

Linking soil process and microbial ecology in freshwater wetland ecosystems

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Abstract Soil microorganisms mediate many processes such as nitrification, denitrification, and methanogenesis that regulate ecosystem functioning and also feed back to influence atmospheric chemistry. These processes are of particular interest in freshwater wetland ecosystems where nutrient cycling is highly responsive to fluctuating hydrology and nutrients and soil gas releases may be sensitive to climate warming. In this review we briefly summarize research from process and taxonomic approaches to the study of wetland biogeochemistry and microbial ecology,

and highlight areas where further research is needed to increase our mechanistic understanding of wetland system functioning. Research in wetland biogeochemistry has most often been focused on processes (e.g., methanogenesis), and less often on microbial communities or on populations of specific microorganisms of interest. Research on process has focused on controls over, and rates of, denitrification, methanogenesis, and methanotrophy. There has been some work on sulfate and iron transformations and wetland enzyme activities. Work to date indicates an important process level role for hydrology and soil nutrient status. The impact of plant species composition on processes is potentially critical, but is as yet poorly understood. Research on microbial communities in wetland soils has primarily focused on bacteria responsible for methanogenesis, denitrification, and sulfate reduction. There has been less work on taxonomic groups such as those responsible for nitrogen fixation, or aerobic processes such as nitrification. Work on general community composition and on wetland mycorrhizal fungi is particularly sparse. The general goal of microbial research has been to understand how microbial groups respond to the environment. There has been relatively little work done on the interactions among environmental controls over process rates, environmental constraints on microbial activities and community composition, and changes in processes at the

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ecosystem level. Finding ways to link process-based and biochemical or gene-based assays is becoming increasingly important as we seek a mechanistic understanding of the response of wetland ecosystems to current and future anthropogenic perturbations. We discuss the potential of new approaches, and highlight areas for further research.

Keywords Microbial ecology · Wetlands · Microbial function · Wetland ecology · Nitrification · Denitrification · Methanogenesis · Microbial communities · Mycorrhizal fungi

Introduction

During the past two decades there has been increasing interest in understanding factors controlling ecosystem processes such as decomposition of organic matter, nitrification, nitrogen fixation, denitrification, methanotrophy, and methanogenesis. Research to date has been primarily focused in two areas: biogeochemical studies of process, and microbial ecological studies of populations and community structure. While significant progress has been made in each area, such as description of processes like methanogenesis (Le Mer and Roger 2001), or the occurrence and population dynamics of the organisms responsible for a given process like methanogenic bacteria (Utsumi et al. 2003), we still lack a mechanistic understanding of the connection between measured processes and the biology of the organisms responsible for those processes. Such a connection is now not only possible, but is also critical in increasing our ability to protect, restore and manage ecosystems.

This linkage is particularly important in freshwater wetland ecosystems. These wetlands, because of their complex hydrology and nutrient cycling and presence in both urban and unmanaged areas, are uniquely positioned to influence biogeochemical cycling in many regions and at many scales. Wetland ecosystems are characterized by hydric soils and hydrophilic plant communities (Mausbach and Parker 2001) and have fluctuating hydrology that gives rise to interplay between aerobic and anaerobic processes

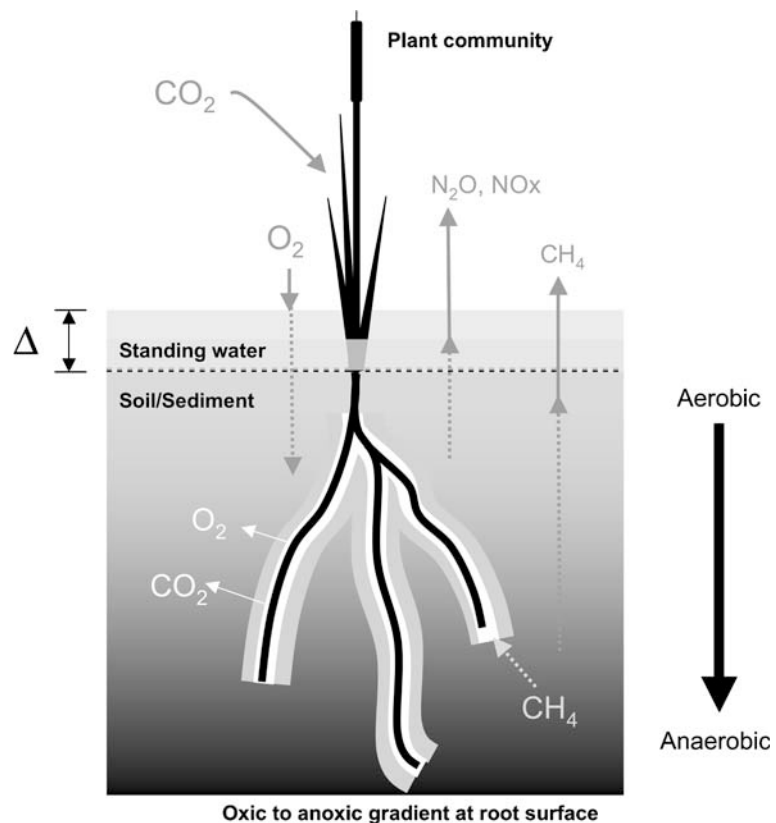
(Davidsson et al. 1997; Stepanauskas et al. 1996) (Fig. 1). Human activities such as alteration of water, sediment, and nutrient loads to wetlands may significantly alter wetland plant communities (Kercher and Zedler 2004), and wetland microbial communities (Mentzer et al. 2006). In high latitude ecosystems, hydric soils currently under permafrost may be critical as sources of radiatively active gases (Freeman et al. 2001). A mechanistic understanding of carbon and nutrient cycling in wetlands is thus important for global scale climate modeling efforts, as well as for regional scale restoration and protection of wetland systems.

In general, wetland studies have tended to focus either on measurement of microbial-mediated process (e.g., measurements of nitrate or methane evolved from a system) or they focus on characterization of microbial (usually bacterial) populations or communities (e.g. using genetic probes to research a specific microorganism or characterizing community lipid or DNA composition). The type of work conducted in managed versus unmanaged wetlands also seems to be split; process-based studies of nutrient and carbon fluxes have more often been focused on unmanaged systems, while wastewater treatment facilities, polluted areas, and constructed wetlands have been the focus of the majority of microbially-based research (Gilliam 1994).

These differences in methodological approach, often dictated by epistemological differences between microbiologists and ecosystem ecologists, have resulted in a limit to our conceptual understanding of the link between wetland microbial community composition, biogeochemical processes rates, and points of control. The lack of interdisciplinary combination may thus be a barrier to a more synthetic understanding of freshwater wetland ecosystem function and instead results in a more qualitative, compartmentalized understanding.

Work to date has laid the foundation for future guiding questions: How do we scale up from microorganisms to regional or global ecosystem function? How can we tie microbial physiology/metabolism to larger scale nutrient cycling and ecosystem function? Is it important to tie the biology of the organisms to their functional processes? The answers to these questions will almost

Fig. 1 Wetland structure. Water table height, depth from surface, and distance from plant roots create oxidic to anoxic gradients. The result is a complex interplay between anaerobic and aerobic conditions that allows for a wide range in processes to occur in wetland soils



certainly require overcoming methodological barriers between microbial taxonomic or phenologic assays (genomics, microscopy, molecular techniques) and process measurements, as well as epistemological barriers (i.e., differences in 'ways of knowing' science) between researchers trying to link these fields (Balsler et al. this issue).

In this review we summarize current research from both process and structural/taxonomic

viewpoints, discuss work to date on combining structural and functional techniques, and finally suggest research areas that will benefit most from the combined approaches. The overall goal is to explore ways to we can increase our mechanistic understanding of wetland system functioning in the context of current anthropogenic changes.

Microbially mediated processes and controls

The dominant processes, studied in a variety of ways (Table 1), that have been the focus of wetland microbial research include denitrification and nitrification, methanogenesis and methanotrophy, sulfate and iron oxidation/reduction, and enzyme activities (Tables 2 and 3). While there are certainly other microbially mediated processes important to wetlands (e.g., nitrogen fixation and the mobilization of secondary nutrients such as copper, manganese and magnesium), these have been less studied and fall outside the scope of this review.

Table 1 Methods used to study wetland microbial processes

Method	Example references
in situ measurements	Chang and Yang (2003)
Isotopic labeling	Stepanauskas et al. (1996)
Laboratory incubation	Lowrance et al. (1995)
Potential assay (lab incubation optimizing conditions for the process of interest)	Groffman and Crawford (2003)
Enzyme activity assays	Groffman et al. (1996) (denitrifying enzyme activity)

Table 2 Wetland denitrification rates

Ecosystem type	Denitrification rate (^a kgN ha ⁻¹ yr ⁻¹ or ^b mgN g soil ⁻¹ d ⁻¹)	Method used	Reference
Maple swamp (SPD) ¹	5.7 ^a	Laboratory incubation	Hanson et al. (1994)
Maple swamp (PD) ¹	6.3 ^a	Laboratory incubation	Hanson et al. (1994)
Maple swamp (VPD) ¹	16.3 ^a	Laboratory incubation	Hanson et al. (1994)
Riparian forest	68 ^a	Laboratory incubation	Lowrence et al. (1995)
Riparian forest (SPD) ^{1,2}	4.9 ^a	Laboratory incubation	Groffman and Hanson (1997)
Riparian forest (PD) ^{1,2}	8.3 ^a	Laboratory incubation	Groffman and Hanson (1997)
Riparian forest (VPD) ^{1,2}	39.3 ^a	Laboratory incubation	Groffman and Hanson (1997)
Wet meadow	2.68 ^a	in situ	Goodroad and Keeney (1984)
Wet meadow	735 ^a	Incubation/isotopic labeling	Stepanauskas et al. (1996)
Wet meadow	546 ^a	in situ	Stepanauskas et al. (1996)
Wet meadow sand	430 ^a	Laboratory incubation	Davidsson and Leonardson (1997)
Wet meadow peat	220 ^a	Laboratory incubation	Davidsson and Leonardson (1997)
Wet meadow peat	562 ^a	in situ	Davidsson and Stahl (2000)
Wet meadow sandy loam	102 ^a	in situ	Davidsson and Stahl (2000)
Wet meadow silt loam	255 ^a	in situ	Davidsson and Stahl (2000)
Coastal wetland ³	205 ^a	Laboratory incubation	Tomaszek et al. (1997)
Riparian forest	5.6 ^b	Potential assay	Pavel et al. (1996)
Riparian forest	86 ^b	Denitrifying enzyme activity	Groffman and Crawford (2003)
Riverine wetlands-silty	1.6 ^b	Laboratory incubation	Johnston et al. (2001)
Riverine wetlands-clayey	2.7 ^b	Laboratory incubation	Johnston et al. (2001)
12 wetlands	0.6–108 ^b	Denitrifying enzyme activity	Groffman et al. (1996)
10 US wetlands	8.2–130 ^b	Laboratory incubation	D'Angelo and Reddy (1999)
Maple swamp (PD) ¹	4.2 ^b	Denitrifying enzyme activity	Duncan and Groffman (1994)
Maple swamp (VPD) ¹	10.2 ^b	Denitrifying enzyme activity	Duncan and Groffman (1994)
Riparian forest ⁴	1.9 ^b	in situ	Clement et al. (2002)

Denitrification rates from a variety of wetlands have been assessed. Rates have been converted to a common unit

- (1) PD = poorly drained soil, VPD = very poorly drained soil, SPD = somewhat poorly drained soil
- (2) Values are averages over two sample years from soils over a toposequence of parent materials
- (3) Values are an average of laboratory incubation rates
- (4) Rates from Clement et al. (2002) are an average over toposequence zones

Denitrification, the anaerobic transformation of nitrate to nitrous oxide and dinitrogen gas (Myrold 2005) has been studied widely due to its potential importance in removal of nitrate (Gilliam 1994) (Table 2). Concern over methane as a greenhouse gas has prompted much of the current research on methanogenesis (the anaerobic production of methane from organic matter breakdown performed by methanogenic archaea), another widely studied wetland process (Table 3; Wolf and Wagner 2005). Aerobic processes such as nitrification and methanotrophy have been studied less in freshwater wetlands and may occur only in surface waters or other aerobic niches in wetland soils (such as near roots, Colmer 2003; Fig. 1). Rates are lower than those for anaerobic processes in wetlands (Tables 2 and 3), but may

still be significant for wetland nutrient cycling (Duncan and Groffman 1994; Le Mer and Roger 2001). Iron and sulfate reduction have been studied primarily because of their importance in acid mine drainage (Sparks 2003), but other than at acid mine sites, these processes have been studied less and are less well understood. Sulfate reduction appears to have similar variability and rates as methanogenesis (Table 3). Finally, enzymatic degradation of large polymers such as cellulose or chitin is particularly of interest in wetland and riparian soils as an indicator of biogeochemical cycling, and as a potential source of soil feedback to climate change (Dick and Tabatabai 1992; Freeman et al. 1997, 2001). Measurements of enzyme activity in wet soils are relatively few, and they vary widely across

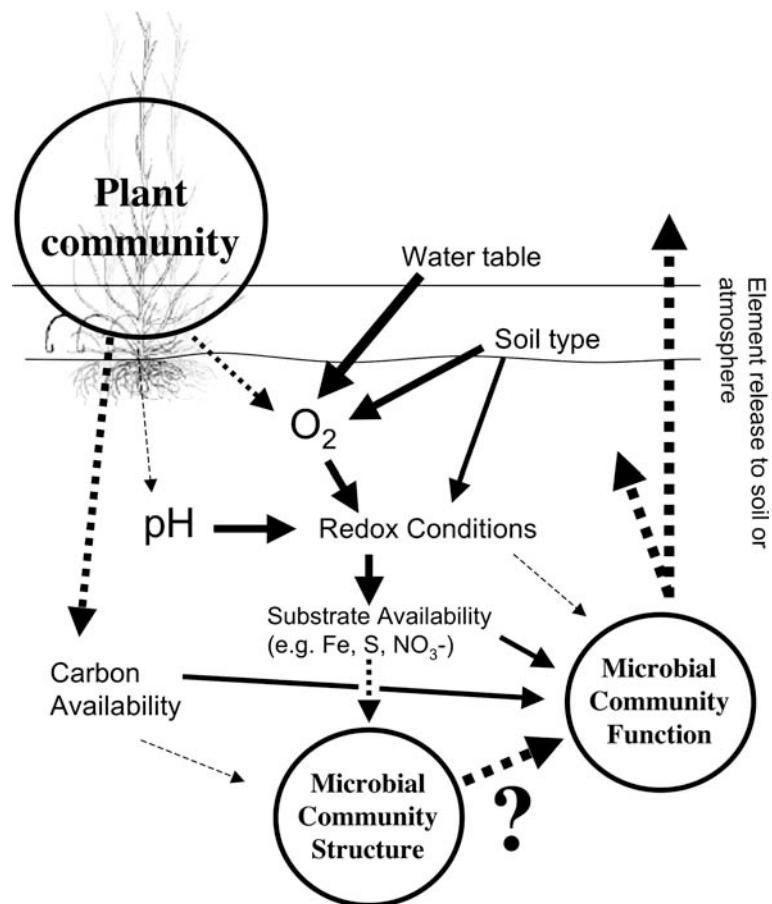
Table 3 Wetland process rates

Process	Ecosystem type	Process rate (^a kg ha ⁻¹ yr ⁻¹ or ^b mg g soil ⁻¹ d ⁻¹)	Method used	Reference
Nitrification	Swamp forest	15 ^a	Potential assay	Zak and Grigal (1991)
Nitrification	Maple swamp PD ¹	0.3 ^b	Potential assay	Duncan and Groffman (1994)
Nitrification	Maple swamp VPD	1 ^b	Potential assay	Duncan and Groffman (1994)
Nitrification	Riparian forest	-0.07 ^b	Potential assay	Groffman and Crawford (2003)
Nitrification	Riparian forest	0.12 ^b	Potential assay	Groffman and Crawford (2003)
Nitrification	Riparian forest	0.1 ^b	in situ	Clement et al. (2002)
Nitrification	Riparian wet meadow	0.1 ^b	in situ	Clement et al. (2002)
Nitrification	12 wetlands	-0.25–1.0 ^b	Potential assay	Groffman et al. (1996)
Methanogenesis	N. Taiwan wetland	159 ^a	in situ	Chang and Yang (2003)
Methanogenesis	N. Taiwan wetland	12.3 ^a	in situ	Chang and Yang (2003)
Methanogenesis	N. Taiwan wetland	20.2 ^a	in situ	Chang and Yang (2003)
Methanogenesis	Boreal peatlands	-10.58–2,883 ^a	Laboratory incubation	Huttunen et al. (2003)
Methanogenesis	Review of many	0–28,470 ^a	Laboratory and in situ	Le Mer and Roger (2001)
Methanotrophy	Review of many	0–620 ^a	Laboratory and in situ	Le Mer and Roger (2001)
Sulfate reduction	10 US wetlands	10–110 ^b	Laboratory incubation	D'Angelo and Reddy (1999)
Iron reduction	Riparian Forest	6379 ^a	Laboratory incubation	Roden and Wetzel (1996)

Several process rates from a variety of wetlands have been assessed. Rates have been converted to a common unit

(1) PD = poorly drained soil, VPD = very poorly drained soil. Values are an average of 3 sites

Fig. 2 Relationships among controls over wetland ecosystem microbial communities and element cycling. Arrows indicate relationships, and width of arrows indicates relative importance of relationship for ecosystem functioning. Dashed arrows represent interactions that are poorly understood, even though they may be important



different wetland ecosystems (Kang and Freeman 1999; Burns and Ryder 2001; Mentzer et al. 2006). All of these processes vary greatly between wetland types (Tables 2 and 3), and the explanation likely lies in greater understanding of process controls.

Factors such as temperature, moisture, and seasonality of temperature and moisture act to control wetland microbial activities, resulting in changes in key biogeochemical cycles (Fig. 2). A review of the factors controlling wetland processes may offer insight into the large variation in processes and rates among wetland types (such as riparian forests, wet meadows, and fens) and provide an overall framework for understanding potentially important factors in wetland ecosystem function.

Hydrology has consistently proved an important controlling variable. Studies with experimentally varied water level have yielded relatively straightforward and predictable results. In general, increased water level increases the rate of anaerobic processes (denitrification, methanogenesis, and sulfate reduction), and decreases rates of aerobic processes (nitrification) presumably by decreasing available oxygen and thereby increasing anaerobic soil microsites (Table 4). Drying/wetting cycles may also be important in increasing enzyme activities (Burns and Ryder 2001; Corstanje and Reddy 2004) and stimulating denitrification in wet cycles and increasing nitrification in dry cycles (Qiu and McComb 1996; Tanner et al. 1999; Eaton 2001; Venterink et al. 2002). Wet-up cycles after seasonal wetland dry-down may be important for nitrogen cycling and loss from the system (Smith and Tiedje 1979). The study not only of water quantity, but also of dynamic processes such as drying/wetting cycles is important in understanding wetland functioning, as fluctuating hydrology is a dominant feature of wetland nutrient cycling. Indeed, researchers are realizing more and more that temporal fluctuations in soil environments are critical in understanding ecosystem processes (Bardgett and Shine 1999; Mentzer et al. 2006).

Soil fertility and/or substrate availability also influences wetland process rates. For the most part, microbial processes in wetlands have higher rates under conditions of higher soil fertility, or when the

substrate of the process in question is added or is abundant (Table 4). Exceptions have been reported by King (1996) for methanotrophy, and by Feng and Hsieh (1998) for sulfate reduction (Table 4). However, the King (1996) study was performed in a peat marsh (distinct from other wetland types), and controls on methanotrophy there may be distinct from non-peat accumulating wetlands. Alternatively, factors other than methane availability control methanotrophy in peat wetlands. The exception in sulfate reduction may simply be the low number of studies on sulfate cycling compared with other freshwater wetland processes (Tables 3 and 4). Feng and Hsieh found that sulfate loading increased sulfate reduction in only one of two swamp soils. They attributed the difference to soil properties.

pH is another important but poorly studied control over wetland process soil pH may regulate methanogenesis (Yavitt et al. 2005), methanotrophy (Dedysh and Panikov 1997b) oxidative enzyme activities (Williams et al. 2000), and nitrogen transformations (Davidsson and Stahl 2000). The role of pH in affecting process rates and in structuring microbial communities has received increased attention, and is an area where there is need for more future research.

Perhaps the least resolved level of control over wetland functioning is the effect of plant species presence and relative abundance (Table 4). While it is relatively well established that the presence of plants usually increases microbial process rates in wetlands (Table 4), the importance of plant species composition or plant community structure remains unclear (Kao et al. 2003; Kao-Kniffin and Balser in press). There is wide variation in results to date, likely due to the extremely limited number of studies in this area. The few that have been done have yielded inconsistent results. While plants can influence microbial activities directly through provision of carbon, and indirectly through rhizosphere ventilation, the mechanistic link between above and below ground community structure has yet to be established (Bardgett and Shine 1999; Wolters et al. 2000). However, examination of plant species effects based on their nutrient content might prove helpful as a framework for this understanding. Work by Hume et al. (2002) indicates

Table 4 Controls over wetland process

Process	Control factors						
	Water	Temperature	Seasonality	Soil fertility	Substrate	Plant presence	Plant species
Denitrification	+ ¹	+ ² /– ³	Spring and, or Fall ⁴ /no effect ⁵	+ ⁶	+ ⁷	+ ⁸	+ ⁹ /– ¹⁰
Nitrification	– ¹¹	nd	Summer ¹² /no effect ⁵	+ ¹³	+ ¹⁴	+ ¹⁵	– ¹⁶
Methanogenesis	+ ¹⁷	+ ¹⁸ /– ¹⁹	Summer ²⁰	+ ²¹	+ ²²	+ ²³	+ ²⁴
Methanotrophy	nd	nd	Summer ²⁵	nd	+ ²⁶ /– ²⁷	+ ²⁸	nd
Iron reduction	nd	nd	nd	+ ²⁹	+ ²⁹	+ ^{30,31}	nd
Sulfate reduction	+ ³²	nd	nd	+ ³³ /– ³³	+ ³³ /– ^{33,34}	nd	nd
Hydrolytic enzyme activity	– ³⁵	+ ³⁶ /– ³⁶	Summer ³⁶ /no effect ³⁶	nd	+ ³⁷ /– ³⁸	nd	nd
Oxidative enzyme activity	no effect ³⁹	nd	nd	nd	nd	nd	nd

Research is summarized to determine whether a process increases (+) or decreases (–) in response to each control factor. Superscript numbers indicate number (below) for references. ‘Water’ and ‘temperature’ indicates a process rate changes when water level or temperature are increased. ‘Seasonality’ is the most active season for each process. ‘Soil fertility’ indicates a process rate change in sites of differing fertility or added fertility (including available organic carbon). ‘Substrate’ indicates response of the given process to substrate additions; for instance, the response of denitrification to nitrate. ‘Plant presence’ indicates process rate change when plants/roots are present. ‘Plant Species’ indicates whether process rates change under different plant species. References: (1) Smith and Tiedje (1979); Ambus and Christensen (1993); Hanson et al. (1994); Groffman and Hanson (1997); Davidsson and Leonardson (1997); Jordan et al. (1998); Flite et al. (2001); Hunter and Faulkner (2001); Groffman and Crawford (2003) (2) Willems et al. (1997) (3) Kuschik et al. (2003) (4) Zak and Grigal (1991); Ambus and Christensen (1993); Hanson et al. (1994); Lowrance et al. (1995); Davidsson and Leonardson (1997); Tobias et al. (2001) (5) Clement et al. (2002) (6) Ambus and Christensen (1993); Verhoeven et al. (1996); Groffman and Hanson (1997); Jordan et al. (1998); Bachand and Horne (2000); Davidsson and Stahl (2000); Van Hoewyk et al. (2000); Casey and Klaine (2001); Brusse and Gunkel (2002); Groffman and Crawford (2003) (7) Ambus and Christensen (1993); Kirkham and Wilkins (1993); Schipper et al. (1993); Hanson et al. (1994); Seitzinger (1994); Davidsson and Leonardson (1997); Delaune et al. (1998); Jordan et al. (1998); White and Reddy (1999); Casey and Klaine (2001); Davidsson et al. (2002) (8) Smith and Delaune (1984); Kristensen et al. (1998); Tanner et al. (1999) (9) Lawrence et al. (1995); Eriksson and Andersson (1999); Bachand and Horne (2000) (10) Otto et al. 1999; Johnston et al. (2001); Clement et al. (2002) (11) Qiu and McComb (1996) (12) Zak and Grigal (1991) (13) Zhu and Ehrenfeld (1999) (14) Matheson et al. (2003) (15) Engelaar et al. (1995) (16) Otto et al. (1999) (17) Coles and Yavitt (2002); Freeman et al. (2002); Rask et al. (2002); Bellisario et al. (1999); Wickland et al. (1999); Van den Pol-Van Dasselaar et al. (1999); Macdonald et al. (1998); Hargreaves and Fowler (1998) (18) Westermann (1993); Granberg et al. (2001); Updegraff et al. (1998); Yavitt et al. (2000) (19) Updegraff et al. (1998); Yavitt et al. (2000) (20) Wieder and Yavitt (1991); Huang et al. (2005) (21) Basiliko and Yavitt (2001); Yavitt and Lang (1990); Weider and Yavitt (1991) (22) Segers (1998); Brauer et al. (2004) (23) Segers (1998); Kim et al. (1998); Coles and Yavitt (2004) (24) Strom et al. (2003); Rask et al. (2002) (25) Segers (1998) (26) Vandernat et al. (1997); Dedysh and Panikov (1997a); Megonigal and Schlesinger (2002) (27) King (1996) (28) Vandernat et al. (1997) (29) Roden and Wetzel (2002) (30) Weiss et al. (2004) (31) Roden and Wetzel (1996) (32) Devito and Hill (1999) (33) Feng and Hsieh (1998) (34) Vile et al. (2003a) (35) Freeman et al. (1996, 1998); Kang et al. (1998); Kang and Freeman (1999); Yavitt et al. (2004) (36) Kang and Freeman (1999) (37) Shackle et al. (2000); Gusewell and Freeman (2003) (38) Wright and Reddy (2001) (39) Freeman et al. (1996); Williams et al. (2000)

that denitrification rates can be related to plant carbon quality. Another useful direction for future research might be to focus not only on empirical measurements of the end-result (process rates), but also on the plant/microbe interactions associated with a given process. Plant species-specific interactions with bacterial or fungal populations can influence process rate and occurrence. For example, nitrogen-fixing bacteria require close association with plant roots and

depend on very specific host–microorganism interactions (Graham 2005; Wolf and Wagner 2005). A small body of research has demonstrated that rhizoplane (root surface) dwelling nitrogen-fixing bacteria have been shown to vary between plant species (Chelius and Lepo 1999; Bergholz et al. 2001; Prieme et al. 2002). In direct contrast, rhizoplane dwelling methanotrophs do not appear to vary between plant species (Calhoun and King 1998). Therefore plant species and plant

community composition may influence nitrogen fixation rates but not methane consumption rates; thus showing the importance of understanding interactions between specific microorganisms, plant species, and the related process rates.

Interactions among biogeochemical cycles have not been well studied, but may be another important control over wetland processes. For example, methane production may be limited by microbial iron oxide reduction (based on a decrease in methanogenesis in rhizosphere samples with high rates of iron reduction) (Roden and Wetzel 1996, 2003). Electron flow can also be diverted from methanogenesis toward iron oxide reduction when microorganisms are in the presence of crystalline iron oxide (Roden 2003). Sulfate reduction may be more important to total anaerobic carbon mineralization than methane production (Vile et al. 2003a, b); and sulfate deposition may even decrease methane production (Blodau et al. 2002; Gauci et al. 2004). Methane production and sulfate reduction may decrease with increased nitrate/denitrification rates (Westermann and Ahring 1987). Studies of multiple processes indicate there may be important interactions that add to the complexity of wetland biogeochemistry. It is difficult, however, to synthesize the contribution of these studies from the small research base currently available.

In conclusion, hydrology and substrate availability are the primary keys to understanding variability in process rate and occurrence. Areas that may be particularly important for future research are the importance of pH and plant community structure in process control. In addition, while functional studies have provided a detailed empirical understanding of many wetland soil process rates and their controls, there are conceptual limitations to studying function alone that become apparent when results among studies are inconsistent or when more complex aspects of wetland ecosystem function are examined. In these cases, the research could provide more insight if it was approached not only from a process standpoint, but from a microbial standpoint as well. Use of methods that combine these two aspects is unfortunately rare. Below, we briefly review microbiological (community and taxonomic) research to date in wetland ecosystems.

Microbial communities and populations in wetland soils

Microorganisms have been characterized in freshwater wetland ecosystems using a variety of approaches and methods (Table 5). General community structure (fingerprints) has been described using biochemical techniques such as phospholipids fatty acid analysis (PLFA) and less often with gene-based fingerprinting techniques (such as terminal restriction fragment length polymorphisms, TRFLP). The majority of microbial studies in wetlands have been focused on bacterial groups that carry out processes of interest. In general, studies of wetland soil microbiology are few, and thus more difficult to synthesize.

PLFA analysis has been used to report differences in community composition in different wetlands (Borga et al. 1994; Sundh et al. 1997; Boon et al. 1996) as well as across gradients of nutrient stress in peatlands (Borga et al. 1994). Lipids have also been used to assess rhizosphere effects on community composition (Halbritter and Mogyorossy 2002). In general these studies suggest that microbial community composition varies between wetland sites and that differences may be due to differences in water level (Sundh et al. 1997; Mentzer et al. 2006).

Wetland microbial research has focused far more on specific microorganisms responsible for key processes than on general microbial community fingerprints. Studies of methanotrophic bacterial communities in wetlands indicate that acidic peatlands have unique genetic composition (Dedysh et al. 1998a, b, 2000, 2003; Dedysh 2002; Warttinen et al. 2003; Sizova et al. 2003; Kemnitz et al. 2004). Methanogenic communities may also be unique in peatlands (Utsumi et al. 2003). The importance of unique communities responsible for key processes has been demonstrated in upland areas (Schimel and Gullledge 1998; Cavigelli and Robertson 2000). In these studies, rather than processes being controlled by environmental factors such as soil water content or methane availability, the physiology of the microorganisms themselves was uniquely adapted to extant conditions and could influence process rates independent of changes in the environment.

Table 5 Methods used to study wetland microbial communities/taxa

Method	Short description	Example reference
Lipid analysis	Analysis of lipid membranes indicating coarse scale community differences	Boon et al. (1996)
Community genetics	16s rRNA genes are amplified to examine genetic diversity in samples	Wartiainen et al. (2003)
Functional genetics	Microbial taxa are distinguished based on functional gene differences	Chelius and Lepo 1999
Physiological tests	Utilization of various substrates such as carbon	Bergholz et al. (2001)
Gram stain	Characterization (+ or –) based on cell wall structure	Casamatta et al. (1999)
Culture techniques	An organism is cultured in a laboratory and characterized	Dedysh et al. (1998a)

These and other recent studies have been seminal in demonstrating that the typical ecosystem ecology approach of ‘black-boxing’ the microbial community can lead to erroneous inference about process control (Balser et al. 2001; Schimel 2004; Balser and Firestone 2005). Further work in wetland ecosystems may prove valuable.

Iron reducing and oxidizing bacteria (IRB) have also been characterized in freshwater wetlands (Lowe et al. 2000; Kusel et al. 2003; Weiss et al. 2003; Emerson et al. 1999). This is significant: prior to the discovery of active iron cycling by bacteria, iron oxidation was thought to be an exclusively physical process (Neubauer et al. 2002). Iron oxidizing bacteria may inhibit abiotic iron oxidation and compete with other rhizosphere microorganisms (Lowe et al. 2000; Neubauer et al. 2002), as well as live in close conjunction to iron reducing bacteria (Sobolev and Roden 2002). The importance of biotic control over what was once thought to be an abiotic process is an area for further study.

Another focus has been sulfate reducing bacteria (SRB), common in salt marshes. While salt marshes are not a focus of this review and SRB may only be important in acidic peatlands having significant sulfur levels, the research approaches used in studying SRB in salt marshes are more complete than many approaches to date in freshwater systems, and may thus be a useful model for how to link community structure and functioning. Salt marsh SRB, abundant in the rhizosphere (Gandy and Yoch 1988), are a diverse group representing both cultured and

non-cultured lineages of sulfate reducing delta-proteobacteria (Banat et al. 1981; Frischer et al. 2000; Klepac-Ceraj et al. 2004; Nedwell et al. 2004; Bahr et al. 2005). Sulfate reducer population size has been correlated with decreases in sulfate concentration (Fortin et al. 2000). In addition, sulfate reducers may (Fortin et al. 2000; Edgcomb et al. 1999) or may not (Koretsky et al. 2003), be more abundant during the winter months. Selective discrimination has been used to suggest the presence of different functional groups of sulfate reducers (acetate versus H₂ oxidizers) present in salt marsh sediments (Banat et al. 1981). Sulfate reducers have been characterized in the rhizosphere of *Spartina alterniflora* using sulfate reduction measurements, MPN, and molecular techniques (Hines et al. 1999) to show that nearly half of the *Spartina* rhizosphere consists of culturable sulfate reducers and that sulfate reduction rates and relative abundance of SRB increase in correlation with plant growth. This interaction among sulfur cycling by bacteria and plant community composition merits further study. In addition, this body of research, connecting population sizes with substrate availability, sulfate reduction rates, and determination of differing SRB functional groups, has yielded a body of knowledge that connects ecosystem-level (process-level) sulfate reduction with the organisms performing the process. More work such as this would substantially help bridge the gap between microbial community structure and wetland nutrient cycling.

It has generally been assumed that fungi are not dominant in wet soil, and there has been little study of mycorrhizal associations in freshwater wetlands (Mentzer et al. 2006). However, mycorrhizae may play an important functional role, and mycorrhizal association was the focus of a recent review (Anupam 2003). A group of studies characterize mycorrhizal abundance in a range of wetlands and find that although fertility is certainly correlated with geographic location, changes in soil characteristics, vegetation zone, and soil matric potential—rates of AMF colonization may be lower in high fertility sites (Wetzel and VanderValk 1996). Wetland AMF colonization may drop significantly under high phosphorus addition (White and Charvat 1999; Cornwell et al. 2001; Stevens et al. 2002). Mycorrhizal fungi have also been characterized at sites with varying hydrologic gradients. Turner and Friese (1998) found significant levels of mycorrhizal–root associations at all moisture levels (including saturated and inundated soils) from rehabilitated fen and wet prairie sites. While AMF can be found at all levels along moisture gradients from dry to excessive moisture, abundance may decrease under very high water content (Rickerl et al. 1994; Miller and Bever 1999). In particular, AMF species accustomed to dry environments may be very sensitive to high water levels (Miller and Bever 1999), indicating that water level is an important factor in AMF colonization.

Mycorrhizal community composition is also likely sensitive to plant community structure. It has been clearly demonstrated that plant species composition is important for AMF colonization (Ingam and Wilson 1999), especially with regard to the extent of aerenchyma (Cornwell et al. 2001). In addition a single plant species may harbor a diversity of mycorrhizal fungi (Bhat and Kavrapa 2003; Wirsal 2004). Several studies have found significant levels of AMF–root association among a variety of plant species using a range of analysis techniques (Glenn et al. 1991; Stenlund and Charvat 1994; Brundrett et al. 1996; Turner et al. 2000; Jayachandran and Shetty 2003; Anupam 2003; Bohrer et al. 2004; Mentzer et al. 2006). However, despite the potential importance of mycorrhizae in wetlands, the significance of mycorrhizal diversity and plant–mycorrhizal

associations in wetland systems is currently unknown.

In conclusion, it is well established that wetland conditions support anaerobic bacteria such as methanogens, denitrifiers, sulfate reducers, fermenters, and acetogens (Conrad 1996). While less well known, it is also possible that aerobic organisms such as nitrifiers and methanotrophs may play an important role in wetland ecosystem functioning. And despite longstanding conventional wisdom that says fungi are not abundant or important in wet systems, it has now been demonstrated that mycorrhizal fungi are often abundant in wetlands and may play a significant role. Therefore, there is need for further research into the role and importance of aerobic bacterial populations and mycorrhizal associations. There have been few studies of general microbial community structure in wetlands, and current understanding of microbial communities extends little beyond description. There is a basic need for more descriptive or exploratory of microbial community structure, as well as for studies that combine process approaches with studies of microbial physiology and taxonomic distribution.

Towards an integrative mechanistic understanding of wetland system functioning

Ultimately the goal in much of wetland research is to understand and predict process rates. Methane and nitrous oxide release may be important feedbacks to atmospheric chemistry. However our understanding of wetland functioning to date remains largely descriptive. A mechanistic understanding will require that we obtain basic information about the ecology of the major organisms that influence nutrient cycling as well as the physiological mechanisms that drive ecological processes within ecosystems, and that we then couple this with process measures. While ecosystem ecologists have traditionally approached soils as a black box in which nutrient transformations are conducted by an uncharacterized community of microbes (Tiedje et al. 1999; Treseder and Allen 2000; Balser et al. 2001), this approach limits our ability to predict how or why belowground processes respond to

environmental conditions. An investigation of mechanisms requires that we ask questions regarding effects of environmental conditions on the ecophysiology and distributions of specific microbial groups (Schimel 2004; Schimel et al. in press). If soils do not respond to perturbations as predicted by ecosystem theory, is it because the relevant microbial groups were not present in the soil, or is it because another factor limited the microbes' ability to respond? We know very little about the roles of individual microbial species in nutrient cycling under field conditions. In addition, we lack information regarding ecophysiology of microbes in situ.

Ultimately, a combination of approaches can lead to greater understanding of population dynamics and role in wetland biogeochemical cycling. Few in number, but important as groundbreaking studies, several research groups have devised innovative strategies using molecular or biochemical approaches coupled with process-based assays or isotope tracers.

For example, analyses of DNA sequences allow us to determine which microbial groups are present in the soil, and characterizations of gene expression enable us to focus on processes. These two can be addressed simultaneously by using other novel techniques such as nucleotide analog labeling (Borneman 1999) and stable isotope probing (Radajewski et al. 2003). In nucleotide analog labeling, bromodeoxyuridine (BrdU) is added to field samples and active microbes absorb the compound and incorporate it into newly-synthesized DNA. BrdU-labeled DNA can then be extracted from the samples and sequenced. In this way, we can characterize microbial groups that respond to varying environmental conditions by proliferating or becoming dormant, and species niches can be mapped (Borneman 1999).

Stable isotope probing involves flushing field samples with ^{13}C - or ^{15}N -labeled substrates. Microbes that take up these substrates will produce labeled cell components (e.g., DNA, RNA, membrane lipids). Analysis of membrane lipid ^{13}C content can directly indicate substrate use by bacteria or fungi (Butler et al. 2003). Labeled DNA can be separated from unlabeled DNA by ultracentrifugation. RNA with specific sequences

can also be isolated for measurement of natural abundance stable isotope signatures (MacGregor et al. 2002).

Other ways to link processes with organisms responsible for the process include the use of selective inhibition techniques or microarrays targeted for a given group of organisms. For example, in the study of sulfate loading by Feng and Hsieh (1998), either selective inhibition of SRB or use of microarrays created to show activity of SRB specific versus other sulfate reduction could allow determination of whether added sulfur was being used by sulfate reducing bacteria (SRB) or by other microorganisms. Competitive PCR techniques have also been used in conjunction with sulfate reduction rates to show a correlation between sulfite reductase abundance and sulfate reduction rates (Leloup et al. 2004). In another example of methodological advance, Roden (2003) quantified methanogenesis and iron reduction rates while simultaneously examining electron flow to methanogens and iron reducing bacteria (IRM).

Biochemical and activity assays can also be combined. Enzyme activities and lipid analysis have been used in combination to better understand microbial community response to disturbance under *Phragmites* and *Spartina* in undisturbed versus anthropogenically affected marshes (Ravit et al. 2003). Significant differences were found in lipid profile and enzyme activities between plant species at each site, with plant species having a larger effect at the undisturbed site. Lipid and enzyme data differed in that enzyme activities varied both by plant species and site groupings, whereas lipid profiles varied mostly by site. The use of enzyme and lipid analyses provided insight not available from each alone.

Other notable studies include work by Castro et al. (2002) in which sulfate reducing bacterial populations and sulfate reduction rates were measured along a nutrient gradient in the Florida everglades. This study reported high diversity of sulfate reducers based on molecular fingerprinting, including members of *Desulfatoma* and uncultured organisms as the dominant members of the community. Agreement between MPN and sulfate reduction rates indicated

greater microbial activity and populations in eutrophic soils (supported by Fortin et al. 2000). Similarly, in a study of salt marsh rhizoplane nitrogen fixing microorganisms, nitrogen fixation was quantified alongside relative abundance measurements of specific rhizoplane diazotrophs in order to determine the effects of fertilization (Bagwell and Lovell 2000). Results indicated that while diazotrophs were responsive to treatments, where there was inhibition of nitrogen fixation the diazotrophs always recovered and showed no lasting impact from fertilization treatments. The conclusion drawn by Bagwell and Lovell (2000) was that the microbial community changed to compensate and maintain function. Last, in a study of activity versus community structure of methanotrophic microorganisms, Horz et al. (2002) used molecular fingerprinting, most probable number (MPN) assays and methane oxidation measurements to characterize the methanotrophic microorganisms from a wet meadow. Cell density (MPN) accounted for measured rates of methane oxidation. Varied community diversity results were reported based on MPN versus molecular fingerprinting techniques (both techniques did report *Methylocystis* with disagreement of other dominant methanotrophs between the methods).

There are many challenges, both conceptual and methodological, in increasing our mechanistic understanding of ecosystem functioning. Further understanding of wetland ecosystems will come from studies that combine process-based and microbial population focused approaches to ecology. This last section of studies demonstrates the power of approaching process study from a microbial perspective. When microbial competition or electron-flow to various organisms in a community is measured in some way, a more mechanistic understanding of overall wetland biogeochemistry can be achieved.

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