Microbial functional capacity among natural and created wetlands in Ohio, USA

Eric J. Saas
University of New Hampshire, Durham

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Microbial functional capacity among natural and created wetlands in Ohio, USA

Abstract
Natural depressional wetlands carry out important functions related to C and N cycling, yet the ability of created wetlands to functionally replace natural wetlands in this capacity is not well understood. My objective was to apply the catabolic response profile (CRP) method to evaluate the functional capacity of the soil microbial community in a series of 15 freshwater depressional wetlands: five naturally-occurring wetlands and 10 created wetlands from 1 to 39 years old. I amended sediment samples with 20 labile carbon sources, and samples were analyzed for CO2 and CH4 efflux following a 4-hr incubation under either aerobic or anaerobic conditions. The richness and evenness of carbon-source utilization by the soil microbial community were both significantly higher in natural wetlands compared to created wetlands when measuring CO2 efflux under aerobic conditions (11.7 vs. 9.18 for evenness and 18.5 vs. 15.1 for richness). Significant differences in overall microbial functional capacity among wetland age-classes, as determined by principal components analysis, were apparent for each treatment. Under aerobic conditions, old wetlands differed from young and mid-aged created wetlands and natural wetlands. Under anaerobic conditions natural wetlands differed from all created wetlands. Functional differences under certain conditions between the soil microbial communities resident in natural and created wetlands support the conclusion that created wetlands are not serving as functional equivalents to their naturally-existing counterparts.

Keywords
Environmental Sciences, Biology, Ecology, Agriculture, Soil Science

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MICROBIAL FUNCTIONAL CAPACITY AMONG NATURAL AND CREATED WETLANDS IN OHIO, U.S.A.

BY

ERIC J. SAAS
Bachelor of Science, Muskingum College, 2004

THESIS

Submitted to the University of New Hampshire
in Partial Fulfillment of
the Requirements for the Degree of

Master of Science
in
Natural Resources

May, 2007
This thesis has been examined and approved.

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DEDICATION

I hope this work does for you, reader, a fraction of what it has for me.

May this work further your knowledge and inspire your curiosity.
ACKNOWLEDGEMENTS

Special thanks to the undergraduate laboratory assistants and graduate students in the laboratories of Serita Frey, Virginie Bouchard and Ruth Varner. Thanks also to my peers, committee and the staff and faculty of the Department of Natural Resources at the University of New Hampshire for their patience and generosity.

This material is based upon work supported by the Cooperative State Research, Education, and Extension Service, U.S. Department of Agriculture, under award number: 2005-35101-15593.
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ABSTRACT

MICROBIAL FUNCTIONAL CAPACITY AMONG NATURAL AND CREATED WETLANDS IN OHIO, U.S.A.

by

Eric Saas

University of New Hampshire, May, 2007

Natural depressional wetlands carry out important functions related to C and N cycling, yet the ability of created wetlands to functionally replace natural wetlands in this capacity is not well understood. My objective was to apply the catabolic response profile (CRP) method to evaluate the functional capacity of the soil microbial community in a series of 15 freshwater depressional wetlands: five naturally-occurring wetlands and 10 created wetlands from 1 to 39 years old. I amended sediment samples with 20 labile carbon sources, and samples were analyzed for CO$_2$ and CH$_4$ efflux following a 4-hr incubation under either aerobic or anaerobic conditions. The richness and evenness of carbon-source utilization by the soil microbial community were both significantly higher in natural wetlands compared to created wetlands when measuring CO$_2$ efflux under aerobic conditions (11.7 vs. 9.18 for evenness and 18.5 vs. 15.1 for richness).

Significant differences in overall microbial functional capacity among wetland age-classes, as determined by principal components analysis, were apparent for each treatment. Under aerobic conditions, old wetlands differed from young and mid-aged created wetlands and natural wetlands. Under anaerobic conditions natural wetlands differed from all created wetlands. Functional differences under
certain conditions between the soil microbial communities resident in natural and created wetlands support the conclusion that created wetlands are not serving as functional equivalents to their naturally-existing counterparts.
CHAPTER I

INTRODUCTION

During the first 200 years following European settlement of the United States, destruction of wetlands resulted in the loss of more than half the original wetland acreage in the contiguous U.S. (Dahl 1990). A growing recognition of the value of wetlands has helped slow the rate of wetland destruction over the last 30 years, particularly through policies which reinforce no net loss of wetlands.

Through compensatory mitigation, ecologists, wildlife managers and engineers have been carrying out thousands of wetland mitigation projects across the United States in recent decades. Between 1998 and 2004, for the first time, the U.S. Fish and Wildlife Service (USFWS) reported that net wetland gains were greater than losses within the contiguous United States. The authors of the USFWS study were careful to point out, however, that any recovery of total wetland acreage does not necessarily translate into recovered wetland quality (Dahl 2006).

Through wetland restoration, wetland practitioners are effectively engaging in a large-scale experiment which tests their ability to create new ecosystems capable of fully replacing natural wetlands. The successes and failures in such ecosystem restoration projects have been referred to as the "acid tests" of our ecological knowledge (Bradshaw 1987). In 2001, the National Research Council...
carried out a study to determine the effectiveness of wetland mitigation policy in the U.S. and concluded that, despite progress, wetland mitigation had fallen short of its no net loss goal. In a 2004 technical report to the Ohio Environmental Protection Agency, Fennessy et al., (2004) analyzed a series of natural and created wetlands in central Ohio (several of which are included in this study) and determined that wetland mitigation is “currently creating a new subclass of wetlands on the landscape” which do not serve as functional equivalents to natural, reference wetlands. These findings are particularly relevant in Midwestern states such as Ohio, where the loss of original wetland acreage exceeds 80% (Zedler 2004). Zedler and Kercher (2005) note that created wetlands could be following a reclamation trajectory toward a dynamic equilibrium in which they differ structurally and functionally from the historical status of the natural wetland they replaced. This study is one contribution to an expanding body of literature which explores properties of created wetlands in relation to reference wetlands in order to assess and understand the results of our nationwide “acid test”.

In wetlands, as in upland terrestrial ecosystems, soil microorganisms and invertebrate species are responsible for providing essential ecosystem services such as decomposing organic matter and recycling nutrients (Wall, et al. 2004). In addition, hydric soils are the principal site of chemical transformation and nutrient exchange on which hydrophytic vegetation depends (Mitsch & Gosselink 2000). The degree to which soil biodiversity affects ecosystem functions such as
primary production, decomposition, and nutrient cycling remains to be fully explored, but Degens, et al. (2001) have found that soils with higher functional diversity are more resistant to stresses such as reduced pH, increased salinity or heavy metal contamination and disturbances such as freeze-thaw cycles than soils with lower functional diversity.

Building upon previous studies of created and reference wetlands, this work focused on establishing a functional characterization of the belowground microbial community in wetlands. Atkinson and Cairns (2001) reported higher decomposition rates for plant litter in late successional vs. early successional created wetlands, and D'Angelo et al. (2005) found differences between soil microbial communities in early and late successional bottomland forest wetlands in Kentucky using phospholipid fatty acid (PLFA) analysis. I applied the catabolic response profile (CRP) method, which has been used in terrestrial soils to examine the functional capacity of microbial communities in numerous studies (e.g. Degens 1998 and 1999; Schipper et al., 2001; Degens et al., 2001; Frey et al., 2004). Ravit et al. (2006) adapted the terrestrial CRP method to analyze microbial functional capacity in estuarine sediments. Rothman and Bouchard (2006) successfully used a similarly modified CRP method to distinguish soil microbial communities in freshwater coastal wetlands of the Great Lakes, USA.

The CRP approach measures the short-term gas efflux from a microbial community following amendment and incubation with a suite of labile organic
compounds (Degens et al., 1997). As the microbial community in a soil catabolizes introduced carbon sources, measurements of richness and evenness of substrate utilization provide an indication of the functional diversity of the microbial community. It has been demonstrated that soils undergoing different levels of disturbance can be differentiated by their catabolic response profiles (Degens 1999), and the same has been shown for soils under differing land use (Degens et al., 1997). An assumption of my study was that the CRP method could, by extension, be applied to distinguish microbial community function among wetland sites at different stages of soil development.

The primary objective of this study was to measure and compare the functional capacities of soil microbial communities in natural, reference wetlands and a series of created wetlands. By sampling soils from 10 wetlands of varying ages since creation (1-39 years) along with five natural wetlands, I additionally sought to determine if created wetlands exhibit any patterns of microbial community development over time. My null hypothesis was that soil microbial communities are functionally indistinct, via the CRP method, in natural wetlands and created wetlands of all ages since creation.
Figure 1. Conceptual diagram of wetland sites

**Young: 5 wetlands (19 sub-sites)**
- Pickerington Ponds A: 1 y.o. (3 sub-sites)
- Pickerington Ponds B: 3 y.o. (4 sub-sites)
- Bluebird: 5 y.o. (5 sub-sites)
- Sacks: 7 y.o. (4 sub-sites)
- Big Island C: 6 y.o. (3 sub-sites)

**Mid.: 3 wetlands (12 sub-sites)**
- Bluebird: 5 y.o. (5 sub-sites)
- J. M. B.: 9 y.o. (4 sub-sites)
- Big Island A: 10 y.o. (5 sub-sites)

**Old: 2 wetlands (9 sub-sites)**
- Big Island B: 32 y.o. (5 sub-sites)
- Big Island C: 6 y.o. (3 sub-sites)

**Natural: 5 wetlands (19 sub-sites)**
- Bailfield Marsh (4 sub-sites)
- Calamus (5 sub-sites)
- Lawrence Woods (3 sub-sites)
- Mishne (3 sub-sites)
- Pickerington Ponds (4 sub-sites)
- Kildeer Plains: 39 y.o. (4 sub-sites)
- New Albany: 12 y.o. (3 sub-sites)
CHAPTER II

METHODS

Sites

Soil cores were collected at 15 wetlands: 10 created wetlands and five naturally-existing, reference wetlands. All wetlands included in this study were classified as palustrine emergent, following Cowardin et al. (1979) and were located within a radius of approximately 100 km from Columbus, Ohio, USA (40° N, 83° W). Five of the created wetlands were considered young (under seven years old at the time of sampling); three were considered intermediate or mid (between nine and 12 years old); and two old wetlands were more than 30 years since creation at the time of sampling (Figure 1).

Mixed emergent vegetation characterized each wetland except for Mishne, which was classified as a cattail marsh dominated primarily by Typha latifolia. Plant biomass varied from a minimum 0.12 ± 0.22 kg m\(^{-2}\) at Pickerington Ponds site A to a maximum of 1.56 ± 0.32 kg m\(^{-2}\) for the natural site at Pickerington Ponds (Table 1). Soil pH for each study site ranged from 5.4 ± 0.8 at New Albany to 6.7 ± 0.3 at J.M.B. Soil moisture ranged from 22.0 ± 2.9% (w/w) at New Albany to 76.4 ± 5.3% at Calamus. The highest soil carbon content was also at Calamus (26.0 ± 5.4%), with the lowest being at Bluebird (2.2 ± 0.2%). Soils at Pickerington Ponds B and Bluebird were the most nitrogen-limited with 0.20 ±
0.01% and 0.20 ± 0.02% soil nitrogen, respectively. The Pickerington Ponds and Calamus natural wetlands each had conspicuously higher soil nitrogen than other wetlands (1.72 ± 0.26% and 2.37 ± 0.50%, respectively) (Katie Hossler, unpublished data).

### Sample Collection

Prior to sampling each wetland, the dominant hydrophytic plant communities were surveyed in order to determine the appropriate number and location of representative sub-sites for each wetland following Magee et al. (1993). A baseline was established parallel to the long axis of each wetland, or perpendicular to any slope, and transects were established at multiples of 0.1, 0.3, 0.5, 0.7 and 0.9 times the baseline length. At regular intervals along the transect (0.05 x baseline length), a quadrat was established using a 0.9-m by 0.9-m frame. Each wetland contained a total of 30 to 40 quadrats, and dominant vegetation type and percent cover data were recorded for each quadrat. A smaller selection of 3-5 quadrats representing the dominant hydrophytic communities from each wetland were deemed sub-sites. In this way, the number of sub-sites established for a given wetland was a reflection of the total area and plant community diversity of that wetland.

Two soil cores (8 cm diameter by 10 cm depth) were taken from each sub-site using a sealable section of PVC pipe. Samples taken from sub-sites where the
soil was deemed to be water-saturated were considered anaerobic \( n = 29 \) and sealed carefully upon removal to limit the introduction of air to the soil core; cores from unsaturated sub-sites were considered aerobic \( n = 30 \). Soil cores from each sub-site were bulked, homogenized, and subsampled within 48 hours of sampling. During the processing stage, anaerobic samples were removed from their PVC corers and handled in a hypoxic glove box, whereas aerobic samples were handled in the ambient laboratory atmosphere. The soil samples were placed in a refrigerator inside sealed, plastic food-storage containers within sealed plastic bags in order to limit their exposure to oxygen. All samples were stored at 4°C and analyzed within two weeks of collection.

**Microbial Functional Capacity**

Functional characteristics of the sediment microbial community were measured using the catabolic response profile (CRP) method established for terrestrial soils by Degens and Harris (1997) and modified by Ravit *et al.* (2006) for wetland soils. In this analysis, a catabolic response profile was derived from each sub-site by detecting patterns of microbial respiration in response to a range of organic carbon sources.

A set of 20 carbon source amendments was selected to represent compounds which: (1) are thought to occur naturally in the wetland rhizosphere, and (2) have been shown in previous studies to effectively differentiate soil microbial communities in terrestrial and wetland ecosystems (see Degens *et al*., 1997;
Carbon sources were prepared in higher concentration than the established terrestrial CRP method, following Ravit et al. (2006). The suite included two carbohydrates at 100 mM (glucose, mannose); six amino acids also at 100 mM (L-asparagine, L-glutamic acid, L-histidine, L-serine, cysteine, leucine); eight carboxylic acids at 200 mM (citric acid, fumaric acid, DL-malic acid, malonic acid, succinic acid, tartaric acid, urocanic acid, acetic acid); two phenolic acids at 100 mM (p-hydroxybenzoic acid, caffeic acid) and two polymers (tannic acid at 0.5% w/w and Typha latifolia root extract at 1.0% w/w). Typha root extract was made following Ravit et al. (2006) and Ladd et al. (1995) by grinding oven-dried root material and, in a 1.0% w/w solution with deionized water, steeping it in a 100°C water bath for 60 min. After this point the mixture was centrifuged at 2000 rpm for 30 minutes. All substrates were adjusted to a pH range similar to the soil samples (5.5 — 6.5) by adding 0.1 or 1.0 M HCl or NaOH dropwise.

Samples from each sub-site were analyzed twice, regardless of their condition at the time of sampling (water-saturated or dry). All soil samples were processed first under anaerobic conditions in a Coy® glove box with a 95% N₂ plus 5% H₂ atmosphere. On the following day the aerobic treatment was performed on a second subsample of homogenized soil from each sub-site. In both treatments, sediment subsamples (3 g dry weight equivalent) for each sub-site were placed into each of 20 amber serum vials (50-ml), capped with rubber septa, and crimp sealed. In the anaerobic process, soil was added to the vials and the vials were
sealed inside the glove box to maintain low oxygen conditions for any soils from sub-sites which were water-saturated at the time of sampling. In the aerobic process, vials were filled with soil in the laboratory, outside of the glove box. In both treatments, after all of the soils had been weighed and placed inside sealed vials, 3 ml of a different substrate was added to each of the 20 vials using a 10 ml syringe. One additional vial per set was injected with 3 ml deionized water for use as a reference blank.

After substrate addition, the vials were vortexed immediately, placed in a 20°C incubator and then vortexed again after 1 hour of incubation. The soils were incubated a total of 4 hours. After the incubation period, each vial was hand shaken and 20 ml of headspace was removed with a 60 ml syringe and injected into a crimp-sealed, 25-ml serum vial for intermediate storage before gas analysis. The storage vials had been prepared by crimp sealing each set inside of a Coy® anaerobic chamber after several hours of stabilization, and empty ‘blank’ vials from each set were analyzed for background gas concentrations in order to correct for final gas concentrations in all vials.

In order to determine concentrations of gas generated during the incubation period, a 20 ml headspace sample was removed from each gas storage vial and 10 ml was analyzed for carbon dioxide (CO₂) concentration using a Shimadzu GC-8A gas chromatograph (Shimadzu Scientific Instruments) equipped with a thermal conductivity detector (GC-TCD). In an adaptation of the CRP procedure
for wetland sediments, the remaining 10 ml was analyzed for methane (CH₄) concentration using a separate Shimadzu GC-8A equipped with a flame ionization detector (GC-FID). Catabolic evenness, a measure of the proportion of carbon sources used by the heterotrophic microbial community, was calculated from the recorded respiration values (Degens et al., 2001) using the Simpson-Yule index. Catabolic evenness is denoted \( E = \frac{1}{\Sigma p_i^2} \) where \( p_i = \frac{(r_i/\Sigma r_i)}{(r_i)} \) and \( r_i \) is the respiration from a single carbon source addition. The respiration response of each carbon source is expressed as a proportion of the total respiration of all substrates and the catabolic evenness is summed for all substrates. In this case, a soil sample with the highest microbial functional diversity would have a catabolic evenness value of 20, while a more scattered respiration response across all carbon sources would yield a lower catabolic evenness value. Prior to any statistical comparisons, each individual gas efflux measurement was standardized by dividing it by the mean of gas effluxes within the same sub-site in order to normalize for differences in microbial biomass (Degens 1998).

**Data Analysis**

Rank analysis of variance (PROC RANK, PROC GLM, SAS Institute, 2002) was used to determine the significance of differences between mean overall CH₄ and CO₂ respiration in wet vs. dry sub-sites. Analysis of covariance (ANCOVA) (PROC GLM, SAS Institute, 2002), with soil moisture content at the time of sampling as a covariate, was used to compare wetland ageclasses (and natural
Principal components analysis (PCA) was used to assess differences in overall microbial functional capacity amongst wetland classes, and principal component scores were compared using ANCOVA. A separate PCA was carried out for each gas measurement (CO₂ or CH₄) in both laboratory treatments (aerobic and anaerobic), and component scores were analyzed for statistical significance using ANCOVA. Given the high sample-volume requirements of the gas chromatograph on which the gas samples were analyzed, only one headspace sample could be removed from each incubated vial. Thus, a small proportion (1.4%) of individual data points was lost as a result of human error. This small proportion of missing data initially caused a disproportionate amount of data (25%) to be excluded from the PCA model; therefore, any missing data points were estimated using imputation by within-wetland gas efflux means from the same carbon source amendment. Linear regression was used to assess the relationship between catabolic richness and evenness measurements and various site characteristics (PROC REG, SAS Institute 2002). All statistical analyses were performed using SAS software (SAS Institute, 2002).
Table 1. Chemical and Physical Characteristics of Wetland Study Sites. Variables age, ageclass, condition at sampling, percent soil moisture, soil pH, plant biomass, percent soil carbon, percent soil nitrogen and soil bulk density with standard errors are listed for each wetland sub-site. From Hossler, et al., unpublished data.

<table>
<thead>
<tr>
<th>Wetland</th>
<th>Age</th>
<th>Ageclass</th>
<th># Subsites</th>
<th>Soil Moisture (%)</th>
<th>SE</th>
<th>Soil pH</th>
<th>SE</th>
<th>Plant Biomass (g m^-2)</th>
<th>SE</th>
<th>Soil C (%)</th>
<th>SE</th>
<th>Soil N (%)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pick. Ponds A</td>
<td>1</td>
<td>young</td>
<td>3</td>
<td>22.7 (6.2)</td>
<td>6.7 (0.603)</td>
<td>197 (219)</td>
<td>3.01 (0.483)</td>
<td>0.250 (0.036)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Pick. Ponds B</td>
<td>3</td>
<td>young</td>
<td>4</td>
<td>25.8 (7.2)</td>
<td>6.6 (0.493)</td>
<td>497 (239)</td>
<td>2.89 (0.607)</td>
<td>0.200 (0.014)</td>
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</tr>
<tr>
<td>Bluebird</td>
<td>5</td>
<td>young</td>
<td>5</td>
<td>29.0 (5.2)</td>
<td>6.0 (0.358)</td>
<td>468 (140)</td>
<td>2.24 (0.242)</td>
<td>0.200 (0.021)</td>
<td></td>
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<tr>
<td>Big Island C</td>
<td>6</td>
<td>young</td>
<td>3</td>
<td>42.3 (8.0)</td>
<td>6.5 (0.109)</td>
<td>582 (143)</td>
<td>4.28 (0.167)</td>
<td>0.350 (0.025)</td>
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<tr>
<td>Sacks</td>
<td>7</td>
<td>young</td>
<td>4</td>
<td>32.0 (3.4)</td>
<td>5.5 (0.103)</td>
<td>364 (59.3)</td>
<td>2.48 (0.300)</td>
<td>0.220 (0.022)</td>
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<tr>
<td>J.M.B.</td>
<td>9</td>
<td>mid</td>
<td>4</td>
<td>25.3 (2.3)</td>
<td>6.7 (0.338)</td>
<td>501 (194)</td>
<td>2.73 (0.114)</td>
<td>0.230 (0.008)</td>
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<tr>
<td>Big Island A</td>
<td>10</td>
<td>mid</td>
<td>5</td>
<td>22.3 (2.0)</td>
<td>5.6 (0.132)</td>
<td>797 (201)</td>
<td>2.97 (0.287)</td>
<td>0.270 (0.019)</td>
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<tr>
<td>New Albany</td>
<td>12</td>
<td>mid</td>
<td>3</td>
<td>22.0 (2.9)</td>
<td>5.4 (0.751)</td>
<td>487 (255)</td>
<td>2.97 (0.233)</td>
<td>0.260 (0.023)</td>
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<tr>
<td>Big Island B</td>
<td>32</td>
<td>old</td>
<td>5</td>
<td>38.1 (3.0)</td>
<td>6.2 (0.394)</td>
<td>1220 (132)</td>
<td>3.33 (0.414)</td>
<td>0.300 (0.036)</td>
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<td></td>
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<tr>
<td>Kildeer Plains</td>
<td>39</td>
<td>old</td>
<td>4</td>
<td>41.5 (3.8)</td>
<td>6.2 (0.377)</td>
<td>990 (264)</td>
<td>2.54 (0.384)</td>
<td>0.240 (0.037)</td>
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<tr>
<td>Ballfield</td>
<td>N</td>
<td>natural</td>
<td>4</td>
<td>64.8 (5.0)</td>
<td>6.2 (0.211)</td>
<td>594 (98.0)</td>
<td>9.03 (0.912)</td>
<td>0.710 (0.090)</td>
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</tr>
<tr>
<td>Calamus</td>
<td>N</td>
<td>natural</td>
<td>5</td>
<td>76.4 (5.3)</td>
<td>5.9 (0.090)</td>
<td>919 (257)</td>
<td>26.0 (5.35)</td>
<td>2.37 (0.497)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Lawrence</td>
<td>N</td>
<td>natural</td>
<td>3</td>
<td>23.6 (0.3)</td>
<td>6.0 (0.167)</td>
<td>683 (349)</td>
<td>5.09 (0.651)</td>
<td>0.460 (0.054)</td>
<td></td>
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<tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Pick. Ponds N</td>
<td>N</td>
<td>natural</td>
<td>4</td>
<td>73.0 (2.1)</td>
<td>5.5 (0.223)</td>
<td>1560 (324)</td>
<td>20.7 (2.93)</td>
<td>1.72 (0.256)</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Mishne</td>
<td>N</td>
<td>natural</td>
<td>3</td>
<td>28.7 (1.5)</td>
<td>6.1 (0.234)</td>
<td>1030 (319)</td>
<td>3.46 (0.533)</td>
<td>0.290 (0.039)</td>
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</table>
CHAPTER III

RESULTS

Carbon dioxide efflux under aerobic conditions had a mean concentration of 417 ± 63 μg g⁻¹ soil hr⁻¹ and ranged from -442 to 1800 μg g⁻¹ hr⁻¹. The mean concentration of CH₄ efflux under anaerobic conditions was 1.62 ± 0.67 μg g⁻¹ with a range of -22.7 to 372 μg g⁻¹ hr⁻¹. Respectively, the mean concentrations of anaerobic CO₂ and aerobic CH₄ were -899 ± 118 μg g⁻¹, ranging from -2.9 x 10⁴ to 6.7 x 10³ and 0.15 ± 0.05 μg g⁻¹, ranging from -4.1 to 22.9 μg g⁻¹ hr⁻¹.

Negative gas efflux values resulted when a given sample’s headspace gas concentration was lower than the deionized water blank amendment for that sample’s particular sub-site; therefore negative values represent a potential inhibition of gas efflux by the carbon source addition.

Gas efflux ranges in this study were consistently wider than those in similar studies, which is likely a result of the diversity of the sampling sites, as the mean gas efflux concentrations were generally on a similar scale to concentrations reported in related studies (Ravit et al., 2006; Degens and Harris 1997). Average CO₂ respiration values under anaerobic conditions were lower than those reported by Ravit et al. (2006), while the mean anaerobic CH₄ efflux was within a similar range. The mean CO₂ respiration under aerobic conditions in this study was within the range reported by Degens and Harris (1997).

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Samples were collected following a stratified random sampling design, wherein soil samples were removed randomly from quadrats which were selected to represent the dominant hydrophytic plant communities of each wetland. The number of these quadrats (referred to here as sub-sites) varied between 3-5 per wetland, depending on plant community diversity and wetland size. Approximately half of the sub-sites in this study were water-saturated. Soil microbial communities from saturated vs. dry sub-sites displayed significantly different amounts of total CO₂ and CH₄ efflux. Concentrations of CO₂ in the aerobic incubation were significantly lower for dry samples than for saturated sub-sites (295 µg g⁻¹ soil for dry samples versus 538 µg g⁻¹ soil for wet samples; \( P = 0.0006 \)). Likewise, mean concentrations of CH₄ were higher in soils from dry sites under anaerobic conditions (3.53 µg g⁻¹ soil for dry samples versus -0.356 µg g⁻¹ soil, relative to the water blank, for wet samples; \( P < 0.0001 \)). To account for gas efflux differences arising from differences in soil moisture, all data were subsequently analyzed by analysis of covariance (ANCOVA) with the proportion of soil moisture at the time of sampling used as a covariate.

For individual carbon sources, many statistical differences were observed between wetland types (Table 2). For every carbon source added, significant differences in microbial respiration existed between wetland ageclasses in at least one category. As an example, for asparagine there were no significant differences among ageclasses in aerobic or anaerobic CO₂ efflux; however there
were ageclass differences in asparagine utilization for both aerobic and anaerobic CH₄ efflux. Natural wetlands were significantly different from all classes of created wetlands in carbon source utilization for 12 of the 20 carbon sources when samples were incubated under anaerobic conditions. Natural wetlands exhibited higher CO₂ efflux in response to urocanic acid, cysteine, leucine, serine and hydroxybenzoic acid, while showing a lower response to histidine, mannose, *Typha* extract and caffeic, fumaric, malic and tartaric acids. A slightly different set of 12 carbon sources showed a significantly different pattern of utilization between natural and created wetland classes for CH₄ efflux under anaerobic conditions. Natural wetlands had higher efflux when amended with acetic and hydroxybenzoic acids and asparagine, cysteine and leucine. Created wetlands had higher gas efflux than natural wetlands in response to fumaric, malic, succinic, tartaric, glutamic and caffeic acids and histidine.

To a lesser degree, old created wetlands stood apart from other wetland types in the aerobic treatment categories. Old wetlands exhibited a higher mean respiration in three of 20 carbon source amendments for the aerobic CO₂ treatment (fumaric acid, leucine and mannose) and in the amendment of malonic acid in mean anaerobic CH₄ efflux. Old wetlands were lower than other wetlands in anaerobic CH₄ efflux when amended with four carbon sources: asparagine, mannose, urocanic acid and glutamic acid.
No single carbon source was effective at differentiating any particular class of wetlands across all four treatments, though 11 of 20 carbon sources were effective in illuminating some kind of difference in utilization between wetland types in all treatments in which they were used (four carboxylic acids: citric acid, fumaric acid, malic acid, malonic acid; four amino acids: cysteine, glutamic acid, histidine and leucine; both phenolic acids: caffeic and hydroxybenzoic, and one polymer: *Typha* extract.)
Table 2. Carbon source utilization patterns in all treatments by wetland ageclass via ANCOVA. (Y = 'young sites': 1-7 years old, M = 'mid-age sites': 9-12 years old, O = 'old sites': 32-39 years old, N = 'natural sites'). Significance: *P < 0.05, **P <0.01, ***P < 0.001. Subscripted letter 'a' denotes a higher mean gas efflux than 'b' and so on.

<table>
<thead>
<tr>
<th>Carbon source</th>
<th>Type</th>
<th>Aerobic CO₂</th>
<th>Aerobic CH₄</th>
<th>Anaerobic CO₂</th>
<th>Anaerobic CH₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>acetic acid</td>
<td>carboxylic acid (CA)</td>
<td>-</td>
<td>**YOᵃ Mᵇ Nᵇ</td>
<td>*Nᵇ Mᵇ (YO)ᵇ</td>
<td>*Nᵇ (YMO)ᵇ</td>
</tr>
<tr>
<td>citric acid</td>
<td>CA</td>
<td>*Oᵇ (YM)ᵇ (ON)ᵇ</td>
<td>*MOᵇ Naᵇ Yᵇ</td>
<td>**(YM)ᵇ Nᵇ</td>
<td>**(YM)ᵇ Nᵇ</td>
</tr>
<tr>
<td>fumaric acid</td>
<td>CA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ Yᶜ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>succinic acid</td>
<td>CA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>tartaric acid</td>
<td>CA</td>
<td>-</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>urocanic acid</td>
<td>CA</td>
<td>-</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>asparagine</td>
<td>amino acid (AA)</td>
<td>-</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>cysteine</td>
<td>AA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>glutamic acid</td>
<td>AA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>histidine</td>
<td>AA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>leucine</td>
<td>AA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>serine</td>
<td>AA</td>
<td>-</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>caffeic acid</td>
<td>phenolic acid (PA)</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>hydroxybenzoic acid</td>
<td>carbohydrate (C)</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>glucose</td>
<td>carbohydrate (C)</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>mannose</td>
<td>C</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>*Oᵇ (MN)ᵇ</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>tannic acid</td>
<td>polymer (P)</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>*MNᵇ Yᶜ Oᵇ</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>Typha extract</td>
<td>P</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>Nᵇ</td>
</tr>
<tr>
<td>carboxylic acids</td>
<td>CA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>amino acids</td>
<td>AA</td>
<td>*Oᵇ (YM)ᵇ</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>phenolic acids</td>
<td>PA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>carbohydrates</td>
<td>C</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>polymers</td>
<td>P</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>*Nᵇ (YM)ᵇ</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>all</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
</tbody>
</table>

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When ageclasses were compared by carbon source class, old created wetlands showed higher amino acid utilization compared to other wetland classes for CO$_2$ efflux, and natural wetlands showed higher respiration in response to polymer addition under aerobic conditions (Table 2). Methane efflux under anaerobic conditions was higher in natural compared to created wetlands for carbohydrates; for polymers, young and old created wetlands had significantly higher mean efflux than mid-aged wetlands which had higher efflux than natural systems. Methane flux under aerobic conditions was higher in old wetlands when the soil was amended with polymers.

The number of carbon sources utilized by the soil microbial community (catabolic richness) and the evenness of substrate use were both significantly higher for CO$_2$ efflux in natural wetlands compared to created wetlands under aerobic conditions (Table 3). Catabolic richness was highest in natural wetlands (18.5), lower in mid-age wetlands (17.0) and lowest in young and old created wetlands (14.4 and 13.9, respectively). Catabolic evenness was higher in natural and mid-aged wetland soils (11.7 and 10.8, respectively) and lower in young and old created wetlands (8.67 and 8.37, respectively). However, no significant differences in patterns of substrate utilization were observed when CO$_2$ efflux was measured under anaerobic conditions. Catabolic richness and evenness in methane efflux did not differ significantly among wetland age categories for either aerobic or anaerobic incubations.
Table 3. Catabolic richness and evenness amongst wetland ageclasses. The data were analyzed by ANCOVA with soil moisture as the covariate. Different superscript letters indicate a significant difference between ageclasses (P < 0.05).

<table>
<thead>
<tr>
<th>Laboratory treatment</th>
<th>Young n = 5</th>
<th>Mid n = 3</th>
<th>Old n = 2</th>
<th>Natural n = 5</th>
<th>Created n = 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aerobic CO₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>14.4&lt;c</td>
<td>17.0b</td>
<td>13.9b</td>
<td>18.5&lt;sup&gt;MA&lt;/sup&gt;</td>
<td>15.1&lt;sup&gt;MN&lt;/sup&gt;</td>
</tr>
<tr>
<td>Evenness</td>
<td>8.37&lt;sup&gt;b&lt;/sup&gt;</td>
<td>10.8a</td>
<td>8.67&lt;sup&gt;b&lt;/sup&gt;</td>
<td>11.7&lt;sup&gt;MN&lt;/sup&gt;</td>
<td>9.18&lt;sup&gt;MN&lt;/sup&gt;</td>
</tr>
<tr>
<td>Anaerobic CO₂</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>15.1</td>
<td>13.67</td>
<td>12.3</td>
<td>11.8</td>
<td>14.1</td>
</tr>
<tr>
<td>Evenness</td>
<td>7.14</td>
<td>8.35</td>
<td>8.43</td>
<td>9.24</td>
<td>7.79</td>
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<tr>
<td>Aerobic CH₄</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>11.0</td>
<td>8.17</td>
<td>10</td>
<td>8.7</td>
<td>9.92</td>
</tr>
<tr>
<td>Evenness</td>
<td>6.02</td>
<td>5.20</td>
<td>3.86</td>
<td>6.17</td>
<td>5.33</td>
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<td>Anaerobic CH₄</td>
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</tr>
<tr>
<td>Richness</td>
<td>9.21</td>
<td>10.3</td>
<td>12.7</td>
<td>12.6</td>
<td>10.3</td>
</tr>
<tr>
<td>Evenness</td>
<td>6.62</td>
<td>9.46</td>
<td>5.03</td>
<td>9.25</td>
<td>7.11</td>
</tr>
</tbody>
</table>

* Catabolic richness indicates the total number of carbon source amendments resulting in respiration values above the water blank, and catabolic evenness is a measure of the proportion of carbon sources used by the heterotrophic microbial community, denoted E = (12π²/3) where π = (r/ζR) and (r) is the respiration of a single carbon source. The maximum value is 20 in each case.

Linear regression analysis was carried out to determine the relationships amongst catabolic evenness, richness and various site characteristics, including wetland age (Table 4). Significant but weak correlations were observed between aerobic CO₂ catabolic evenness and plant biomass ($r^2 = 0.158$, $P = 0.002$), percent soil carbon content ($r^2 = 0.007$, $P = 0.035$), and soil nitrogen ($r^2 = 0.068$; $P = 0.049$). Plant biomass and percent soil carbon were directly related to aerobic CO₂ catabolic evenness, whereas there was a weak negative correlation between catabolic evenness and percent soil nitrogen. There was no relationship between catabolic evenness or richness and wetland age in any treatment.
Table 4. Linear regression of aerobic CO₂ and anaerobic CH₄ catabolic richness and evenness vs. site age, plant biomass, soil carbon and nitrogen content, soil pH and soil moisture. P and r-squared values are listed at the intersection of each pair of variables. Significant P values (< 0.05) denoted by an asterisk.

<table>
<thead>
<tr>
<th>Wetland Age (created only)</th>
<th>Wetland Age (created only)</th>
<th>Plant biomass (g m⁻²)</th>
<th>Soil C (%)</th>
<th>Soil N (%)</th>
<th>Soil pH</th>
<th>Soil Moisture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aerobic CO₂:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>r² = 0.005</td>
<td>0.002</td>
<td>0.033</td>
<td>0.030</td>
<td>0.049</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>P = 0.664</td>
<td>0.759</td>
<td>0.172</td>
<td>0.191</td>
<td>0.084</td>
<td>0.438</td>
</tr>
<tr>
<td>Evenness</td>
<td>r² = &lt; 0.001</td>
<td>0.158</td>
<td>0.007</td>
<td>0.068</td>
<td>0.024</td>
<td>0.029</td>
</tr>
<tr>
<td></td>
<td>P = 0.980</td>
<td>0.002*</td>
<td>0.035*</td>
<td>0.049*</td>
<td>0.245</td>
<td>0.204</td>
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<tr>
<td><strong>Anaerobic CH₄:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>r² = 0.023</td>
<td>0.057</td>
<td>0.023</td>
<td>0.024</td>
<td>0.013</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>P = 0.352</td>
<td>0.070</td>
<td>0.255</td>
<td>0.242</td>
<td>0.395</td>
<td>0.352</td>
</tr>
<tr>
<td>Evenness</td>
<td>r² = 0.056</td>
<td>0.002</td>
<td>0.002</td>
<td>0.001</td>
<td>0.001</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>P = 0.247</td>
<td>0.757</td>
<td>0.728</td>
<td>0.782</td>
<td>0.868</td>
<td>0.550</td>
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</table>

Significant differences in overall microbial functional capacity among wetland ageclasses as determined by principal components analysis were apparent along the first principal component axis of each treatment and also in the second principal component axis for CH₄ efflux measured under aerobic conditions (Figure 2). Old created wetlands were significantly different from all other ageclasses along the first axis for both CO₂ and CH₄ efflux under aerobic conditions. In the aerobic CH₄ treatment, old wetlands were distinct from young while each was distinct from a grouping of the natural and mid ageclasses. All ageclasses were distinct from one another along the second axis (CO₂: PC1 P = 0.04, λ = 54.9%; CH₄: PC1 P < 0.0001, λ = 80.2%; PC2 P = 0.0001, λ = 16.8%).

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In the anaerobic treatments the natural wetlands were significantly different from all other ageclasses along the first principal component axis (CO$_2$: PC1 $P = 0.001$, $\lambda = 98.2\%$; CH$_4$: PC1 $P = 0.0001$, $\lambda = 94.9\%$.)

Carbon sources driving the first principal component axis for aerobic CO$_2$ in the positive direction were primarily fumaric acid and cysteine, a carboxylic acid and an amino acid, respectively and in the negative direction tannic acid and urocanic acid, a polymer and a carboxylic acid respectively. An amino acid and a carboxylic acid, asparagine and malic acid, were most associated with negative loading of the first component axis for anaerobic methane. *Typha* root extract, a polymer, and citric acid, a carboxylic acid, were most closely associated with the positive loading of the first principal component axis (Table 5).
Figure 2. Principal components scores sorted by wetland class for aerobic and anaerobic CO$_2$ and CH$_4$ efflux. Note that the axes differ between plots. In the aerobic CO$_2$ treatment, old is significantly different from all other ageclasses ($P = 0.04$) in PC1. Aerobic CH$_4$ PC1: old is different from natural and mid which are all different from young ($P < 0.0001$); PC2: all classes are significantly different ($P = 0.0001$). Anaerobic CO$_2$ PC1: natural wetlands are significantly different from others ($P = 0.001$). Anaerobic CH$_4$ PC1: natural wetlands are different from all other ageclasses ($P = 0.0001$).
Table 5. Principal component loading scores for carbon sources in each treatment. The two main carbon sources associated with each direction on the first two principal component axes are listed along with their Eigenvector value. AA = amino acid; C = carbohydrate; CA = carboxylic acid; P = polymers; PA = phenolic acids

<table>
<thead>
<tr>
<th>PC 1</th>
<th>Negative loading</th>
<th>Positive loading</th>
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<tbody>
<tr>
<td></td>
<td>Carbon Source</td>
<td>Type</td>
</tr>
<tr>
<td></td>
<td>CO₂</td>
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</tr>
<tr>
<td>Aerobic</td>
<td>tannic</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td>urocanic</td>
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<td></td>
<td>caffeic</td>
<td>PA</td>
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<td>leucine</td>
<td>AA</td>
</tr>
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<td>asparagine</td>
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<table>
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<td>CO₂</td>
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</tr>
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<td>Aerobic</td>
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CHAPTER IV

DISCUSSION

**Aerobic and Anaerobic Incubations**

The soil microbial community responded differently under two different atmospheric conditions used for sample processing in this study. These results support the use of an anaerobic chamber to preserve anaerobic conditions for the analysis of wetland sediments. For example, when CO$_2$ respiration and CH$_4$ efflux were each measured after samples had been processed in an anaerobic atmosphere, differences in patterns of overall microbial functional capacity (via PCA, Figure 3) were evident between natural wetlands and all classes of created wetlands. In contrast, old created wetlands showed distinction from other wetland ageclasses for both gas measurements under ambient, aerobic conditions. Popp *et al.* (2000) indicated that significant differences arose in methane production rates from peat samples when handled under anaerobic conditions in a nitrogen-filled glove bag compared to ambient conditions. They hypothesized that oxygen toxicity to methanogens led to the difference, and the differences in CH$_4$ efflux and CO$_2$ respiration between anaerobic and aerobic conditions in my study support their hypothesis. Any alteration of the methanogen community in a soil could alter the degree to which CO$_2$ is taken up as an electron acceptor and methane is formed as a byproduct of anaerobic respiration.

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Natural vs. Created Wetlands

The first objective of this study was to determine if microbial functional capacity differed between natural and created wetlands. Catabolic evenness and catabolic richness were calculated to illuminate patterns, or capacities, of carbon source utilization by wetland soil microbial communities. Significant differences in catabolic richness and evenness between natural and created wetlands were evident when CO$_2$ efflux was measured after samples had been processed under aerobic conditions in the laboratory showing that under some conditions the soil microbial community in created wetlands has a lower functional diversity than natural wetlands.

Additionally, when all efflux data points from samples handled under anaerobic conditions were fit to a principal components model, natural wetlands were distinct from every ageclass of created wetlands, having principal components scores significantly different from other wetland classes along the first axis of variation. From this, it is apparent that the overall functional capacity of the microbial community in the natural sites differs significantly from that of created wetlands.

The five natural wetlands stood apart from created wetlands in several, general site characteristics, which holds one possible explanation for why the natural wetlands harbor a microbial community which functions differently in some aspects from created wetlands. The individual wetlands having the highest soil
moisture, soil carbon content, soil nitrogen content and plant biomass were all natural wetlands (Table 1), and natural wetlands as a class had significantly higher amounts of soil moisture, carbon and nitrogen than any class of created wetland (Katie Hossler, unpublished data). It has been shown that differences in the catabolic response of a given soil sample is a reflection of both: 1) the genetic diversity of the soil microbes present and 2) an indication of soil conditions (Degens 1999). In a later study, Degens et al. (2000) found the amount of soil organic carbon in a given site to be an important influence on microbial functional diversity. These findings are in accord with natural wetlands in this study exhibiting higher evenness and richness in carbon source catabolism while at the same time having higher soil carbon content.

**Age Effect in Created Wetlands**

A second goal of this study was to determine whether there was any evidence of a shift in microbial community function across the different ageclasses of created wetlands. The question being: Do created wetlands more closely resemble natural systems as created wetlands age?

The *young, mid, and old* categories assigned to the created wetlands in this study were arbitrary designations related more closely to the history of wetland mitigation policy rather than any particular ecological factor. The terms *young, mid* and *old*, used in this study to refer to the relative ages of created wetlands, begin to lose meaning when considering a wetland such as the natural site at
Pickerington Ponds which is thought to be part of a remnant system formed during the retreat of the Wisconsinian glaciations, between 10 and 20 thousand years ago. The created wetlands studied in this work represent ecosystems created as a result of contemporary public policy, and they are at the very beginning of ecosystem establishment relative to their natural counterparts. Data from created wetlands were compared to site age in linear regression analysis to determine if wetland age as a continuous variable, rather than wetland ageclass as a categorical variable, was a more reliable predictor of the functional capacity of a wetland’s soil microbial community function. There was no relationship between the age of a created wetland and the catabolic evenness or richness of its microbial community (see Table 4, column 1). Age since creation, taken by itself, is apparently not a good indicator of the catabolic richness and evenness of the soil microbial community in these created wetlands.

Under aerobic conditions, old wetlands were distinct from other wetland classes, among which there were significant differences between young wetlands and a grouping of both mid and natural wetlands. If the functional capacity of the soil microbial community in a wetland showed successional development over time, one would expect that any groupings of similar wetland ageclasses in a PCA model would be consecutive (i.e., young and mid would be similar to one another but not to old and natural wetlands). It does not support the hypothesis that microbial function in created wetlands is developing in a linear trajectory when the oldest created wetlands in this study are more dissimilar to natural wetlands.
than mid-aged created wetlands. PCA results of the soil microbial communities under anaerobic conditions suggest that created wetlands do not become more similar to natural wetlands with time because all created wetland ageclasses were grouped together (no significant differences). Alternatively, any succession that would occur in microbial community development may take place over a longer timeframe than that which is represented in this study (wetlands created up to 39 years ago).

The two wetlands in the *old* ageclass, Big Island B and Killdeer Plains, differ in several qualitative characteristics from the other created wetlands included in this study, which correlate with the differences observed via the PCA analysis of respiration under aerobic conditions in soil microbial community function between old wetlands and all others. The *old* category in this study only consists of two wetlands which exhibit certain structural characteristics that are unique from other wetlands in this study. The *old* wetland class is the only ageclass where all wetlands included are impoundments (most other sites in this study are classified as depressional, except for the Big Island wetlands, A-C, and New Albany which are all mixes of impoundment and depressional designs). The old wetlands are also unique in soil texture being the only sites, aside from Big Island A, which have clay soils. The two mid-aged created wetlands in this study were created prior to the popularization of wetland mitigation, and their construction included the use of dikes and open water patches for use by waterfowl. That the old wetlands could exhibit differences in physical characteristics due to structural
differences and their intended function is one possible explanation for old created wetlands harboring a soil microbial community with functions distinctly from other classes of wetlands.

Conclusions

The goal of this study was to compare the functional characteristics of soil microbial communities in natural wetlands and a series of created wetlands. The null hypothesis stated that soil microbial communities in natural and created wetlands share the same functional characteristics and that soil microbial communities amongst the study sites were functionally indistinct via the catabolic response profile method. Using the catabolic response profile technique, I was able to detect differences between soil microbial communities in a suite of natural and created wetlands, thus I can reject the null hypothesis that soil microbial communities are functionally indistinct among natural wetlands and created wetlands of all ages.

Results from this study correspond with other recent studies of early-successional and late successional wetland ecosystems by Campbell et al. (2002), Atkinson and Cairns (2001) and D'Angelo et al. (2005) where significant differences in site characteristics or microbial community structure and function were measured. Campbell et al. (2002) measured soil and vegetative characteristics in 12 created wetlands of varying ages and 14 reference wetlands and found differences between natural and created wetlands as well as...
differences between younger and older created wetlands. Similar to this study, the authors found that older wetlands were not necessarily becoming more similar in condition to reference sites. Atkinson and Cairns (2001) found a set of 20 y.o. created wetlands had higher litter decomposition rates than a set of 2 y.o. wetlands, but that neither group of wetlands exhibited decomposition rates which approached that of natural wetlands. D'Angelo et al. (2005) found differences in microbial community structure between young (under seven years old) created wetlands compared to natural wetlands using the phospholipid fatty acid method (PLFA) and were able to link these community distinctions to differences in moisture regime between wetland types.

Current wetland mitigation policy relies on the assumption that created wetlands are capable of acting as surrogates for natural wetland ecosystems which have been removed from the landscape. Wetland restoration ecology emphasizes the need to restore degraded (or destroyed) systems along both structural and functional trajectories (see Zedler and Kercher 2005) to achieve a historical or 'natural' wetland status. Central to a created wetland's function is its ability to carry out local, watershed-level and global nutrient cycling functions, such as denitrification and carbon sequestration, in the same capacity as the previously-existing wetland which has been replaced. If a series of created wetlands does not harbor a soil microbial community with the capacity to function in a manner indistinct from similar natural wetlands, which this research suggests, then the ability of these created wetlands to contribute to carbon and nitrogen cycling in a
similar fashion, and ultimately the ability of created wetlands to functionally replace natural wetlands, is called into question.

Created wetlands may well be following a 'reclamation' trajectory toward a dynamic equilibrium which is significantly different from the historical status of lost original wetlands (Zedler and Kercher 2005). The differences in soil microbial community function between natural and created wetlands, with the absence of a clear successional trend support the conclusion that created wetlands are indeed "a new subclass of wetlands on the landscape" (Fennessy et al., 2004), at least within the timeframe of wetland creation encompassed by this study.
REFERENCES


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