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ORIGINAL PAPER

Influences of upland timber harvest on aquatic invertebrate communities in seasonal ponds: efficacy of forested buffers

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Abstract We assessed community responses of aquatic invertebrates in 16 small, seasonal ponds in a forested region of north central Minnesota, USA, to evaluate potential influences of timber harvest and efficacy of uncut forested buffers in adjacent uplands. Invertebrate data gathered before (2000) and during the first 4 years following clearcut timber harvest (2001–2004) indicated that tree removal was followed by shifts in aquatic invertebrate communities in adjacent seasonal ponds. Retention of forested buffers appeared to partially mitigate influences of tree removal, but benefits of buffers may be limited by wind throw or other factors. Additional research is needed to clarify relationships between ecological characteristics of seasonal ponds and upland silviculture activities, and to better document efficacy and longevity of forested buffers.

Keywords Aquatic invertebrates · Buffers · Indicator species analysis · Multiple response permutation procedure · Ordination · Seasonal forest pond · Timber harvest

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Introduction

Small seasonally flooded wetlands (sensu Stewart and Kantrud 1971, hereafter seasonal ponds) are abundant in many forested landscapes and provide unique habitat for biological communities (Gibbs 1993; Brooks et al. 1998; Palik et al. 2003, 2007; Tiner 2003). This habitat dependence results, in part, from the short hydroperiods in seasonal ponds that exclude fish and other predators, favoring communities of organisms with little tolerance for vertebrate (and even invertebrate) predation (Wiggins et al. 1980; Wellborn et al. 1996). These sites typically occur in localized depressions, are usually isolated from adjacent waters, fill during spring from snow-melt, and then dry due to evapotranspiration by early-midsummer, sometimes filling again in the fall. Until recently, these sites were often overlooked by forest

managers who were unaware of their ecological significance or the potential consequences of silviculture in adjacent uplands (Batzer et al. 2000).

Palik et al. (2001) suggested that processes and organisms in small seasonal ponds are strongly influenced by adjacent forested uplands. As for small streams, the potential for influence of the adjacent upland forest on seasonal ponds is large due to high edge-to-area ratios (Polis et al. 1997). High amounts of edge increase the importance of functional linkages with the adjacent forest through evapotranspiration, shading, and organic matter inputs. For example, seasonal ponds gain much of their energy from litter originating in adjacent uplands (Oertli 1993; Palik et al. 2006), thus annual leaf fall may be the major energy source for many resident organisms. An adjacent overhead canopy also mediates light availability at the pond surface and may influence vegetation composition and dynamics (Palik et al. 2001, 2007).

It follows that timber harvesting in adjacent uplands has potential to alter ecological processes and communities in embedded seasonal ponds by modifying light regimes, water chemistry, and litter inputs (Semlitsch and Bodie 1998; Batzer et al. 2000; Palik et al. 2001) and perhaps pond hydrology (Hanson et al. 2009). These changes in turn may influence resident organisms and communities as they do in small streams (Webster et al.1990; Wallace et al. 1997; Kiffney et al. 2003). For instance, timber harvest adjacent to small depressional ponds in Georgia increased light availability, water temperatures, pH, and coverage by emergent macrophytes (especially *Carex*, Batzer et al. 2000). It seems plausible that such chemical, physical, and biological responses have potential to induce changes in aquatic invertebrate abundance or community composition. In fact, abundances of several macroinvertebrate taxa in small seasonal ponds in northern Minnesota have been shown to vary as a function of canopy openness (Palik et al. 2001; Batzer et al. 2004; Hanson et al. 2009). Macroinvertebrates in seasonal ponds provide a key protein source for female and immature ducks (Krapu and Reinecke 1992), thus changes in abundance and composition of invertebrates have implications for waterfowl nutrition and recruitment throughout forested regions of North America and elsewhere.

Retention of buffers around small seasonal ponds may mitigate invertebrate responses by limiting environmental changes following adjacent timber harvest. Philippi et al. (1998) suggested that changes in species composition may be a useful indicator of environmental disturbance. Along these lines, retention of riparian buffers along headwater streams has been shown to maintain pre-harvest light regimes, litter and nutrient inputs, water temperature patterns, primary production, periphyton characteristics, and other processes (Wallace and Gurtz 1985; Stone and Wallace 1998; Wenger 1999; Kiffney et al. 2004). Stream insects, in turn, benefit from forested buffers, at least if this can be inferred from lack of change in these communities following timber harvesting (Kiffney et al. 2003). It is reasonable to expect that aquatic invertebrate communities in small seasonal ponds should also benefit from retention of upland forested buffers. In fact, forested buffers, or aggregate patches of mature trees adjacent to small seasonal ponds, have been suggested as a tool useful for minimizing effects of pond disturbance associated with timber harvesting (Dodd and Cade 1998; Semlitsch 1998; Minnesota Forest Resources Council 1999). However, we are aware of no previous studies evaluating efficacy of forested buffers as a means of limiting community change, thus protecting the integrity of aquatic invertebrate communities in small seasonal ponds.

With this need in mind, we studied influences of upland timber harvests on invertebrate communities of small seasonal ponds in north central Minnesota, specifically assessing whether retention of forested buffers (uncut and partially cut) mitigated short-term changes in these communities. We evaluated these relationships using a planned silvicultural experiment including both replicated treatments and control ponds to measure mitigating effects of forested buffers. We hypothesized that (1) adjacent upland timber harvest would lead to changes in invertebrate communities of embedded seasonal ponds during years immediately following harvest and (2) uncut forested buffers around ponds would mitigate resulting changes, while partially cut buffers would mitigate changes to a lesser extent.

Methods

Study sites and experimental design

Seasonal ponds were selected for study in Aitkin and Cass Counties, in north central Minnesota. This

region has been classified as the Northern Minnesota Drift and Lake Plains Section and is characterized by thick but variable (60–180 m) glacial till forming extensive areas of lakes, deep wetlands, and shallow, seasonal ponds (Almendinger and Hanson 1998). Vast forests remain, especially in till plains and moraine areas. Fire and weather extremes were historically the major disturbance mechanisms, but management activities, and especially timber harvesting, are currently the most important determinants of forest composition, age structure, and extent (White and Host 2003).

Study ponds were chosen to be as similar as possible in terms of hydroperiods, extent and composition of hydrophytes, and cover types of adjacent upland forest. Ponds flooded during snow-melt and most dried by 1 July each year. Sedges (*Carex* spp.) were the predominant non-woody hydrophytes, but occurred only in small stands in some sites. All ponds were embedded within mature (60–70-year-old) aspen (*Populus tremuloides* Michx.) forest prior to timber harvest. Our design included 4 blocks of mature upland forest, each containing at least 4 seasonal ponds. Each block was approximately 64 ha in area and was divided into 4 16-ha treatment stands. One pond within each stand was assigned to each of the following treatments; control (uncut forest), full buffer, partial buffer, and clearcut. The full buffer treatment consisted of an upland clearcut with a 15-m uncut zone around the pond margin, beginning at the seasonal high water mark and extending into the adjacent upland forest. The partial buffer treatment was similar, except that 50% of the basal area was removed within the 15-m buffer zone. In the clearcut treatment, the forest was harvested up to the pond margin. Prior to harvest, mean canopy openness was measured over each pond using spherical densiometers. All harvesting was done during December 2000–January 2001 on frozen ground with an approximately 60-cm snowpack.

Aquatic invertebrate sampling and enumeration

Aquatic invertebrates were collected at least 3 times each growing season during April–May 2000–2004 using surface-associated activity traps (SATs) (Hanson et al. 2000). SATs perform well in shallow water, accommodate water level fluctuations, and simultaneously gather organisms at and below the water surface. At each sampling, we deployed 1 SAT along each of five randomly chosen transects in each pond. Water depths at SAT locations varied, but were rarely >0.5 m, and depths often decreased to <10 cm by late May. SATs were deployed for 24 h by attachment to PVC frames fastened in sediments. Trap contents were retrieved and condensed in the field using a 0.4 mm-mesh sieve, then stored in 80% ethanol. We combined numbers of invertebrates collected from 5 SATs, producing a single relative abundance value for each pond on each sampling date. Sampling began each year approximately 2 weeks after ice-out, and each pond was then sampled every 2-weeks until no standing water remained. This resulted in a total of 3–5 sampling efforts each year. Sample contents were examined under a dissecting microscope. Invertebrates were identified to the lowest feasible taxonomic level, typically family or genus using the keys of Thorp and Covich (2001), Hilsenhoff (1995), Merritt and Cummins (1996), and Pennak (1989). To reduce complexity of the invertebrate data, we aggregated related organisms, and the resulting 16 variables were used as responses for all analyses. Aggregate taxa corresponded to feeding guilds and life-history groups and were generally similar to those reported by Hanson et al. (2009) from work in similar pond sites. We chose peak seasonal abundance (highest annual abundance count from among 3–5 sampling dates) for each of these 16 taxa in each pond and these values were averaged across replicate sites for each treatment group (control, full buffer, partial buffer, and clearcut), resulting in a single peak abundance estimate for each treatment in each year. Temporal variability is a major source of variance in wetland invertebrate communities and differences among sampling periods sometimes exceed that among wetland sites (Miller et al. 2008). We used peak seasonal abundance to guard against bias resulting from our inability to simultaneously sample all pond sites on a single date.

Data and statistical analysis

To assess efficacy of forested buffers, we compared aquatic invertebrate communities in study ponds assigned to control, full buffer, partial buffer, and clearcut treatments. Our primary concern was detecting community-level responses to harvest. We reasoned that patterns among treatment groups (for example, similarity between control and buffer

ponds) would indicate whether buffers were preventing community changes following adjacent harvest. We used several multivariate techniques to assess changes among harvest treatments, in other words, to determine whether treatment groups differed and which invertebrate taxa were affected by harvest.

First, we used nonmetric multidimensional scaling (NMS) to determine whether forested buffers mitigated community-level changes in pond invertebrates in response to adjacent treatments. We chose this ordination approach because it relaxes assumptions of normality and linear relationships to environmental variables, provides a biologically meaningful visual summary of data, and preserves distance properties among sample units (ponds, in our case) (Clarke 1993; McCune and Grace 2002). NMS was performed using PC-ORD 5.0 (McCune and Mefford 1999). We used Sorenson (Bray-Curtis) distance measures, and specified 6 dimensions and 250 iterations (with actual data) for initial analyses. Significance of dimensional solutions was assessed using Monte Carlo permutation procedures (based on 249 interactions). Our final ordination was restricted to 3 dimensions based on stress reduction and examination of scree plots (McCune and Grace 2002). Lines connecting treatment/year combinations in our final ordination (NMS) depicted chronological sequences, illustrating trends among treatment groups during the 5 years of our study.

Following NMS, we used a multi-response permutation procedure (MRPP, Biondini et al. 1988) to test differences among treatments indicated by the NMS ordination. MRPP is a nonparametric procedure useful for comparisons among previously defined groups of sampling units (McCune and Grace 2002). Using MRPP, we compared mean peak abundance of our response taxa during 2003 and 2004 because treatments during these years showed the most separation along NMS axes. MRPPs were based on Sorenson (Bray-Curtis) distance measures and performed using PC-ORD 5.0. Following significant *P*-values, we used pair-wise comparisons to clarify differences among treatment groups; significance of MRPP results was inferred at $P < 0.05$.

Finally, to identify taxa responsible for treatment patterns (NMS and MRPP), we performed Indicator Species Analysis (ISA, Dufrêne and Legendre 1997) using PC-ORD 5.0. Again, we used mean peak abundance from 2003 and 2004 (post-harvest years 3 and 4, as for MRPP) because NMS showed most separation between invertebrate scores during these years. ISA is a randomization technique that calculates indicator values for each taxon based on its relative abundance and relative frequency within each treatment. Indicator values represent % of perfect indication of a taxon in user-defined treatments and range from 0 to 100. An indicator value of zero means that no members of a taxon were found within a treatment group; a value of 100 means that a taxon is always present (thus is a perfect group indicator). ISA values for each taxon are calculated independently of other taxa, thus indicator values based upon the a priori groups is a significant advantage of ISA (McGeoch and Chown 1998). Trends in resulting values were then tested using Monte Carlo permutation procedures and we assessed significance based on 4,999 random permutations. Significance of ISA results was inferred at $P < 0.1$ in order to minimize potential of type II error, especially given our limited number of study units (ponds). All invertebrate taxa were $\log_{10}$ transformed prior to NMS, MRPP, and ISA to prevent abundant taxa from having too much influence on the results (Jongman et al. 1995; ter Braak 1995; McCune and Grace 2002).

Results

A total of four sets of samples were collected from each pond in 2000 and 2001, and three sets from each site during 2002, 2003 and 2004. One control pond remained dry throughout 2003 and 2004, thus our control treatment group contained three replicate sites during these years. Predominant invertebrates collected included aquatic earthworms (Oligochaeta), leeches (Hirudinea), fairy shrimp (*Eubranchipus*), clam shrimp (Conchostraca), Copepoda, seed shrimp (Ostracoda), water fleas (cladocera), water mites (Hydracarina), springtails (Collembola), various aquatic insects (Odonata, Hemiptera, Trichoptera, Coleoptera, Diptera), snails (Gastropoda), and fingernail clams (Sphaeriidae). Total numbers of each of these aggregate taxa were determined for each pond on each sampling date (summarized in Appendix).

Before tree removal, we observed no trends in mean canopy openness among harvest treatments (i.e., control, full buffer, partial buffer, clearcut), although clearcut ponds did show highest openness

prior to harvest (openness values 7–21%). Harvest treatments were restricted to the uplands and riparian forest surrounding each pond, yet they increased canopy openness above the pond basins in a pattern paralleling the intensity of harvesting in each treatment (i.e., control < full buffer < partial buffer < clearcut). Two years after harvest (2002), mean canopy openness was lowest in the controls (2%), higher in the full buffers (9%), intermediate in the partial buffers (25%) and highest in the clearcut (44%) (Fig. 1). A similar trend and difference was still evident in 2006 (control = 7%; full buffer = 18%; partial buffer = 21%; clearcut = 48%) (Fig. 1).

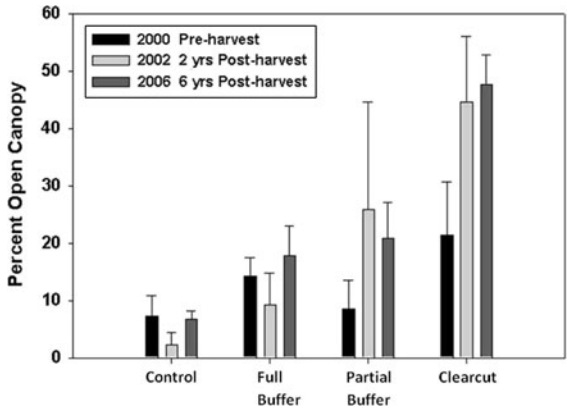

Fig. 1 Mean values of % canopy openness above 16 study ponds near Remer, MN, during pre-harvest (2000) and at 2- and 4-year intervals following tree removal (2002 and 2006, respectively). *Error bars* depict 2SEs

Ordination of pond/year scores using NMS identified a final 3 dimensional solution (Table 1) with the first 3 axes explaining approximately 27, 18, and 38% of the variance in our original invertebrate data matrix (cumulative $R^2 = 0.828$). Mean stress of this final ordination was near 10 (11.2), indicating that our model results were reliable (Clarke 1993; McCune and Grace 2002). NMS revealed no obvious pattern in invertebrate communities among treatments prior to timber harvest during 2000 (Fig. 2). However, contrast (higher dissimilarity of treatment/year scores) was evident between control and clearcut ponds during 2003 and 2004 (years 3 and 4 after tree removal), with full and partial buffer treatments showing characteristics intermediate between control and clearcut treatments. Interestingly, partial buffer scores converged with those from clearcut ponds during study year 5, while full buffer treatments remained intermediate between clearcuts and controls (Fig. 2). Invertebrate communities in clearcut ponds also appeared to reflect less interannual variability than did other treatments (Fig. 2).

Several groups of crustaceans (cladocera, Copepoda, Conchostraca, and *Eubranchipus*), aquatic insects (Coleoptera, Diptera, Hemiptera), gastropod snails, fingernail clams (Sphaeriidae), and Hirudinea (leeches) showed moderate ($R^2 > 0.30$) to strong associations with NMS axes (Table 2). Highest axis correlations were observed for *Eubranchipus* ($R^2 = 0.70$, axis 1), Hemiptera ($R^2 = 0.54$, axis 2) and Hirudinea ($R^2 = 0.84$, axis 3). This suggests that presence and abundance of these taxa had considerable

Table 1 Summary of model fitting results for non-metric multidimensional scaling using peak seasonal abundance of 16 taxa of aquatic invertebrates in ponds near Remer, MN, during 2000–2004

Axes	Stress in source data						*P*-value
	Actual data (250 runs)			Monte Carlo tests (249)			
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	
1	36.394	48.259	54.772	33.165	49.052	54.772	0.0200
2	18.729	19.926	30.753	17.948	23.913	37.675	0.0160
3	11.143	11.591	13.922	10.586	14.387	27.782	0.0120
4	6.406	6.458	8.153	6.927	9.557	12.945	0.0040
5	4.222	4.377	17.976	4.762	6.724	18.347	0.0040
6	2.974	3.090	14.480	3.226	4.719	6.403	0.0040

Values indicate dissimilarity (stress) with site/year scores and results are summarized for actual and randomized (Monte Carlo) data; *P*-values indicate improvement in actual data relative to randomized. Preliminary models were performed for 6 axes; final model included 3 dimensions (axes) based on methods described by McCune and Grace (2002)

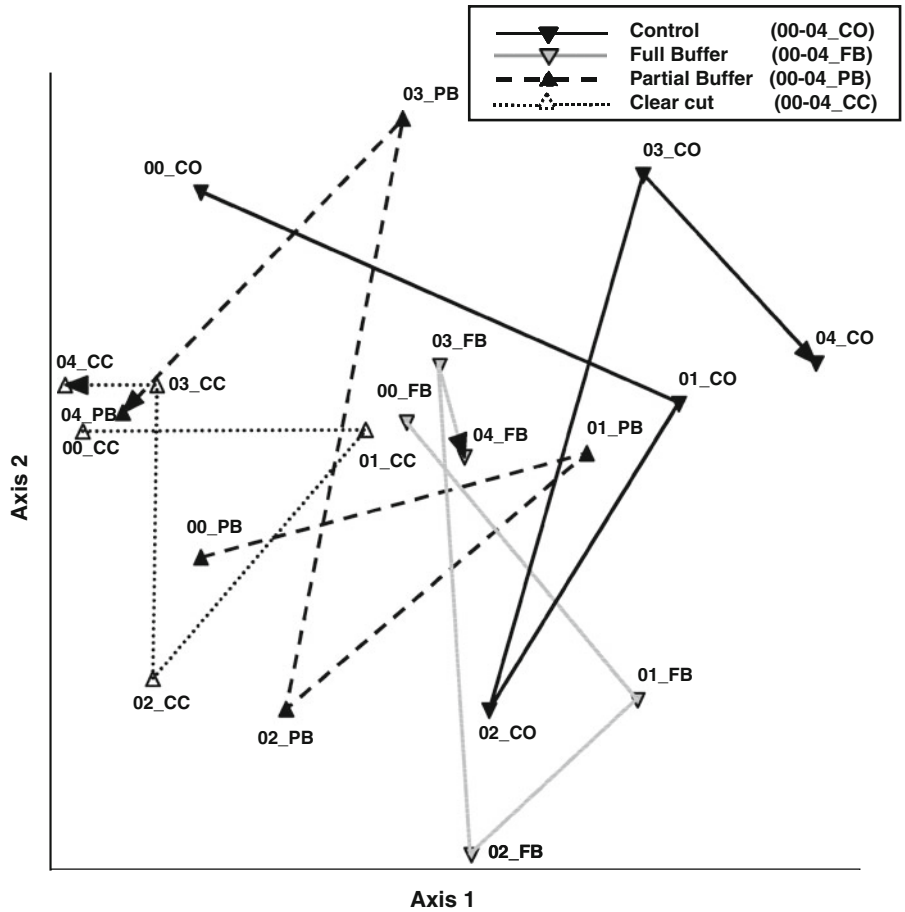

Fig. 2 Site scores from non-metric multidimensional scaling of mean peak annual abundance of invertebrates captured in 16 study ponds near Remer, MN, during 2000–2004. Treatments included ponds embedded in control (*solid black lines*), full buffer (*grey lines*), partial buffer (*heavy dash*) and clearcut (*light dash*) upland areas. *Symbol labels* indicate year_treatment combinations; lines connect annual means, forming chronosequence for each treatment group. For example, scores from control sites during 5 years are depicted as a line connecting 00_CO, 01_CO, 02_CO, 03_CO, 04_CO

influence on observed patterns in our final NMS model.

MRPP comparisons during 2004 indicated significant heterogeneity of invertebrate communities among harvest treatment groups ($P = 0.04$), with lowest distance values observed for our control ponds (Table 3). Pair-wise comparisons indicated similarity in invertebrate communities of clearcut and both buffer treatments, but these differed from control (unharvested) pond sites ($P < 0.05$). No such differences were observed among treatment groups during 2003 ($P = 0.23$, data not shown).

ISA analysis of the peak abundance data during 2003 and 2004 identified patterns in mean peak abundance of some pond invertebrates among harvest treatment groups. For example, *Eubranchipus* was the only taxon significantly associated with control ponds during 2003 and 2004 (Tables 4 and 5). Cladocera and Collembola (spring tails) were also associated with control sites, but only during 2004 ($P = 0.06$ and 0.06, respectively). In contrast, Hemiptera and Ostracoda were more abundant in clearcut ponds during 2003 ($P = 0.03$, $P = 0.01$, respectively), but these trends were not evident during 2004. Oligochaeta were associated with partial-buffer ponds during 2003, but showed no relationships to treatment during 2004. No taxa showed associations with full buffer treatments during 2003 or 2004 (Tables 4 and 5).

Table 2 Summary of R^2 values showing linear associations between $\log_{10}$ $(n + 1)$ invertebrate groups in ponds near Remer, MN, and 3 axes identified in final non-metric multi-dimensional scaling models

Taxa		R^2 values		
		Axis 1	Axis 2	Axis 3
Oligochaeata		0.14	0.12	0.29
Hirudinea		0.01	0.02	0.84
Crustacea	*Eubranchipus*	0.70	0.05	0.25
	Conchostraca	0.43	0.15	0.02
	Cladocera	0.44	0.18	0.00
	Copepoda	0.31	0.07	0.02
	Ostracoda	0.08	0.12	0.06
Hydracarina		0.09	0.22	0.18
Insecta	Collembolla	0.01	0.23	0.19
	Odonata	0.24	0.00	0.09
	Hemiptera	0.19	0.54	0.09
	Trichoptera	0.01	0.08	0.00
	Coleoptera	0.16	0.35	0.07
	Diptera	0.33	0.03	0.22
Mollusca	Gastropoda	0.25	0.38	0.00
	Sphaeriidae	0.05	0.08	0.53

Table 3 Results of multi-response permutation procedure comparisons of invertebrate communities sampled in ponds near Remer, MN, during 2004

Treatment group	Average distance
Control	$^{A}0.15$
Full buffer	$^{B}0.19$
Partial buffer	$^{B}0.19$
Clearcut	$^{B}0.18$

Values are shown for harvest treatment group distances with $T = -2.00$; chance-corrected within-group agreement ($A = 0.08$) indicated within-group variability approximated that expected by chance. Global $P = 0.04$, indicated that treatment group differences exceeded those expected by chance (see discussion of McCune and Mefford 1999). ^{A} Values with different letters indicate invertebrate community differences ($P < 0.05$)

Discussion

Our data indicated that invertebrate communities of seasonal ponds in clearcut forests differed from those in similar sites in unharvested uplands, but only after 3–4 years following tree removal. Partial and full buffer treatments showed more equivocal relationships, with intermediate NMS (treatment/year) scores, thus indicating shared community characteristics with both control and clearcut treatments. These results support our first hypothesis, suggesting that, in absence of forested buffers, upland forest harvest would induce changes in invertebrate communities of embedded ponds. Data also provided modest support for our second hypothesis, that retention of 15-m forested buffers would mitigate changes in seasonal pond invertebrates following adjacent clearcut harvesting. This is informative because the influences of adjacent forest harvesting on invertebrate communities in seasonal ponds, and the effectiveness of buffers mitigating these impacts, have not been well evaluated (Batzer et al. 2000; Minnesota Forest Research Council 2007).

Previous studies of aquatic invertebrates in seasonal ponds of North America have reported weak, sometimes variable relationships between community patterns and environmental gradients. For example, Batzer et al. (2004) described a negative relationship between abundance of Dytiscidae (predacious Coleoptera) and extent of canopy closure, but Hanson et al. (2009) observed opposite trends in seasonal ponds located within 50 km of the former sites.

We suspect a combination of direct and indirect mechanisms were responsible for contrasting similarity patterns we observed among harvest treatment groups, especially during years 3 and 4 following tree harvesting (2003 and 2004). For example, *Eubranchipus* was often most abundant in control ponds (Appendix) and ISA values reflect this for both 2003 and 2004 (Tables 4 and 5). *Eubranchipus* are year-round pond residents, consume bacteria, protozoans, algae, and detritus (Pennak 1989), and winter as resting eggs. Distribution and densities of these crustacean branchiopods often reflect extent and intensity of vertebrate and invertebrate predation (Bohonak and Whiteman 1999), thus populations are restricted to ephemeral waters where adults complete their life cycles quickly to avoid predators (Wiggins et al. 1980). These life history requirements may mean that unusual fluctuation in seasonal water temperature patterns or duration of flooding in response to tree removal has potential to reduce recruitment of *Eubranchipus* populations. In addition, resident wetland invertebrates have been shown to be especially sensitive to sediment overburden (Gleason

Table 4 Results of indicator species tests assessing distribution of pond invertebrate taxa among harvest treatments near Remer, MN, during 2003

Taxa		Highest group indicator value	Randomized indicator value	SD	*P*-value
Oligochaeta		39.9 (PB)	32.5	4.19	0.07
Hirudinea		45.0 (FB)	34.2	12.73	0.18
Crustacea	*Eubranchipus*	35.2 (CO)	30.7	2.20	0.02
	Conchostraca	25.1 (PB)	37.7	7.44	0.99
	Cladocera	29.2 (CO)	28.6	1.48	0.32
	Copepoda	27.7 (CC)	27.0	0.93	0.21
	Ostracoda	28.9 (CC)	27.1	0.86	0.01
Hydracarina		27.5 (CC)	27.2	1.09	0.37
Insecta	Collembolla	29.1 (CO)	29.5	1.80	0.57
	Odonata	30.1 (CO)	31.6	3.23	0.67
	Hemiptera	37.8 (CC)	31.6	3.02	0.03
	Trichoptera	39.6 (FB)	33.3	5.25	0.12
	Coleoptera	25.9 (CC)	26.0	0.56	0.57
	Diptera	27.1 (CO)	27.2	1.03	0.49
Mollusca	Gastropoda	27.2 (CO)	32.6	3.51	0.97

Indicator values reflect % perfect agreement (McCune and Mefford 1999). $P < 0.10$ indicates improvement using actual vs. randomized data and treatment groups with highest indicator values shown in parentheses (*CO* control, *PB* partial buffer, *FB* full buffer, *CC* clearcut); *P*-values from Monte-Carlo simulations using 4,999 permutations. Standard deviation values are also shown (SD)

Table 5 Results of indicator species tests assessing distribution of pond invertebrate taxa among harvest treatments near Remer, MN, during 2004

Taxa		Highest group indicator value	Randomized indicator value	SD	*P*-value
Oligochaeata		27.4 (FB)	30.9	2.26	0.94
Hirudinea		17.1 (PB)	29.8	11.24	0.91
Crustacea	*Eubranchipus*	39.5 (CO)	32.5	4.09	0.03
	Conchostraca	33.9 (PB)	34.8	7.78	0.50
	Cladocera	31.1 (CO)	28.9	1.47	0.06
	Copepoda	27.8 (CC)	27.1	0.99	0.24
	Ostracoda	26.9 (PB)	27.2	0.93	0.60
Hydracarina		27.4 (CC)	27.2	1.05	0.39
Insecta	Collembolla	29.6 (CO)	27.5	1.21	0.06
	Odonata	45.6 (PB)	31.3	11.99	0.15
	Hemiptera	33.3 (CC)	30.6	2.51	0.15
	Trichoptera	28.5 (CO)	33.6	7.05	0.73
	Coleoptera	25.9 (PB)	26.3	0.70	0.74
	Diptera	29.4 (CO)	28.1	1.45	0.17
Mollusca	Gastropoda	31.7 (CC)	1.82	1.82	0.14
	Sphaeriidae	36.2 (PB)	33.3	5.23	0.30

Indicator values reflect % perfect agreement (McCune and Mefford 1999). $P < 0.10$ indicates improvement using actual vs. randomized data and treatment groups with highest indicator values shown in parentheses (*CO* control, *PB* partial buffer, *FB* full buffer, *CC* clearcut); *P*-values from Monte-Carlo simulations using 4,999 permutations. Standard deviation values are also shown (SD)

et al. 2003) and upland disturbance producing even slight increases in sedimentation is likely to reduce egg viability of *Eubranchipus* and perhaps other crustaceans.

In contrast, Hemiptera were associated with clearcut treatments in 2003 (Table 4). Corixidae often become very abundant in disturbed wetlands (Gernes and Helgen 2002), although causal mechanisms are unknown. Our Hemiptera variable included predatory families such as Belostomatidae and Notonectidae and these disperse actively, thus hemipteran abundance probably reflects differential colonization rates among pond sites, and perhaps food availability. It seems plausible that by removing canopy cover, timber harvest enhanced visibility of seasonal ponds, thus increasing colonization rates for taxa that disperse by flight. We speculate that greater abundance of Hemiptera and other predators may increase predation rates and this might help explain lower numbers of *Eubranchipus* in clearcut upland ponds. Changes in predation, along with physical features of seasonal ponds such as hydroperiod (Williams 1997), light availability, temperature dynamics, extent and quality of litter inputs (Palik et al. 2003), and predominant vegetation (Batzer et al. 2000), probably contributed to the community differences we observed.

Our results provide some evidence that 15-m buffer strips mitigate against short-term effects of upland clearcuts. We are not aware of previous research on efficacy of buffers for conserving natural invertebrate communities in seasonal ponds, although buffers have been shown to limit changes in benthic insect communities following tree removal adjacent to streams (Kiffney et al. 2003). Studies of birds, ungulates, and other vertebrates suggest that buffers serve as habitat and travel corridors for mobile species (O'Connell et al. 2000; Hanowski et al. 2005, 2006). However, research on highly mobile vertebrates may have only limited usefulness for understanding within-pond responses to disturbance. Dufrêne and Legendre (1997) suggest that studies of invertebrates may provide better information about site-level consequences of habitat disturbance than does research on vertebrates or even plant communities, since responses of the latter are complicated by habitat size requirements or lag effects.

Differences among treatments in our study were not evident until 2003 and 2004, 3 and 4 years following timber harvest, apparently indicating belated invertebrate responses. We are aware of no similar observations from seasonal ponds although data such as ours are rare. Aquatic oligochaetes and cladocera increased and decreased (respectively) following tree removal adjacent to small ponds in Georgia and trends appeared shortly after harvesting (Batzer et al. 2000). Palik et al. (2001) studied invertebrates in similar ponds (Minnesota, USA), but tree removal occurred at least 7 years prior to the onset of their data collecting. We suspect lags we observed reflect time required for development of complex responses, especially those induced by changes in hydrophytes within ponds. For example, Batzer et al. (2000) reported increased emergent hydrophytes in small hybrid Cyprus/gum ponds (Georgia, USA) following adjacent tree removal. We observed similar responses of *Carex* spp. in some ponds in clearcuts during several years following tree removal and changing invertebrate communities in these sites probably resulted from increased habitat complexity, altered litter inputs, and increased periphyton (M. Hanson and B. Palik, personal observation). Blow-down of residual trees within the partial buffers was considerable in some of our study ponds, sometimes removing up to 50% of remaining basal area. It may be that similarity between invertebrate communities of clearcut and buffer treatments was due, in part, to wind throw within the latter, essentially creating conditions that were similar to the clearcut treatment.

Expectation of stronger trends towards differences among harvest treatments may be unwarranted for several reasons. First, densities of resident invertebrate populations in seasonal ponds are highly variable and temporal variance alone may overwhelm treatment-induced changes (Batzer et al. 2004; Miller et al. 2008). Second, because seasonal ponds are harsh environments, many resident taxa have high tolerance for extreme and variable conditions. Seasonal pond environments may change in response to disturbance from clearcutting, but even then, resulting conditions may be well within ranges tolerated by most invertebrates in these communities (Williams 1997; Batzer et al. 2004). Third, it is plausible that our 15-m buffers were insufficient to reduce influences of adjacent clearcut harvesting (for example, Kiffney et al. 2003 recommended retention of 30-m buffers for conservation of stream invertebrates). Finally, many taxa we collected were active

dispersers (Hemiptera), and some of these did appear to have affinities for certain treatments. However, this may also reflect geographic proximity of pond sites to permanent waters serving as wintering areas, or other characteristics that were unrelated to timber harvest.

Elsewhere we suggest that functional linkages between seasonal ponds and upland areas are strong and may result from complex relationships among adjacent forest canopy, light availability, pond water temperature, and litter and nutrient inputs (Palik et al. 2001, 2006). However, recent work has identified only weak associations between wetland invertebrate communities and environmental gradients, etc. (Tangen et al. 2003; Batzer et al. 2004; Hanson et al. 2009). This may indicate that current approaches based on use of invertebrates as disturbance indicators hold only limited potential to elucidate responses or identify complex relationships and that better methods are needed for gathering and interpreting invertebrate community data.

Management implications

Our results indicated that clearcutting upland forest adjacent to seasonal ponds resulted in measurable changes in aquatic invertebrate communities, compared to ponds in uncut forest, and uncut buffers around seasonal ponds partially mitigated these changes. As far as we know, these results represent a first evaluation of buffer efficacy for invertebrate communities in seasonal ponds in the northern forest region of North America. We caution that changes in animal communities do not elucidate causal mechanisms or consequences of such responses, or reflect trends in other ecosystem characteristics. We also recognize that community change does not necessarily connote ecological impairment. Implications of the changes we observed probably depend on the abundance and distribution of seasonal ponds in the landscape, specific characteristics of forests, harvests, and buffers, and extent to which harvest responses are scale-dependent. Even deleterious changes in individual seasonal ponds may have little consequence beyond site-level scales if nearby (unaltered) habitats provide alternative habitats for organisms, functional redundancy of ecosystem features, etc. On the other hand, seasonal ponds in forest landscapes clearly provide food-chain support functions that extend well beyond boundaries of individual ponds or even local landscape areas. For example, many female breeding ducks and young ducklings rely almost exclusively on aquatic invertebrates for protein and other nutrients (Krapu and Reinecke 1992) and seasonal ponds probably provide access to critical food resources before larger, permanently flooded habitats become ice-free. Because growth and survival of young mallard ducklings are positively related to abundance of aquatic invertebrates (Cox et al. 1997), changes in temporal abundance or availability of invertebrates in seasonal ponds may make it more difficult for some waterfowl to satisfy nutritional requirements in forested landscapes.

We recommend that uncut buffers of at least 15 m be retained around a portion of seasonal ponds in extensive harvests areas to help conserve integrity of pond invertebrate communities over the short-term. Use of pond buffers is not without problems. For example, narrow buffers are prone to blow down and thus may have only limited effectiveness over time. We encourage future research to (1) target spatially dependent consequences of timber harvesting adjacent to seasonal ponds, (2) address sampling and analytical problems currently limiting use of invertebrates as disturbance indicators, (3) improve understanding of natural variation (short- and long-term) in pond invertebrate communities to clarify how often disturbance responses exceed normal conditions, and (4) help identify forest management strategies to minimize impacts on wetland-dependent species. More specifically, we believe future work should evaluate specific strategies for increasing retention and efficacy of forested buffers around seasonal ponds.

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Appendix

See Table 6.

Table 6 Relative peak abundance of aquatic invertebrates captured each year (year) in 16 study ponds near Remer, MN, during 2000–2004

Year	Trt	Taxa													
		Oligochaeta	Hirudinea	*Eubranchipus*	Conchostraca	Copepoda	Cladocera	Hydracarina	Collembolla	Odonata	Hemiptera	Trichoptera	Coleoptera	Diptera	Mollusca
00	PB	15.8	256.0	29.3	231.5	764.8	6,241.3	52.5	33.3	6.5	16.5	5.5	58.8	954.5	70.3
	CC	12.8	80.0	7.5	17.0	589.3	845.8	117.0	23.3	52.3	43.0	2.3	49.5	422.8	82.5
	FB	14.0	20.7	85.0	22.3	810.3	1,317.5	65.5	9.5	1.3	5.3	2.5	38.3	1,350.0	36.1
	CO	3.5	251.3	4.0	68.5	299.3	1,914.0	74.0	16.0	1.8	5.0	2.3	45.0	418.8	122.6
01	PB	8.5	57.8	49.0	1.0	377.0	15,923.5	49.3	27.3	1.5	12.8	3.5	45.3	2,261.3	32.3
	CC	4.0	43.5	46.5	13.8	818.0	4,891.3	51.3	19.0	0.8	25.3	2.3	38.0	245.5	63.8
	FB	1.5	10.3	134.5	22.3	787.0	6,258.8	33.3	9.5	0	33.5	1.8	56.8	559.3	16.0
	CO	2.3	40.3	368.5	1.3	560.8	6,177.3	44.5	18.8	1.3	5.8	3.3	29.8	2,401.3	39.5
02	PB	38.3	32.5	37.5	36.0	7,269	5,142.0	57.3	35.8	7.3	44.0	21.0	65.8	3,470.0	46.0
	CC	21.3	4.3	32.5	1,098	883.5	3,952.3	57.3	26.0	4.0	202.3	7.5	49.5	566.8	65.6
	FB	4.3	5.3	281.3	188.0	880.3	18,798.5	38.8	2.8	3.8	62.5	1.8	51.0	1,649.8	8.3
	CO	6.3	24.3	300.0	46.0	217.5	6,833.8	48.8	17.5	6.8	9.8	16.3	46.0	941.8	23.1
03	PB	7.3	1.0	38.0	11.5	478.8	2,649.0	58.3	22.5	7.8	3.0	1.0	40.8	5,993.5	29.3
	CC	3.0	0	30.8	87.0	1,013	1,041.0	104.5	33.8	4.0	11.5	3.5	45.8	1,024.5	36.0
	FB	1.5	17.5	107.3	70.0	511.5	6,231.8	76.0	23.0	2.0	3.3	11.8	35.0	1,094.0	67.8
	CO	2.0	1.0	327.3	2.3	265.3	6,043. 7	113.0	192.7	6.0	2.7	5.0	38.7	2,436.7	82.3
04	PB	2.0	1.3	21.5	123.0	853.3	777.8	85.8	73.5	4.5	13.0	5.0	48.3	741.0	60.3
	CC	2.0	0.5	24	131.8	2,081.6	1,065.3	269.0	85.3	0.8	13.0	2.0	40.0	691.0	57.8
	FB	2.3	1.0	252	69.0	912.5	2,921.0	169.8	47.5	0.5	4.8	1.8	40.8	3,957.5	18.3
	CO	1.7	0.8	417	8. 7	260. 7	5,229.0	121.0	239.3	0	2.0	10.7	36.7	7,823.7	22.0

Values represent mean peak abundance of organisms summarized separately for each harvest treatment (Trt; *CC* control, *FB* full buffer, *PB* partial buffer, *CC* clearcut). Mollusca includes Sphaeriidae and Gastropoda

References

Almendinger JC, Hanson DC (1998) Ecological land classification handbook for the Northern Minnesota drift & lake plains and the chippewa national forest. Minnesota Department of Natural Resources, Division of Forestry, St. Paul

Batzer DP, Jackson CR, Mosner M (2000) Influences of riparian logging on plants and invertebrates in small, depressional wetlands of Georgia, USA. Hydrobiologia 441:123–132

Batzer DP, Palik BJ, Buech R (2004) Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota. J North Am Benthol Soc 23:50–68

Biondini ME, Mielke PW Jr, Berry KJ (1988) Data-dependent permutation techniques for the analysis of ecological data. Vegetatio 75:161–168

Bohonak AJ, Whiteman HH (1999) Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. Limnol Oceanogr 44:487–493

Brooks RT, Stone J, Lyons P (1998) An inventory of seasonal forest ponds on the Quabbin Reservoir watershed, Massachusetts. North East Nat 5:219–230

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austral Ecol 18:117–143

Minnesota Forest Resources Council (1999) Sustaining Minnesota forest resources: voluntary site-level forest management guidelines for landowners, loggers, and resource managers. Minnesota Forest Resources Council, St. Paul, Minnesota

Minnesota Forest Research Council (2007) Analysis of the current science behind riparian issues: report to the Minnesota forest resources council, St. Paul

Cox RR Jr, Hanson MA, Roy CC, Euliss NH Jr, Johnson DH, Butler MG (1997) Mallard duckling growth and survival in relation to aquatic invertebrates. J Wildl Manag 62: 124–133

Dodd CK Jr, Cade BS (1998) Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conserv Biol 12:331–339

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Gernes MC, Helgen JC (2002) Indices of biological integrity (IBI) for large depressional wetlands in Minnesota. Minnesota pollution control agency, Saint Paul

Gibbs JP (1993) Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13:25–31

Gleason RH, Euliss NH Jr, Hubbard DE, Duffy WE (2003) Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23:26–34

Hanowski J, Danz N, Lind J, Niemi G (2005) Breeding bird responses to varying amounts of basal area retention in riparian buffers. J Wildl Manag 69:689–698

Hanowski J, Danz N, Lind J (2006) Response of breeding bird communities to forest harvest around seasonal ponds in northern forests, USA. For Ecol Manag 229:63–72

Hanson MA, Roy CC, Euliss NH Jr, Zimmer KD, Riggs MR, Butler MG (2000) A surface associated activity trap for capturing water-surface and aquatic invertebrates in wetlands. Wetlands 20:205–212

Hanson MA, Bowe SE, Ossman FG, Fieberg J, Butler MG, Koch R (2009) Influences of forest harvest and environmental gradients on aquatic invertebrate communities of seasonal ponds. Wetlands 29:884–895

Hilsenhoff WL (1995) Aquatic Hydrophilidae and Hydraenidae of Wisconsin (Coleoptera). 2. Distribution, habitat, life cycle and identification of species of Hydrobiini and Hydrophilini (Hydrophilidae: Hydrophilinae). Great Lakes Entomol 28:97–126

Jongman RH, ter Braak CJ, van Tongeren OF (1995) Data analysis in community and landscape ecology. Cambridge University Press, Melbourne

Kiffney PM, Richardson JS, Bull JP (2003) Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. J Appl Ecol 40: 1060–1076

Kiffney PM, Richardson JS, Bull JP (2004) Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. J North Am Benthol Soc 23:542–555

Krapu GL, Reinecke KJ (1992) Foraging ecology and nutrition. In: Batt BD, Afton AD, Anderson MG, Ankney CD, Johnson DH, Kadlec JA, Krapu GL (eds) Ecology and management of breeding waterfowl. University of Minnesota Press, Minneapolis, pp 1–29

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach

McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach

McGeoch MA, Chown SL (1998) Scaling up the value of bioindicators. Trends Ecol Evol 13:46–47

Merritt RW, Cummins KW (1996) An introduction to the aquatic insects of North America. Kendall Hunt, Dubuque

Miller AT, Hanson MA, Church JO, Palik BJ, Bowe SE, Butler MG (2008) Invertebrate community variation in seasonal forest wetlands: implications for sampling and analyses. Wetlands 28:874–881

O'Connell MA, Hallett JG, West SD, Kelsey KA, Manuwal DA, Pearson SF (2000) Effectiveness of riparian management zones in providing habitat for wildlife. Timber/fish and wildlife, CMER committee, report TFW-LWAG1-00-001

Oertli B (1993) Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). Oecologia 96:466–477

Palik BJ, Batzer DP, Buech R, Nichols D, Cease K, Egeland L, Streblow DE (2001) Seasonal pond characteristics across a chronosequence of adjacent forest ages in Northern Minnesota, USA. Wetlands 21:532–542

Palik BJ, Buech R, Egeland L (2003) Using an ecological land hierarchy to predict seasonal-wetland abundance in upland forests. Ecol Appl 13:1153–1163

Palik BJ, Batzer DP, Kern C (2006) Upland forest linkages to seasonal wetlands: coarse particulate organic matter flux, litter processing, and food quality. Ecosystems 9:141–151

Palik BJ, Streblow D, Egeland L, Buech R (2007) Landscape variation of seasonal pool plant communities in forests of northern Minnesota, USA. Wetlands 27:12–23

Pennak RW (1989) Fresh-water invertebrates of the United States: protozoa to mollusca, 3rd edn. Wiley, New York 628 pp

Philippi TE, Dixon PM, Taylor BE (1998) Detecting trends in species composition. Ecol Appl 8:300–308

Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Ann Rev Ecol Syst 28:289–316

Semlitsch RD (1998) Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conserv Biol 12:1113–1119

Semlitsch RD, Bodie JR (1998) Are small, isolated wetlands expendable? Conserv Biol 12:1129–1133

Stewart RE, Kantrud HA (1971) Classification of natural ponds and lakes in the glaciated prairie region, Bureau of sport fisheries and wildlife resources publication no. 92, Washington, DC

Stone MK, Wallace JB (1998) Long-term recovery of a mountain stream from clearcut logging: the effects of forest succession on benthic invertebrate community structure. Freshw Biol 39:151–169

Tangen BA, Butler MG, Ell MJ (2003) Weak correspondence between macroinvertebrate assemblages and land use in prairie pothole region wetlands, USA. Wetlands 23: 104–115

ter Braak CJ (1995) Ordination. In: Jongman RH, ter Braak CJ, van Tomgeren OF (eds) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, pp 91–173

Thorp JH, Covich AP (2001) Ecology and classification of North American freshwater invertebrates. Academic Press Inc, San Diego

Tiner RW (2003) Spatially isolated wetlands of the United States. Wetlands 23:494–516

Wallace JB, Gurtz MS (1985) Response of *Baetis* mayflies (Emphemeroptera) to catchment logging. Am Midl Nat 115:25–41

Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104

Webster JR, Golladay SW, Benfield EF, D'Angelo DJ, Peters T (1990) Effects of forest disturbance on particulate organic matter budgets of small streams. J North Am Benthol Soc 9:120–140

Wellborn GA, Skelly DK, Werner EE (1996) Mechanisms creating community structure across a freshwater habitat gradient. Ann Rev Ecol Syst 27:337–363

Wenger S (1999) A review of the scientific literature on riparian buffer width, extent, and vegetation. Office of Public Service & Outreach, Institute of Ecology, University of Georgia, Georgia

White MA, Host GE (2003) Changes in disturbance frequency, age and patch structure from pre-Euro-American to settlement to present in north central and northeastern Minnesota. Report to the Minnesota forest resources council, St. Paul, Minnesota, Unpublished report

Wiggins GB, MacKay RJ, Smith IA (1980) Evolutionary and ecological strategies of animals in annual temporary pools. Arch Hydrobiol Suppl 58:97–207

Williams DD (1997) Temporary ponds and their invertebrate communities. Aquat Conserv Mar Freshw Ecosyst 7: 105–117