

Effects of wetland plants on denitrification rates: a meta-analysis

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Abstract. Human activity is accelerating changes in biotic communities worldwide. Predicting impacts of these changes on ecosystem services such as denitrification, a process that mitigates the consequences of nitrogen pollution, remains one of the most important challenges facing ecologists. Wetlands especially are valued as important sites of denitrification, and wetland plants are expected to have differing effects on denitrification. We present the results of a meta-analysis, conducted on 419 published estimates of denitrification in wetlands dominated by different plant species. Plants increased denitrification rates by 55% on average. This effect varied significantly among communities as defined by the dominant plant species, but surprisingly did not differ substantially among methods for measuring denitrification or among types of wetlands. We conclude that mechanistically linking functional plant traits to denitrification will be key to predicting the role of wetlands in nitrogen mitigation in a changing world.

Key words: community structure; ecosystem services; functional traits; global change; nitrogen cycle.

INTRODUCTION

Identifying general relationships between biotic community structure and ecosystem function is a key challenge facing ecologists. Changes to biotic communities that result from global climate change, sea-level rise, species introductions, or selected harvesting are likely to have a substantial effect on biogeochemical processes (Chapin et al. 2000, Lavorel and Garnier 2002, Kremen and Ostfeld 2005). Nonetheless, attempts to link simple measures of community structure to ecosystem process have often met with limited success (Lawton 1999, Simberloff 2004). For example, a large number of studies have found that relationships between biodiversity and a number of biogeochemical processes are often complex and statistically weak (Hooper et al. 2005). Such a result is not necessarily surprising. Ecosystem processes are often most strongly influenced by those organisms in a community that contribute most to biomass and productivity, or which play unique biogeochemical roles (Lavorel and Garnier 2002, Suding et al. 2008). Due to differences in key traits, dominant organisms can vary widely in their effects on the local chemical and physical environment, as well as on other species in the community (Eviner and Chapin 2003, Laughlin 2011). Therefore, we may expect ecosystem processes to be closely linked to the identity of the dominant species in an ecosystem.

We apply meta-analytic techniques to relate published values of wetland denitrification to plant community composition as defined by the dominant species present.

Manuscript received 29 September 2014; revised 23 June 2015; accepted 17 August 2015; final version received 14 September 2015. Corresponding Editor: D. Schimel.

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This study represents an important first step in a broader effort to develop a more mechanistic incorporation of community structure into models of the nitrogen cycle. Humans have more than doubled the amount of nitrogen fixation on a global basis, with highly industrialized areas experiencing mineralized nitrogen concentrations up to 25 times that of pre-development concentrations (Vitousek et al. 1997, Hinga et al. 2005). Movement of excess fixed nitrogen into downstream ecosystems, particularly nitrogen-limited coastal ecosystems, results in eutrophication, hypoxia, and harmful algal blooms, all of which may have severe consequences for the economy and human health (Hooper and Vitousek 1997, Vitousek et al. 1997, Hinga et al. 2005, Howarth et al. 2011). Denitrification, a microbial process in which nitrate is permanently removed from ecosystems to the atmosphere as inert dinitrogen gas (N_2), can help to mitigate the effects of mineralized-nitrogen pollution (Zedler 2003, Jordan et al. 2011). Consequently, estimating denitrification at landscape scales is a critical goal for managers of aquatic and coastal ecosystems (Hinga et al. 2005, Groffman et al. 2009). Wetland sediments are particularly important sites of denitrification because their anaerobic nature favors complete reduction of mineralized nitrogen to N_2 gas, while minimizing the release of the intermediate product, N_2O , a powerful greenhouse gas (Kralova et al. 1992, Schlesinger 2009).

Wetland plants are generally understood to play an important role in nitrogen removal by altering the sediment environment in which denitrification occurs (Caffrey et al. 2007). Denitrification is an anaerobic bacterial respiratory process that requires nitrate (NO_3^- , an oxidizing agent), organic carbon (as a reducing agent), and low O_2 concentrations to proceed. In several cases,

plants have been shown to control sediment denitrification dynamics by competing for nitrate (Schimel et al. 1989, Kirk and Kronzucker 2005), supplying labile organic carbon (Hume et al. 2002), and introducing oxygen via diffusion from roots (Caffrey and Kemp 1990, 1992). Research on plant invasions has further revealed that changes in the composition of plant communities can have a major effect on sediment microbial processes (Ehrenfeld 2003), including denitrification (Windham and Meyerson 2003). The extent and composition of wetland plant communities are changing rapidly due to species' introductions, land-use changes, sea level rise, and climate change (Bertness et al. 2002, Ehrenfeld 2003). Because plants differ in functional characteristics that may influence denitrification, broadscale changes in the composition of plant communities may substantially alter denitrification rates of future landscapes.

Despite the growing realization that vegetation may exert considerable control over denitrification rates, to date no attempts have been made to assess the generality of plant-mediated effects and incorporate these effects into predictive denitrification models (Boyer et al. 2006). Instead, efforts have more typically focused on abiotic factors, such as hydrography, water chemistry, and sediment characteristics, which are relatively easy to characterize and whose potential influence on denitrification is often more clearly understood. The influence of plant communities on denitrification may be hard to disentangle from the influence of abiotic variables because plant community structure may be correlated to a number of physical and chemical variables. Methodological concerns also pose problems for attempts to build predictive models from existing observations. Researchers have developed diverse techniques for measuring small rates of N_2 production against the enormous background concentrations in the atmosphere (Groffman et al. 2006). Whether these various methods provide comparable estimates of denitrification rates remains one of the greatest concerns in denitrification research. As an example, acetylene-inhibition methods have been found to underestimate denitrification rates relative to direct measurements of nitrogen gas production (Watts and Seitzinger 2000). If any type of method tends to be used more in a given plant community, spurious correlations between plant communities and measured denitrification could result. Alternatively, variation among methods may obscure any relationships between plant community structure and denitrification that actually exist.

We synthesize the results of a large number of denitrification studies conducted in well-characterized plant communities from across the ecological and engineering literature. Using this extensive database, we determine whether denitrification rates differ among communities dominated by specific plant species. We also evaluate the relative importance of the type of wetland system in which the studies were conducted and the methods used to measure denitrification in explaining the variation in denitrification rates among studies. The presence

of nearby non-vegetated control plots or treatments in a number of studies allow us to control for geophysical context and methodology by calculating an effect size for vegetation on denitrification rates. Using the effect-size metric, we test for generality in the effect of vegetation on denitrification rates among plant communities. We conclude by exploring possible approaches for predicting what effects specific plant communities will have on sediment denitrification rates.

METHODS

To develop an exhaustive data set, we performed a systematic review using Web of Science and Google Scholar databases, using the key terms "wetland AND plant AND denitrification." We expanded this search by including all studies cited in key review papers examining variation in denitrification rates or the effects of plants on geochemical processes (Cornwell et al. 1999, Ehrenfeld 2003, Caffrey et al. 2007), and we searched for all papers citing any of these reviews. Publication dates ranged from earliest available publications to studies published in 2010. Once a list of potentially useful studies was compiled, we examined each study systematically to include only those that measured denitrification rates within well-characterized plant communities. Among these studies, plant communities were most often characterized by the dominant species inhabiting the community; therefore, we only included studies that reported a denitrification rate measurement associated with a dominant species in the community. Where percent composition was specified, the "dominant species" classification was only used if the species comprised >50% of the biomass or cover within a plant community. On several occasions in which the inputs to a wetland system were known or easily determined, investigators quantified other fates of nitrogen, such as plant uptake, and calculated denitrification by mass balance. If studies used either nitrogen removal (ammonium or nitrate removal) or mass balance to calculate denitrification, we required that they quantify other fates of nitrogen inputs or justify that denitrification was the dominant form of nitrogen removal within their system. Mass-balance studies that failed to meet these criteria were assumed to overestimate denitrification rates and were discarded.

For each plant community studied in an article, the average denitrification rate, as well as the error and sample size for that average, was recorded. Where multiple averages were recorded, we included only those averages that were collected during the growing season at independent wetland locations (or in separate laboratory or field containers). For each average denitrification measurement, we recorded the type of wetland system within which the measurement was made, as well as the method used to measure denitrification. Denitrification rates were converted to common units ($g\ N\ m^{-2}\ h^{-1}$) prior to analyses. For studies that measured denitrification per volume of sediment, volume measurements were

converted to area equivalents, given the dimensions of sediment cores analyzed. Studies that failed to report error or sample size, or failed to provide enough methodological information to convert denitrification rates to common units were excluded from further examination. Our search yielded average measurements of denitrification in vegetated sediments from 419 independent sites or mesocosms collected from 55 publications. Ninety-two of these measurements could be paired with estimates of denitrification from nearby non-vegetated control plots or treatments. A final list of measurements included in this analysis is provided in Appendix S1: Table S1.

Effect sizes were calculated as the average denitrification rate for each measurement, weighted by the inverse of the sampling variance. This calculation gives greater weight to measurements of denitrification rates with greater precision or greater replication (Osenberg et al. 1999). Data were then grouped by plant community, wetland system, and method of denitrification measurement. Any differences observed in average denitrification rates among plant communities may be the result of physiological differences in the plants themselves; however, they could also be an artifact of geophysical conditions (e.g., hydrology, nitrogen loading, salinity), which influence denitrification and, coincidentally, affect the composition of wetland plant communities. Unfortunately, geophysical conditions such as nitrogen loading were rarely reported in a way that would facilitate inclusion in this analysis. To estimate the effect of vegetation independent of geophysical context, we made use of the subset of 92 measurements that included denitrification measurements in non-vegetated control sites or treatments. For each of these measurements, we calculated the logarithm of the ratio of denitrification rate in vegetated sediments to that in nearby non-vegetated sediments. This ratio provided us with a measure of the local effect of vegetation on denitrification (Hedges et al. 1999). To test whether functional or taxonomic groupings of plant communities may explain variation in vegetation effects, we repeated this analysis, grouping plant communities at the family and genus level and into functional groups based on growth form. Growth-form categories included trees and shrubs, emergent forbs, submersed macrophytes, and floating plants. Q tests of heterogeneity were performed to test the ability of each grouping variable to explain both the variation in the effect of plants on denitrification and the variation in average denitrification rates among all measurements. A random effects model was used for these tests (Gurevitch and Hedges 2001). In the context of meta-analysis, a random effects model is a more conservative test of differences among groups in that it does not assume that a common true effect size exists for each group among measurements; rather, it includes an additional variance term that accounts for random variation in the effect of interest among measurements

(Gurevitch and Hedges 2001). For both sets of analyses, confidence intervals and probability values were estimated by bootstrapping, using 999 iterations of the data. All calculations were performed in MetaWin 2.0 (Rosenberg et al. 2000).

RESULTS

Overview of the data

Average net denitrification rates reported among all the measurements included in this analysis varied over six orders of magnitude, from -6.4 to $880 \text{ mg N}\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. Studies varied widely in purpose from documenting the effects of species invasions on denitrification rates to comparing treatment-wetland designs employing different plant species. Often, the dominant plant species at a site was reported under site characterization and was not the main focus of the study. Results were obtained from a variety of wetland systems, including 168 constructed wetland sites, 53 experimental microcosms or mesocosms, and 198 naturally occurring wetlands (including salt marshes, tidal freshwater marshes, riparian wetlands, and depression wetlands). More than 82% of the measurements involved emergent plant communities dominated by monocots, with 49% of the monocot species belonging to the family Poaceae.

Of the many methods available to measure denitrification (for a complete review, see Groffman et al. 2006), the most commonly used method was denitrification enzyme activity (DEA) and other similar acetylene-reduction techniques (Appendix S1: Table S1); DEAs and other acetylene reduction techniques accounted for over 59% of the measurements included in our analysis. The methods used to measure denitrification and the systems in which measurements were made did not appear to be strongly associated with any particular type of plant community (for complete list, see Appendix S1: Table S1). However, instances in which investigators have used multiple denitrification measurements to investigate the same plant community, or instances in which the same community was investigated in multiple wetland systems, were rarely available. Consequently, we were unable to calculate interaction terms or perform multiple regression analyses with our predictor variables.

Do denitrification rates differ among plant communities?

Measurements of denitrification differed significantly among plant communities, with differences among dominant plant species ranging over four orders of magnitude (Fig. 1a). The highest observed denitrification rates occurred in sites dominated by *Spartina alterniflora* and *Oryza sativa* (Fig. 1a). Grouping by the dominant species in a plant community explained 28% of the variation in denitrification rates among measurements (Table 1). These results were not sensitive to the removal of high-denitrification and low-denitrification plant communities from the analysis. Because we were unable to

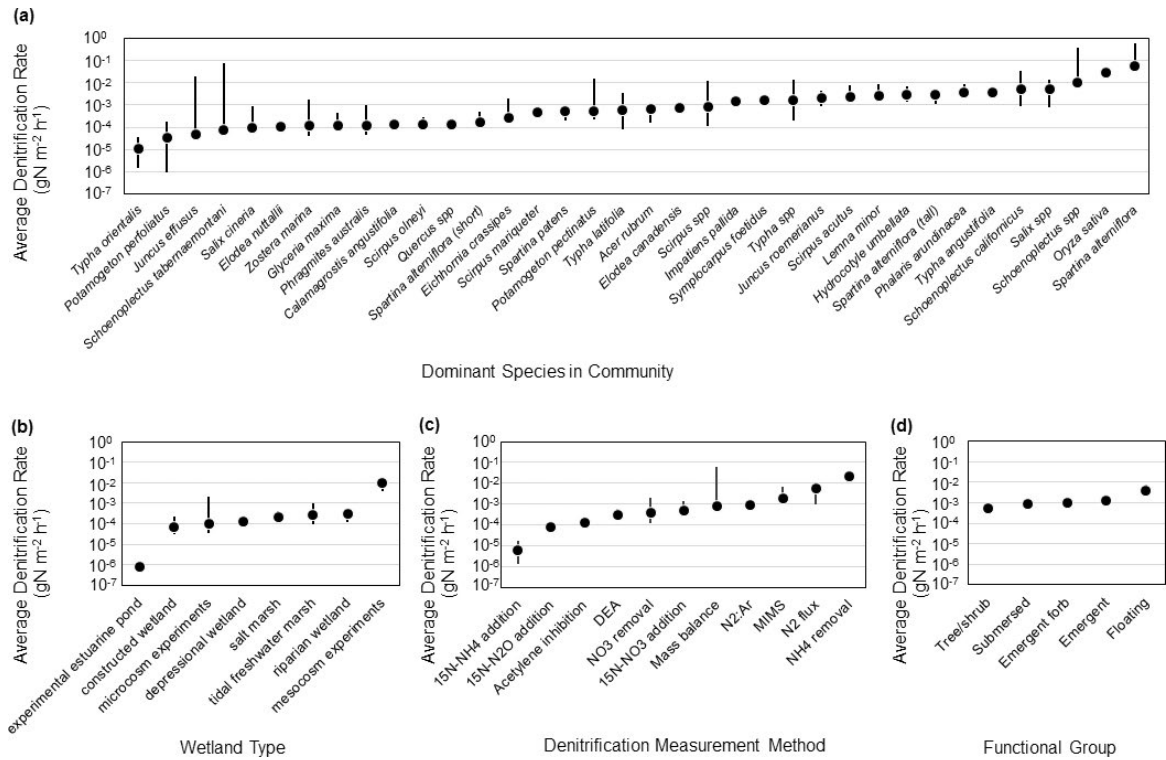


FIG. 1. Weighted average denitrification rates among (a) dominant species in the wetland plant community, (b) types of wetland in which the studies were conducted, (c) methods used to measure denitrification rates (DEA is denitrification enzyme activity, and MIMS is membrane inlet mass spectrometry), and (d) functional groups based on growth forms. Average rates are plotted on a log₁₀ scale. Error bars show bootstrapped confidence intervals, generated from 999 sampling iterations.

determine if there was an interaction between plant communities and denitrification measurements using the whole data set, we repeated this analysis for only those studies using DEA and similar acetylene-reduction methods in order to rule out a confounding effect of variation in methods among studies. This subset analysis provided statistically similar results to an analysis of the full data set ($P = 0.002$; $df = 23, 221$; variance explained = 31%).

A notably large amount of variation remained within many of the plant community groupings, including cases for which a large number of measurements were available. For example, denitrification rates observed at sites dominated by *Phragmites australis* ($n = 55$) varied by over an order of magnitude (Fig. 1a). Grouping denitrification measurements by the wetland type explained only 14% of the total variation in denitrification rates, less than half of the variation explained when grouping by plant community (Table 1). Most of this variation was explained by very low denitrification rates in experimental estuarine ponds and very high denitrification rates in mesocosm experiments (Fig. 1b). When studies conducted in experimental ponds and mesocosm experiments were removed from the analysis, differences among the remaining wetland types ranged within only one order of magnitude and explained only 2.1% of the variation in denitrification measurements.

Denitrification measurements were found to differ significantly among the various methods used to measure denitrification, but grouping by method explained only 8% of the variation in denitrification rates among measurements. The greatest estimates of denitrification were based on ammonium removal, although denitrification measurements obtained by direct N_2 flux methods, including membrane inlet mass spectrometry (MIMS) and $N_2:Ar$ measurements, also appeared higher than those obtained by acetylene reduction methods (including DEA) and ^{15}N tracer methods. When studies employing ammonium removal were removed from our analysis, grouping by denitrification measurement method explained only 2.3% of the variation in denitrification measurements (Fig. 1c). Though average denitrification rates varied significantly among functional groups (Table 1), grouping dominant species into functional groups based on their growth forms explained only 2% of the variation in denitrification measurements (Fig. 1d).

Does “the effect of vegetation” on denitrification rates differ among plant communities?

When normalized to rates in nearby non-vegetated sediments, denitrification rates in vegetated sediments varied over three orders of magnitude and differed significantly among plant communities. Average denitrification

TABLE 1. Summary of Q tests of heterogeneity for each of the three grouping variables, performed on weighted average denitrification rates.

| Source of heterogeneity | Plant community | | Wetland system | | Method | | Functional group | |
|-----------------------------------|-----------------|-----|----------------|-----|--------------|-----|------------------|-----|
| | Q | df | Q | df | Q | df | Q | df |
| Among | 4865 | 37 | 2533 | 7 | 1479 | 10 | 174 | 4 |
| Within | 12 773 | 355 | 15 330 | 402 | 16 471 | 405 | 7899 | 382 |
| Total | 17 637 | 392 | 17 863 | 409 | 17 950 | 415 | 8073 | 386 |
| P | 0.004 | | 0.004 | | 0.041 | | 0.043 | |
| Percentage of variation explained | 28 | | 14† | | 8‡ | | 2 | |

Notes: P -values are estimated from bootstrapping, using 999 iterations. Results significant at $\alpha = 0.05$ are shown in bold.

†Percentage of variation explained is equal to 2.1% when studies conducted in experimental estuarine ponds and constructed wetlands are excluded from analysis.

‡Percentage of variation explained is equal to 2.3% when measurements obtained by ammonium removal are excluded from analysis.

among communities with different dominant species ranged over two orders of magnitude (Fig. 2a), a reduction from the four orders of magnitude variation observed in non-normalized average denitrification rates. Grouping plant communities by the dominant species accounted for 38% of the variation in the effect of vegetation (Table 2). This result was not sensitive to the removal of high-denitrification and low-denitrification plant communities from the analysis. Significant variation remained within individual community groupings, most notably in *Salix*-dominated communities, for which the greatest average effect of vegetation was observed but for which this effect varied over two orders of magnitude (Fig. 2A). Vegetation effects on denitrification rates were positive for 12 out of the 16 plant communities included in this analysis, with nine of these having a positive effect on denitrification that differed significantly from zero. In four plant communities, denitrification rates were lower than those in non-vegetated sediments, but none of these differences were statistically significant. The same analysis failed to detect differences among plant communities when dominant species were grouped at either the family ($P = 0.551$, $df = 9, 59$) or genus level ($P = 0.271$, $df = 12, 57$) or by growth form (Table 2, Fig. 2d).

When normalized to denitrification rates in non-vegetated sediments, denitrification rates in vegetated sediments did not differ significantly either among different types of wetland systems or among the various methods used to measure denitrification (Table 2). Average vegetation effects ranged within one order of magnitude (Fig. 2b, c). These variables also explained far less variation in the vegetation effect than did the dominant species in the plant community (Table 2). Because this data set contained little to no overlap in predictor variables among studies, we were unable to compute interaction terms between predictors or to perform the subset analysis described for denitrification rates.

On average, we found that denitrification rates were 55% higher in vegetated sediments, relative to denitrification

rates in non-vegetated sediments ($\ln R = 0.4380$, confidence interval = 0.1460–0.7357). Thus the overall “effect of vegetation” was a 1.55 factor increase in denitrification rates.

DISCUSSION

The data set used in this study is the largest currently available on wetland denitrification, bridging extensive literatures in both ecology and environmental engineering. Our analysis of this huge data set established several key points regarding controls on denitrification. First, we found that the type of wetland studied and the method used to measure denitrification was poorly related to variability in denitrification rates. Instead, what mattered most was the presence of vegetation, which caused denitrification to be on average ~50% greater than in nearby non-vegetated sediments. Furthermore, we found that the size of this vegetative effect varied widely with plant community composition as defined by the dominant species, suggesting that the characteristics of dominant species need to be considered in future models of wetland denitrification. In the following discussion, we will discuss the implications of our main findings and their ramifications for estimation of denitrification at a landscape level.

The general lack of a systematic effect of methodology on denitrification rates was perhaps the most surprising finding to us. While we found some influence of methodology on raw denitrification estimates, differences in denitrification between vegetated and adjacent non-vegetated sediments were unrelated to the methods employed. Attempts to predict denitrification across ecosystems have been limited because of uncertainty concerning the comparability and accuracy of different methods, and because many methods can only be used under certain circumstances (Groffman et al. 2006). For example, the technique widely believed to be most accurate, changes in $N_2:Ar$ as measured by membrane inlet mass spectrometry, is technically challenging and can only be used routinely in saturated environments where

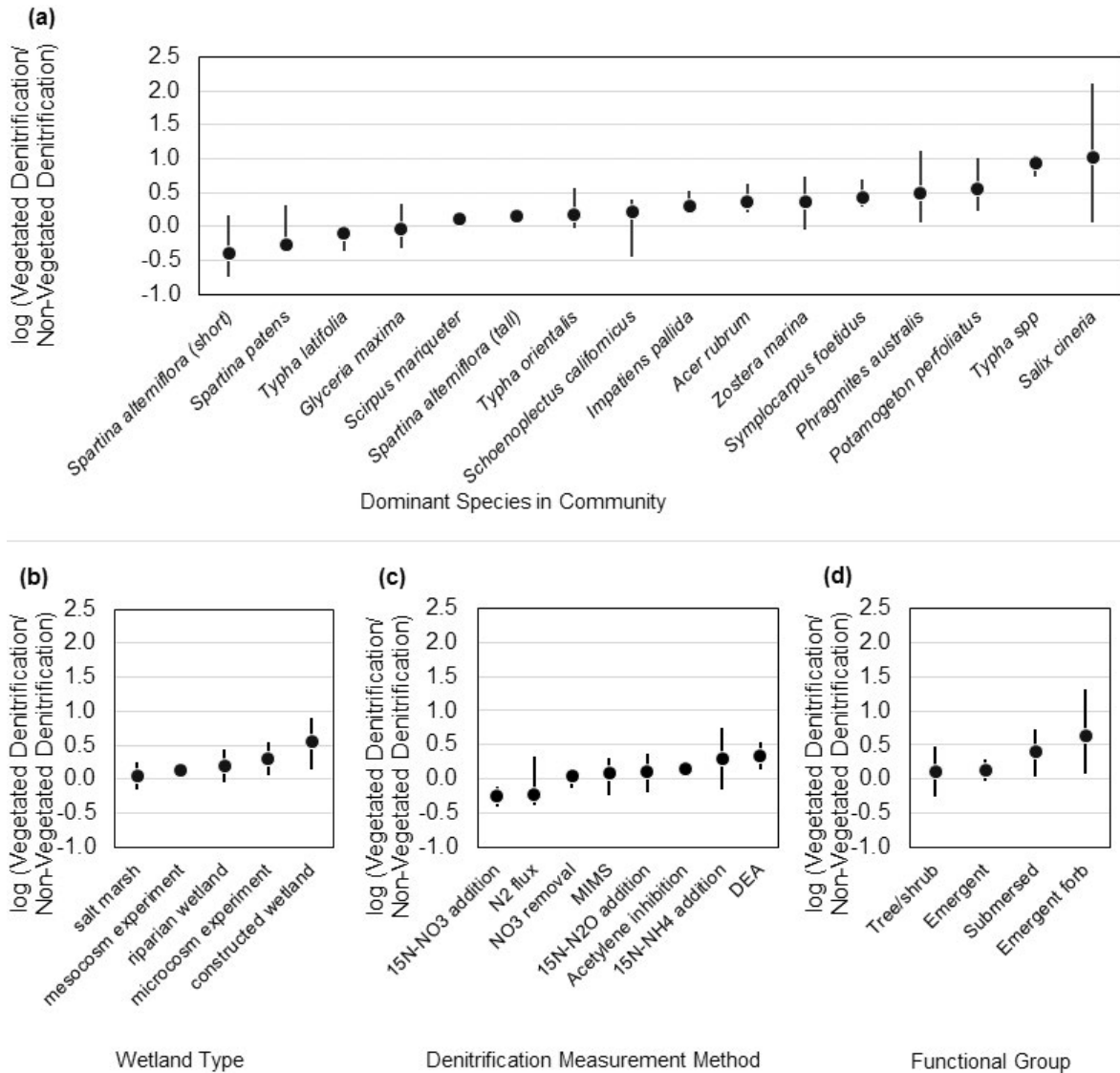


FIG. 2. Denitrification rates in vegetated sediments, normalized as a log response relative to denitrification rates in paired non-vegetated plots or treatments. Weighted means are grouped by (a) the dominant species in the wetland plant community, (b) the type of wetland system in which the studies were conducted, (c) measurements used to measure denitrification rates (DEA is denitrification enzyme activity, MIMS is membrane inlet mass spectroscopy), and (d) functional groups based on growth forms. Error bars show bootstrapped confidence intervals, generated from 999 sampling iterations.

interference from atmospheric N_2 is minimal (Kana et al. 1994). Our analysis suggests that the measurement of denitrification potential using acetylene reduction, which is cheap, technically straightforward, and feasible in most environments, can be used to assess wide-scale variation in relative denitrification rates, making broad comparative studies feasible. It also raises the possibility that absolute rates may be estimated from relative measures by calibrating them against more robust and intensive methods, such as change in $\text{N}_2:\text{Ar}$, in reference habitats that allow the use of both methods. Future analyses would strongly benefit from a greater availability of studies that estimate denitrification rates for the

same plant community using multiple measurement techniques (Watts and Seitzinger 2000, Hopfensperger et al. 2009). With these data, one could more conclusively assess relative differences in the estimates that various denitrification methods provide, without the confounding influence of differences among plant communities.

A major goal of this study was to determine if vegetation exerted a positive influence on denitrification. While enhancement of denitrification by vegetation had been observed in previous experimental studies, it was not clear that it would be broadly observed across wetland ecosystems. In addition to promoting denitrification by

TABLE 2. Summary of Q tests of heterogeneity for each of the three grouping variables, performed on log response ratios of denitrification in vegetated and non-vegetated sediments.

| Source of heterogeneity | Plant community | | Wetland system | | Method | | Functional group | |
|-----------------------------------|-----------------|----|----------------|----|--------|----|------------------|----|
| | Q | df | Q | df | Q | df | Q | df |
| Among | 81 | 15 | 16 | 4 | 23 | 7 | 9 | 3 |
| Within | 134 | 39 | 149 | 59 | 144 | 56 | 84 | 55 |
| Total | 214 | 54 | 165 | 63 | 166 | 63 | 93 | 58 |
| P | 0.04 | | 0.187 | | 0.284 | | 0.207 | |
| Percentage of variation explained | 38 | | 10 | | 14 | | 10 | |

Notes: P values are estimated from bootstrapping, using 999 iterations. Results significant at $\alpha = 0.05$ are shown in bold.

adding organic substrates and introducing oxygen that enhances generation of nitrate from nitrification, plants may inhibit denitrification by flooding the sediments with oxygen or competing with nitrifying and denitrifying bacteria for nitrogenous compounds (Schimel et al. 1989, Kirk and Kronzucker 2005). This competition for nitrogen should be particularly important in wetlands since primary production in these systems is often limited by nitrogen (Howarth 1988, LeBauer and Treseder 2008). That such competition was not sufficient to offset the positive effect of plants on denitrification would seem at first to suggest that nitrifying and denitrifying microbes significantly out compete the plants for nitrogen. However, other studies have suggested that nitrifiers are in fact poor competitors for ammonium (Verhagen et al. 1994, 1995). Alternatively, at the scale of microbes, both nitrogen sufficient and nitrogen deficient conditions could coexist side by side in soils over relatively small spatial scales. Over the larger scales experienced by plants, however, the actions of denitrifying microbes may result in an overall deficit of nitrogen relative to plant needs, resulting paradoxically in the limitation of primary production by nitrogen in an ecosystem with enough free nitrate to allow substantial denitrification.

Our data indicate that over a third of the variability in the effect of vegetation can be explained by the dominant species in the plant community. Along with previous studies of pair-wise species comparisons (Caffrey and Kemp 1990) and studies of species invasions (Ehrenfeld 2003, Windham and Ehrenfeld 2003), our findings make a clear case that community composition plays an important role in determining denitrification. That effect may actually be larger than observed here. The identity of the dominant species is an incomplete description of plant community structure, and the composition and biomass of the subdominant community, as well as interactions among dominant and subdominant species, could vary substantially within one of our community categories in ways that could significantly influence denitrification. In any case, community structure should be considered when making landscape-scale assessments of denitrification from remote sensing data or when predicting the effects of sea-level rise or species invasions on denitrification.

One obvious approach for including species composition in future assessments of denitrification would be to estimate the average rates associated with each dominant species using analyses like those conducted here. It might be possible to do so using factorial laboratory experiments under controlled conditions and technically straightforward denitrification methods, such as denitrification potential. While conceptually simple, such an approach may be complicated in practice. Relevant traits like oxygen production, nitrogen demand, and root:shoot allocation can be very plastic and may vary substantially with ambient conditions in ways that are particular to each species. Moreover, the effects of these important traits on denitrification could vary substantially with abiotic variables, such as hydrologic regime, or sediment and water chemistry. Establishing separate, context-specific relationships to predict denitrification for each community type, even for the limited number of dominant species included in this analysis, could soon prove to be a quixotic effort. Even if successfully obtained, such relationships would not necessarily account for the influence of subdominant species and may therefore fail to replicate real patterns in nature.

An alternative approach would be to identify a few distinct functional groupings of species based on their effects on denitrification. For example, emergent plants, whose leaves are in contact with the atmosphere and whose roots penetrate sediments, would be expected to have very different effects on sediment oxygen relative to submerged or floating plants that have little or no rooting structure. Consequently, functional groupings based on morphology are often expected to explain variation in the influence of plant communities on sediment processes like denitrification (Keddy 1992, Boutin and Keddy 1993). Contrary to this expectation, we found that morphological groupings of dominant species did not explain significant variation in raw denitrification rates or in the influence of plant communities on denitrification. This result is perhaps not surprising given that the highest and lowest denitrification rates observed in this study occur in emergent plant communities dominated by species in Poales (Fig. 1a), while plant communities dominated by different species in the genus *Typha* are associated with low, intermediate, and high

effects on denitrification rates (Fig. 2a). Furthermore, vegetation effects were not found to differ significantly when measurements were grouped by either the family or the genus of the dominant plant in the community. These results are consistent with previous assessments that conventional functional or taxonomic groupings are relatively less useful in predicting rates of ecosystem processes than is information about plant community composition or functional trait composition (Eviner and Chapin 2003, Wright et al. 2006).

A third approach is to describe the plant community along several continuous functional trait axes that may be relevant to denitrification, rather than by the dominant species (Eviner and Chapin 2003, Suding et al. 2008). These “aggregate functional traits” would be those likely to influence denitrification through specific effects on oxygen concentrations, nitrogen availability, or labile carbon in associated sediments. A list of such traits could include aboveground or belowground biomass, rooting area or depth, elemental composition of tissues, litter quality, etc. When applied at the community level, a trait-based approach promises to address the effect of the dominant species on denitrification while accommodating for plasticity within species and for some of the influence of subdominant species. By addressing only a few relevant functional traits at a time, it also simplifies the task of characterizing the community in ways that are relevant to denitrification. Moreover, determining how specific traits relate to denitrification can reveal which critical factors seem to be the most important determinants of this process.

Although we wanted to explore the possibility of using functional traits to predict denitrification on a preliminary basis, most denitrification-relevant traits were not reported consistently enough among taxa to be of use in our meta-analysis. Wetland plants also tend to be under-represented in online plant trait databases (Wright et al. 2004, Kleyer et al. 2008, Kattge et al. 2011). Nonetheless, we were able to find information on “average shoot height” for 16 of the taxa in our analysis belonging to the order Poales in the United States Department of Agriculture (USDA) Plants Database ([available online](http://www.plants.usda.gov))². Over some timescale, we expect that average shoot height should be correlated to nutrient demand and photosynthetic rate, which may be relevant for oxygen and nitrogen levels in associated sediments. Below a certain value, shoot height should be positively related to denitrification due to the effects of diel oxygenation of sediments on denitrification (Fig. 3a). Above a certain shoot height, we may expect sediment oxygenation will be enough to inhibit denitrification or that plants will sequester enough nitrogen that they effectively compete with nitrifiers and denitrifiers. Consequently, we expect a unimodal relationship between denitrification and shoot height. When we plot weighted average denitrification rates calculated in our analysis to average shoot heights from the USDA

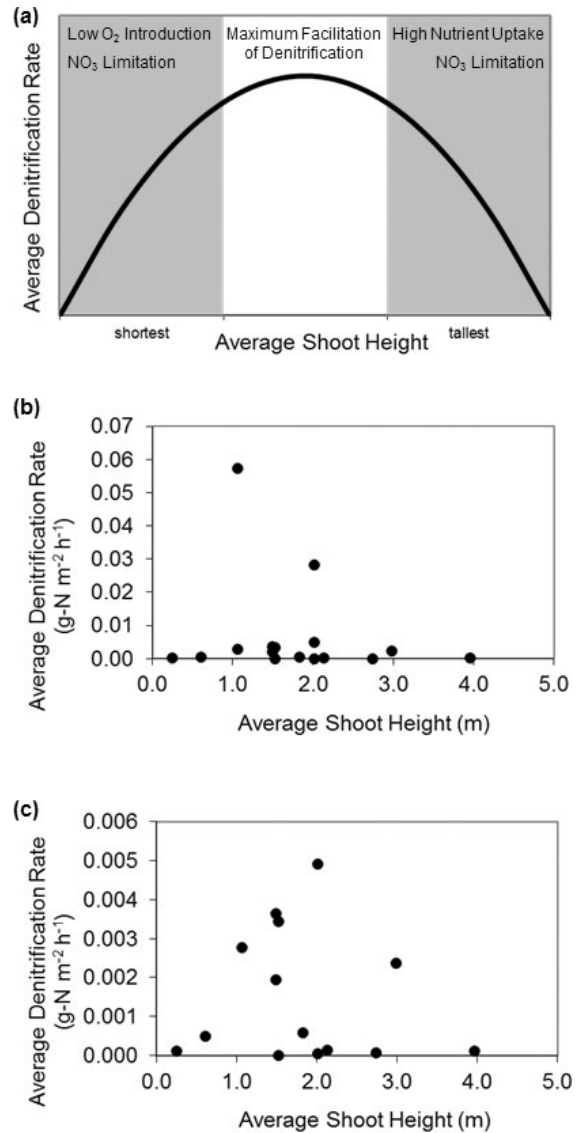


FIG. 3. (a) Denitrification may be expected to vary with plant size such that small plants introduce insufficient oxygen to sediments to facilitate production of nitrate and larger plants compete with denitrifiers for nitrate, both limiting denitrification rates. Maximum rates of denitrification would occur at intermediate plant size. (b) Among emergent plant communities, maximum rates of denitrification are observed in communities dominated by 1.0–2.0 m plants. (c) When the highest rates in *Spartina alterniflora* (1.0 m) and *Oryza sativa* communities (2.0 m) are excluded, the pattern persists. Data for average shoot height for grasses, sedges, and rushes were obtained from the USDA database.

database, we do observe a general trend of maximum denitrification rates occurring in communities dominated by species of intermediate height (Fig. 3b); this pattern is even clearer when we remove the extremely high denitrification measurements obtained in *Oryza sativa* and *Spartina alterniflora* communities (Fig. 3c).

Clearly, much more information is required in order to understand how various other plant traits, as well as

²www.plants.usda.gov

sediment properties and site history, interact to influence the effects of plant communities on denitrification. However, the patterns observed here suggest that a functional-trait approach may offer a promising way forward, particularly as the characterizations of wetland plant species that are already underway continue to become available. Functional-trait variables offer many of the same advantages as abiotic factors, in that they are relatively easy to quantify using established methods and can be generalizable, in this case according to physiological trade-offs for plants that have been shown to operate independently of plant functional type, growth form, or environment (Wright et al. 2004). A focus on key plant traits offers a general and, therefore, flexible way to link plant community composition and structure to important ecosystem process such as denitrification. Such approaches will become increasingly important as plant community distributions and compositions are expected to change in the future.

ACKNOWLEDGMENTS

We would like to thank Dianna Padilla, Jessica Gurevitch, Alistair Rogers, Stuart Findlay, and several anonymous reviewers for helpful comments on earlier versions of this manuscript, as well as Kerrie Mengersen and Jessica Gurevitch for statistical advice. This work was supported by a Tibor T. Polgar Fellowship and Graduate Research Fellowship from the Hudson River Foundation, New York Sea Grant (R/CMC-10) and a Robert R. Sokal Award for Research in Statistical Biology from the Department of Ecology and Evolution, Stony Brook University. This paper is number 1230 contributed by the Stony Brook Ecology and Evolution Graduate program.

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DATA AVAILABILITY

Data associated with this paper have been deposited in figshare: <http://dx.doi.org/10.6084/m9.figshare.1541106>