>Laccophilus</i>	7.5 (0–19)	5.3 (4–8)	3.0 (0–8)		
<i>Rhantus</i>	14.3 (0–38)		0.8 (0–4)		
Unidentified		0.8 (0–4)			1
Hydrophilidae <i>Berosus</i>	3.8 (0–15)	0.8 (0–4)			
<i>Laccobeus</i>		0.8 (0–4)			
<i>Tropisternus</i>	1.5 (0–4)	0.8 (0–4)	0.8 (0–4)		
Unidentified	3 (0–15)	1.5 (0–8)			
Diptera (flies)					
Ceratopogonidae (biting midges)	79.6 (15–146)a	0.8 (0–4)b	4.4 (0–11)b	0.0001	2
Chironomidae (midges; total)	2,008.5 (705–3,375)a	45.9 (0–199)b	12.8 (0–30)b	0.0001	27
Tanytopodinae	21.8 (0–36)a	0.8 (0–4)b	b	0.016*	2
Orthocladiinae	2.4 (0–8)	0.8 (0–4)			18
Chironomini	44.4 (0–84)a	b	b	0.016*	
Tanytarsini	1,939.9 (611–3,220)a	44.3 (0–184)b	12.0 (0–26)b	0.0001	3
Culicidae (mosquitoes; total)	11.3 (4–19)a	b	b	0.001*	
<i>Anopheles</i>	6.8 (0–19)a	b	b	0.007*	
Culicinae	4.5 (0–11)				
Tabanidae (deer and horse flies)	0.8 (0–4)				
Isopoda (sowbugs)					6
Total invertebrates	2,702.9 (1,549–4,339)	393.2 (229–638)	424.3 (180–810)		512

Different letters denote significant differences among means at the given *p* value. Treatment values are means/m² (range) and wetland values are number per sample. *Kruskal-Wallis test statistic.

lowing arcsine transformation; Sokal & Rohlf 1995). Because the mesocosms and the natural wetland were sampled differently, it is important to note that accurate estimates of similarity were not possible. However, our interest was in making relative comparisons among the treatments regarding their similarity to the natural wet-

land. Because all mesocosms were sampled identically and were compared with the same composite sample from the natural wetland, any differences among treatments in their relative similarity to the natural wetland must represent real effects of the treatments, rather than differences in sampling methodology.

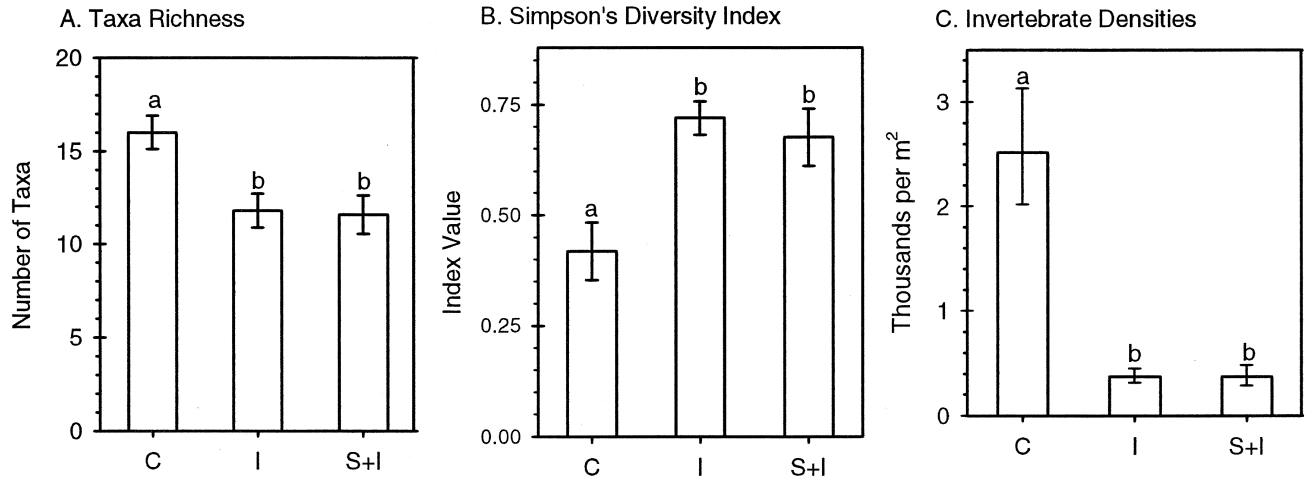


Figure 1. (A) Richness, (B) diversity, and (C) abundance of macroinvertebrate communities in wetland mesocosms (mean \pm SE). C, control; I, inoculated; S+I, stocked + inoculated. Different superscripts denote significant differences among means ($p \leq 0.01$).

Results

After 82 days of the experiment, 32 aquatic invertebrate taxa had colonized the wetland mesocosms (Table 1). There were significant differences in the taxonomic richness of the communities in control mesocosms and those in the inoculated and stocked + inoculated mesocosms. Communities in control mesocosms had an average of 16 taxa, whereas inoculated and stocked + inoculated mesocosms averaged 11.8 and 11.6 taxa, respectively (Fig. 1A). Several of the taxa found in control mesocosms were not collected from the natural wetland, suggesting they had arrived from more distant locations. Indeed, most of these taxa (genera of mosquitoes [Culicidae], beetles [Coleoptera], and dragonflies/damselflies [Odonata]) are adapted for migrating long distances to colonize small temporary wetlands (Barnes 1983; de Moor 1992; Batzer & Wissinger 1996).

Although control mesocosms contained more taxa, diversity (Simpson's index) was higher in inoculated and stocked + inoculated treatments (Fig. 1B). Higher diversity in inoculated and stocked + inoculated treatments was due to a more even distribution of densities among taxa. Low diversity in control mesocosms was caused by the dominance of *Tanytarsini* (midges [Diptera: Chironomidae]), whose presence contributed to the much higher invertebrate densities in these mesocosms (Fig. 1C). In contrast, *Tanytarsini* were nearly absent from inoculated and stocked + inoculated mesocosms (Fig. 2A, Table 1). Significantly higher densities in controls were also observed for five other groups of invertebrates: biting midges [Ceratomyxidae], mosquitoes [Culicidae], true bugs [Hemiptera], dragonflies and damselflies [Odonata], and beetles [Coleoptera]; Fig. 2, B–F). Gastropods (snails) were the only group with higher densities in inoculated

and stocked + inoculated mesocosms (Fig. 2G, Table 1). The only macroinvertebrate group whose densities were not significantly different among treatments was Ephemeroptera (mayflies; Fig. 2H), even though there was a trend toward lower densities in the controls.

Treatment differences were also apparent in the colonization pattern of aerial and non-aerial invertebrates in that more aerial taxa were collected from control mesocosms (Fig. 3). Fifteen aerial taxa were identified from the natural wetland; however, only an average 9.7 taxa colonized the control mesocosms. Even fewer aerial taxa (6.5 or less) were found in the inoculated and stocked + inoculated mesocosms (Fig. 3A). Conversely, inoculated and stocked + inoculated mesocosms contained a greater number of non-aerial invertebrates. Invertebrates without aerial dispersal abilities comprised less than 3% of control communities but dominated inoculated and stocked + inoculated communities (50 and 65%, respectively; Fig. 3C). Stocked + inoculated mesocosms averaged 4.2 non-aerial taxa (Fig. 3B), representing almost half of the nine non-aerial colonists found in the natural wetland (Table 1). Inoculated mesocosms had significantly fewer non-aerial taxa than stocked + inoculated mesocosms (2.8 vs. 4.2) but a slightly higher number than controls (2.8 vs. 1.6).

Community composition was also quite distinct among treatments due to differences in the relative abundance of several taxonomic groups. Gastropods, the primary non-aerial taxa facilitated by stocking and inoculation, became the dominant invertebrates in facilitated mesocosms, whereas chironomids dominated control mesocosms (Fig. 4). Hemiptera, Coleoptera, and Odonata were subdominant groups in control communities, whereas these groups plus Ephemeroptera were the subdominant components of facilitated communities.

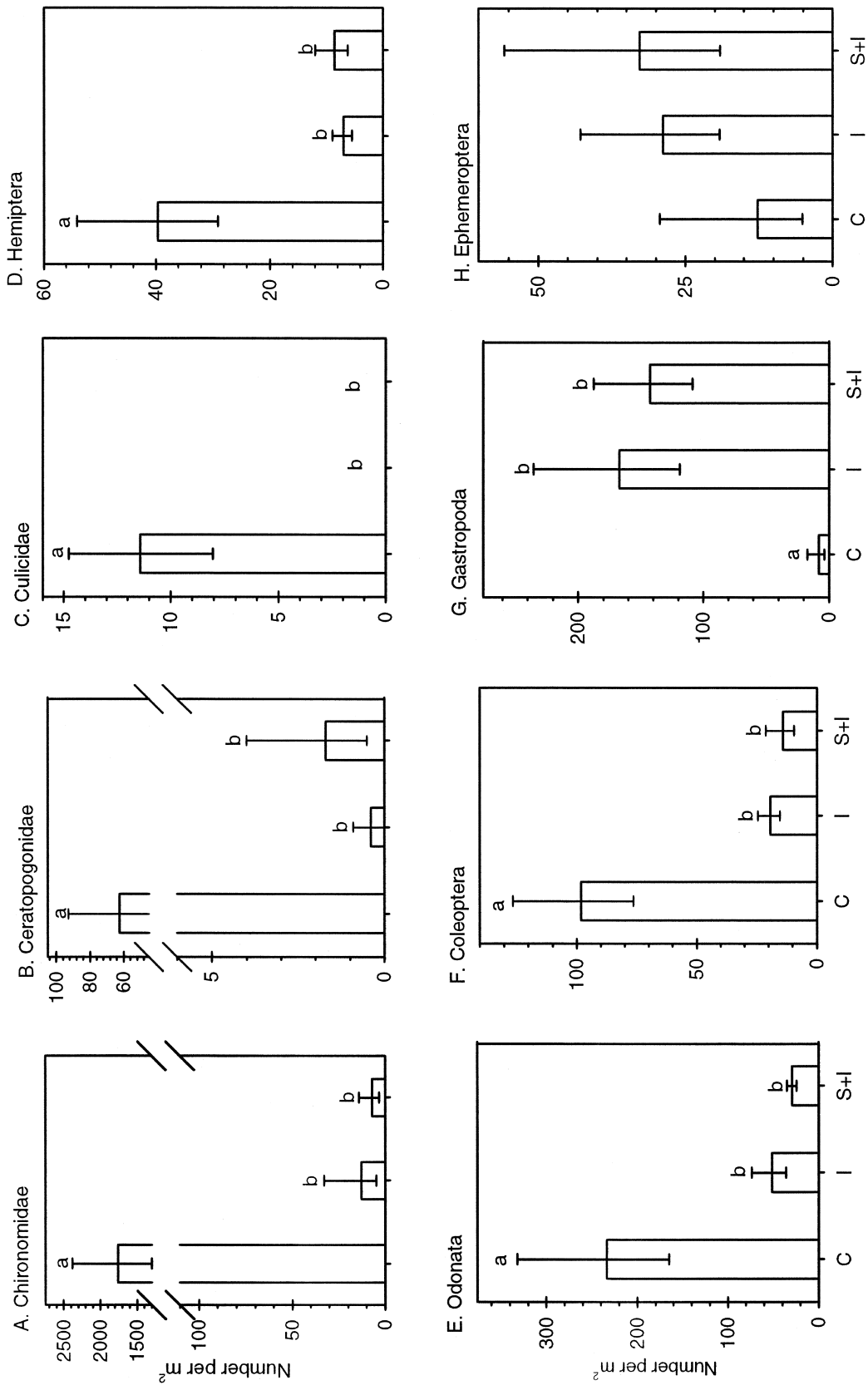


Figure 2. (A-H) Abundance differences (mean \pm SE) of selected macroinvertebrate taxa in wetland mesocosms. C, control; I, inoculated; S+I, stocked + inoculated. Different superscripts denote significant differences among means ($p \leq 0.005$).

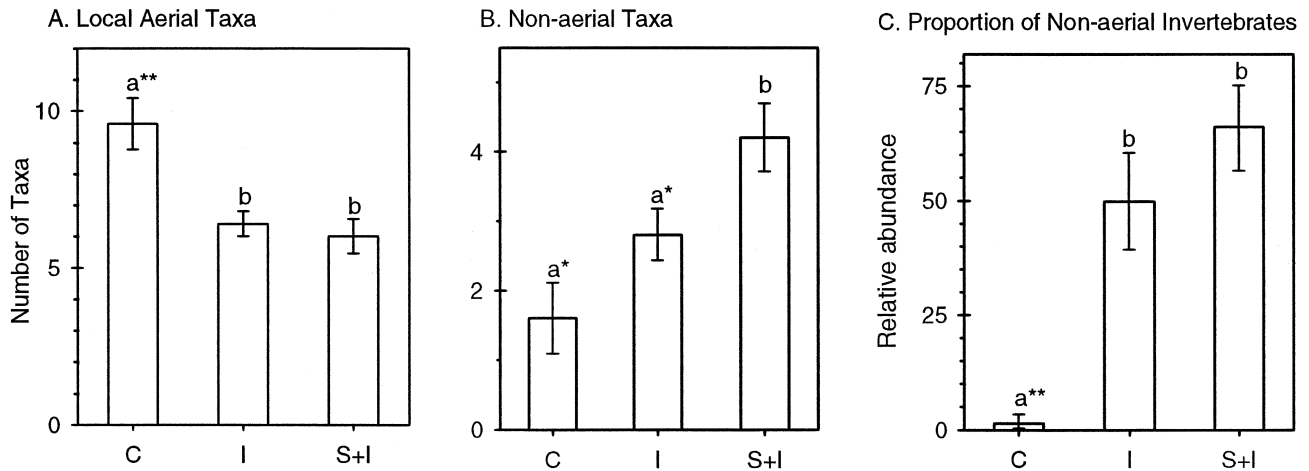


Figure 3. (A-C) Richness and proportional abundance of (A) aerial and (B) non-aerial invertebrates in wetland mesocosms. C, control; I, inoculated; S+I, stocked + inoculated. Different superscripts denote significant differences among means: * $p \leq 0.05$, ** $p \leq 0.01$.

Mesocosm communities were compared with the invertebrate community in the natural wetland using community similarity indices. To determine whether treatments differed in their similarity to the natural wetland, we tested for differences among similarity values. Tests of the PSI and Morisita's index showed that controls were less similar to the natural wetland than were the other two treatments. The PSI, which compares the relative abundances of shared taxa, showed that inoculated and stocked + inoculated treatments averaged 17 or 20% similarity, respectively, to the natural wetland community, whereas controls averaged only 7% similarity (Fig. 5A). Low similarities were due,

in large part, to the absence of caenid mayflies, Sphaeriidae (fingernail clams), Isopoda (sowbugs), and Hirudinea (leeches) in all treatments (Table 1, Fig. 4). An identical pattern was found using Morisita's index, which gives greater weight to rare taxa (Fig. 5B). These indices suggest that community structure was closer to that of the natural community in the inoculated and stocked + inoculated mesocosms.

Discussion

Restoration efforts have often assumed that small organisms such as invertebrates, fungi, and bacteria are

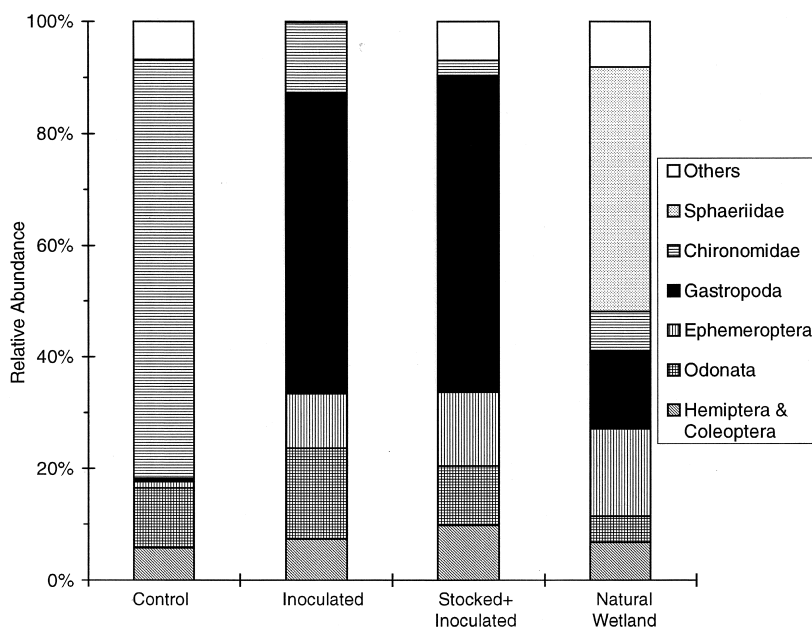


Figure 4. Macroinvertebrate community composition in wetland mesocosms. The community in a nearby natural wetland is included for comparison.

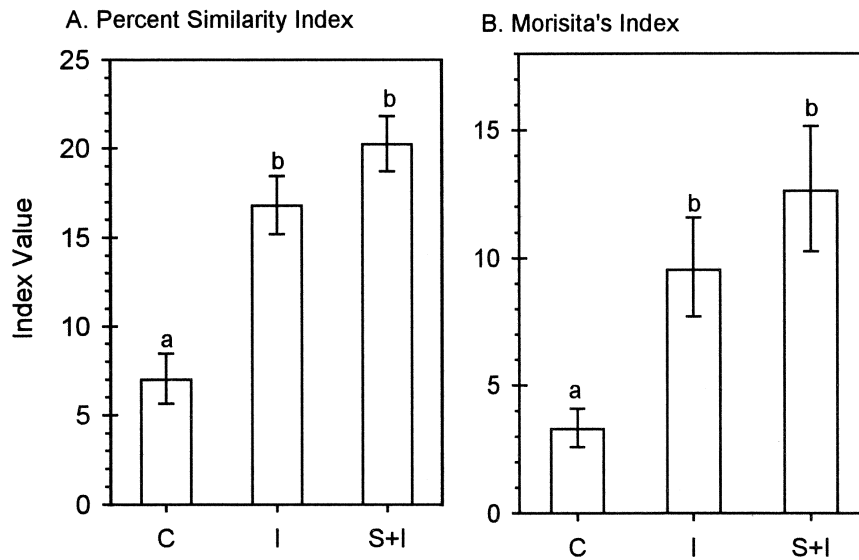


Figure 5. (A-B) Community similarity comparison between each treatment community and the natural wetland community. Values represent index means \pm SE. C, control; I, inoculated; S+I, stocked + inoculated. Different superscripts denote significant differences among means ($p \leq 0.005$).

ubiquitous—able to naturally recolonize a restored area if the proper habitat is provided (Keesing & Wratten 1998). Indeed, the predominant logical sequence that underlies most restoration efforts is as follows: (1) Providing proper habitat will (2) naturally lead to recolonization of fauna, which will (3) lead to normal community structure, which (4) then leads to proper “functioning” of a restored site (e.g., Bradshaw 1996; Palmer et al. 1997; Keesing & Wratten 1998). Yet, there is growing evidence that this sequence of logic is fundamentally flawed (e.g., Palmer et al. 1997; Keesing & Wratten 1998). Just one of many problems is that it does not account for the potential barriers to dispersal that might limit the successful reestablishment of taxa in a restored site. For example, aquatic invertebrates that lack an aerial dispersal stage in their life cycle may have difficulty recruiting to a restored site. This can lead to major differences in community structure between restored and natural wetlands (e.g., Layton & Voshell 1991; Christman & Voshell 1993; Brown et al. 1997) that can persist for long periods of time (e.g., Barnes 1983). Such differences could lead to dominance by different functional groups of organisms with major consequences for the recovery of ecological processes in a restored wetland site.

One potential solution to the problem of recruitment limitation is to assist colonization by “seeding” or “inoculating” isolated restored sites with small amounts of material from similar natural systems (Touart 1987; Brown et al. 1997). Because the effectiveness of this method has not been studied, one goal of our experiment was to investigate whether development of a wetland invertebrate community could be altered by inocu-

lating wetland mesocosms with fragments of a natural wetland. We found that, after 82 days of colonization, mesocosms inoculated with cores of wetland vegetation and sediment were dominated by non-aerial taxa whose colonization had been facilitated by inoculation. Mesocosms allowed to colonize naturally, in contrast, were dominated by invertebrates with an aerial dispersal stage. As a result, there were significant differences in community structure between inoculated and control mesocosms.

Although adding an inoculum did increase non-aerial invertebrate colonization of mesocosms, this inoculation only assisted a select few invertebrate taxa, primarily gastropods. Mesocosm colonization by several other major groups of non-aerial invertebrates inhabiting the natural wetland (Sphaeriidae, Isopoda, Hirudinea, and Hydracarina) was not assisted by inoculation. We are uncertain as to whether these taxa did not recruit because of the lack of propagules in the cores added to the mesocosms or because of low survival after addition. Brown et al. (1997) also found that inoculation of wetland restoration sites with soil from vegetated drainage ditches provided little assistance to many non-aerial invertebrates. These results suggest that inoculum should be collected over a sufficient area to encounter propagules of scarce taxa and that successive inoculations may be necessary.

Another solution to low recruitment by poorly dispersing taxa is to collect and directly stock individuals to a restored site. We found that stocking four gastropod genera into mesocosms resulted in little change beyond simple inoculation. Because the target taxa for stocking

(gastropod genera) were the same taxa most facilitated by inoculation, few differences were apparent between these two techniques. Stocked + inoculated and inoculated treatments were indistinguishable from each other with respect to taxonomy, community structure, and their similarity to the natural wetland. Although we would conclude from this experiment that there was no additional benefit to be gained from stocking relative to simple inoculation, we emphasize that this conclusion might have been different had we chosen to stock other taxa such as sphaeriids or isopods.

Our experiment did, however, provide clear evidence that facilitation of colonization through inoculation with plugs of sediment and vegetation resulted in very different communities from those that were allowed to develop naturally. These communities differed from unfacilitated communities in many ways: They had lower species richness but higher diversity as a result of greater evenness, they contained more non-aerial invertebrates, and they had community structures that were more similar to those in the natural wetland. Perhaps the most striking difference between facilitated and control mesocosms was community dominance: Facilitated mesocosms became dominated by Gastropoda, whereas control communities became dominated by a single group of Chironomidae (Tanytarsini). Numerical dominance by Chironomidae in newly created or restored wetlands is quite common (e.g., Street & Titmus 1979; Barnes 1983; Layton & Voshell 1991). Thus, the virtual lack of chironomids in the facilitated treatments seems quite unusual and may be related to the dominance of these mesocosms by gastropods. Other researchers have shown that gastropods can reduce chironomid densities by 33 to 90% due to both competition for food and interference (Cuker 1983; Harvey & Hill 1991). Tube-dwelling taxa such as the Tanytarsini are particularly vulnerable to "bulldozing" by snails (Cuker 1983; Hawkins & Furnish 1987; Harvey & Hill 1991). So it seems plausible that assisting gastropod colonization resulted in decreased chironomid density that, in turn, led to major shifts in the taxonomic structure of the facilitated communities. It is also possible that reduced chironomid density had bottom-up effects on the densities of predators such as Ceratopogonidae, Odonata, Hemiptera, and some Coleoptera, which were much less abundant in facilitated mesocosms. To the extent these hypotheses are true, they provide a mechanism by which facilitation of poorly dispersing taxa can result in substantial changes to the structure and potentially the biological functioning of a community.

Overall, similarity between mesocosms and the natural wetland community was fairly low, possibly due to the short duration and timing of our experiment. The duration of this study was less than that of other studies comparing restored and natural wetlands (e.g., Barnes

1983; Howick et al. 1992; Brown et al. 1997), and this may have precluded colonization by some slowly dispersing taxa. The timing of our experiment may have also precluded colonization by aerial invertebrate taxa that have fall or spring emergence. Despite these potential limitations, it is interesting that community structure was more similar among facilitated mesocosms and the natural wetland than between control mesocosms and the natural wetland. Two indices that emphasize different aspects of community structure showed that, with respect to the controls, the facilitated mesocosms were more similar to the natural wetland in the relative abundances of their shared taxa. This greater community similarity suggests that inoculation provided facilitated mesocosms with a "jump start" that resulted in the development of more natural communities by the end of the experiment. However, it is impossible to predict whether this difference between facilitated and control communities would have persisted had the experiment been allowed to continue or if it would have diminished as a greater fraction of the regional species pool colonized the mesocosms.

In summary, the results of this study show that addition of inoculum from a natural wetland to sites being restored can alleviate recruitment limitation of some important taxa that are poor dispersers and can lead to communities that are very different from those of unassisted communities. Our data also suggest that assistance of invertebrate colonization may lead to communities that more closely approximate those of a natural wetland, at least in the short term. Because inoculation potentially assists invertebrate community development, it may also speed the restoration of many wetland ecosystem functions. We agree with Brown et al. (1997) and give guarded endorsement of inoculation to assist invertebrate community development in situations where there are no remnant populations to aid non-aerial colonization and where inoculum can be obtained without destroying extant wetlands.

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