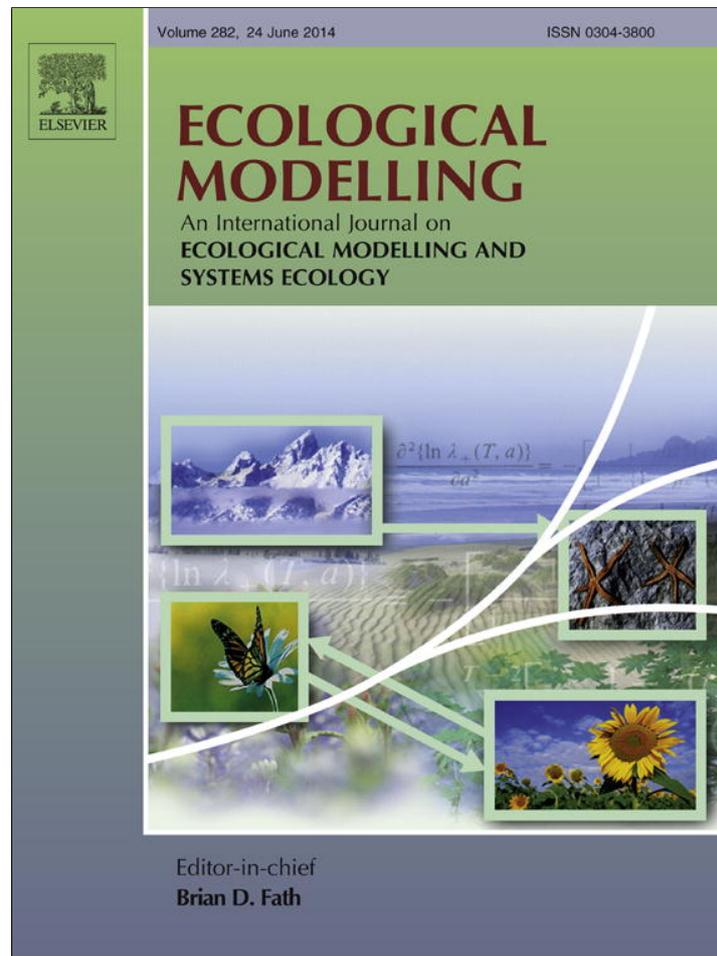


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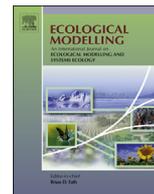
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Emergence of nutrient-cycling feedbacks related to plant size and invasion success in a wetland community–ecosystem model



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ABSTRACT

Invasive plants in wetlands may alter community composition through complex interactions related to elevated N inflows, plant size, litter production, and ecosystem N retention and recycling. To investigate these interactions, we constructed an individual-based model, MONDRIAN, that integrates individual growth and clonal reproduction, nutrient competitive interactions among species, and ecosystem processes. We conducted in silico experiments, parameterized for Great Lakes coastal marshes, where invaders that differed only in size attempted to invade native communities across a range of N inflows. Small invaders were able to persist only at low N inflow and never dominated. Large invaders were not able to reproduce clonally at low N inflow but they successfully coexisted with natives at intermediate N inflow and dominated at high N inflow, excluding natives in some cases. In both native and invaded communities, a positive feedback in plant–detritus N cycling emerged, amplifying ecosystem N cycling to nearly 2× the range of N inflows. The largest invaders augmented this N-cycling feedback over the native community by up to 23%, increasing with greater N inflow, driving community NPP higher than the native community by 33% and litter mass higher by 35%. In communities dominated by the largest invader, wetland N retention was increased but species diversity decreased. Results demonstrate that a single trait difference, plant size, simultaneously allows natives to resist invasion at low N inflows and allows invaders to dominate at high N inflows, partly through augmenting ecosystem N-cycling feedbacks.

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1. Introduction

Coastal freshwater wetlands along rivers, embayments, and on lakeshores in the Laurentian Great Lakes region of the USA were historically oligotrophic, providing habitat for plant communities adapted to low nutrient conditions. In this region, as in many regions worldwide, flows of nitrogen into coastal wetlands have increased substantially in the past half-century. The widespread use of agricultural fertilizer, the cultivation of N-fixing crops, and combustion of fossil fuels have produced elevated fluxes of nitrogen in atmospheric deposition, in groundwater flow, and in surface water runoff (Vitousek et al., 1997; Galloway et al., 2008; Han et al., 2009). Because coastal wetlands occur at the terrestrial–aquatic interface, the extent of N inputs to them depends on their landscape position, hydrology, and the types of human activities that

take place in their watersheds (Mitsch, 1992; McClain et al., 2003; Zedler and Kercher, 2004; Morrice et al., 2004).

Coastal wetlands have also been strongly affected by invasions over the past several decades by large-size clonal plants including *Typha x glauca*, *T. angustifolia*, and *Phragmites australis*. In many locations, these large-sized invasive plants grow in such dense stands over such large areas that they largely or completely exclude native marsh plants. In both field surveys and wetland experiments, dominance of invasive plants and reduced diversity of native plants often co-occur with high nutrient conditions (Galatowitsch et al., 1999; Zedler and Kercher, 2004; King et al., 2007; Trebitz and Taylor, 2007; Woo and Zedler, 2002; Tuchman et al., 2009; Farrer and Goldberg, 2009).

Disentangling the causes and effects of plant community change, including plant invasion, across wide-ranging differences in N availability is far from straightforward in these ecosystems. Causes and effects interact across several levels of organization, from individual plant physiology that drives clonal growth and reproduction, to population–community interactions and ecosystem processes such as litter production, wetland N retention, and

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N recycling. Under wide-ranging regional differences in N inflows from oligotrophic to eutrophic (hereafter referred to as a gradient in N inflows), N availability for plant uptake in any particular location is determined through complex interactions among N inflow, ecosystem-level losses of N driven by hydrologic flushing and denitrification, and N immobilization and mineralization from litter and sediment organic matter (Morrice et al., 2004; Arheimer and Wittgren, 2002; Pastor et al., 2002; Daufresne and Hedin, 2005). Ecosystem N retention, driven partly by NPP (net primary productivity) and litter production, works together with N inflow to control N availability over the long term, while at the same time elevated N availability drives greater NPP and litter production.

Where plant invasion is involved, the situation is further complicated because plant–litter–sediment cycling of N can be altered by species changes and can include community–ecosystem feedbacks (Miki and Kondoh, 2002; Ehrenfeld, 2003; Daufresne and Hedin, 2005; Liao et al., 2008; Laungani and Knops, 2009). Invasive plants frequently increase overall community NPP (Ehrenfeld, 2003; Herr-Turoff and Zedler, 2005; Liao et al., 2008). In a meta-analysis of 94 experimental studies, Liao et al. (2008) found that plant invasions significantly increased both community NPP and the availability of inorganic N in soils of forests, grasslands, and wetlands.

Invasion at elevated N availability and NPP may involve the physical effects of development of a massive litter layer that could inhibit the growth of small-statured plants. On shores of Lakes Michigan and Huron, the large-sized, fast-growing invasive *Typha x glauca* produces prodigious amounts of plant litter that can be held in voluminous layers rising 1 meter or more above the ground, supported by rigid stems that remain standing over the winter. *Typha*-invaded stands contain more than ten times the litter found in native communities in the field (see Table 4; Angeloni et al., 2006; Tuchman et al., 2009; Farrer et al., unpublished data). In a field experiment in a native oligotrophic marsh in our study region, Farrer and Goldberg (2009) found a strong reduction in light availability at the soil surface and inhibition of native species density by cattail (*T. x glauca*) litter, whereas live cattails produced no such effects on light levels or native stem density. While massive litter layers are likely to inhibit regeneration from seed of most plants, horizontal expansion of clonal stems (ramets) may be able to escape inhibition because of subsidies by maternal ramets, especially for large-stemmed clonal plants that can translocate larger amounts of resources such as C and N. This benefit of large size in clonal plants could provide an additional positive feedback for large-size clonal invaders to displace small-size natives.

Whether or not the accumulation of a massive litter layer occurs in a particular location, in these wetlands clonal translocation of C and N are likely to be key in understanding nutrient competition and thus population-level growth or decline where plant species coexist or invade (Travis et al., 2011; Kettenring and Mock, 2012). A parent ramet that is able to acquire N through uptake, or to retain it via resorption from senescing stems, can translocate N to daughter ramets, thus raising the nutrient-use efficiency (NUE) of the genet. The clonal habit is also significant because the plants do not need to regenerate from seed in each new generation. Inter-connected clones may have the ability, once well established, to inhibit the establishment of later arrivals by depleting available resources (Grace, 1987; Fukami, 2010). Such a linkage between pre-establishment and nutrient depletion could be a factor in determining degrees of invasion success at different locations along an N inflow gradient.

These complex interactions among plant size, clonal translocation, NPP, litter layer mass, and the retention, availability, and cycling of N include processes and phenomena that occur across four levels of organization: the individual, population, community, and ecosystem levels. In such a situation, it is difficult to establish causal interactions from empirical work alone. There are multiple

relevant variables and potential interactions and also typically a lack of detailed empirical data over multiple points in time (Fukami, 2010). Mechanistic models can provide insight into interwoven processes and outcomes by precisely controlling plant traits and nutrient inflows in a manner not possible in field studies, while examining detailed differences among contrasting simulations.

1.1. Objectives and approach

Our first objective in this paper is to present a fully mechanistic modeling approach to simulate the interplay of individual plant, population–community, and ecosystem processes in clonal, herbaceous wetlands. We introduce a new model, MONDRIAN (Modes Of Nonlinear Dynamics, Resource Interactions, And Nutrient cycling), that includes a suite of processes not typically combined in a single model. Individual-based models have long been proposed as providing a means to unify ecological theory from the level of the individual to the community and ecosystem (Huston et al., 1988; Judson, 1994). MONDRIAN allows examination of plant traits and individual interactions that scale to regulate community dynamics and produce ecosystem services, including maintenance of biodiversity, retention of N, and storage of C. Our second objective in this paper is to report on results of a set of *in silico* experiments using MONDRIAN to gain insight into the interwoven causes and effects across levels of organization involving plant sizes, native community pre-establishment, N inflows, and N cycling. We designed a set of model experiments around the following questions:

- (1) Does the success of potential invaders into established communities depend on their size and how does invader size interact with N inflow?
- (2) Across a range of external N inputs (inflows), does N cycling in the plant–litter–soil cycle amplify the local consequences of differences in external N inputs over time through a positive feedback?
- (3) If thicker litter layers inhibit the establishment of new stems of smaller-size species in the model, does this alter either the dependence of invasion success on plant size or the effects of invasion on N cycling in the ecosystem?
- (4) As an emergent community–ecosystem phenomenon (*sensu* Levin, 1998; Currie, 2011), does wetland N retention change with N inflow or with community change related to invader size or invasion success?

2. Methods

2.1. Overview of the MONDRIAN model

MONDRIAN is an individual-based model with an internal source–sink sub-model of C and N translocation within each plant, including intra-clonal transfers, in hundreds to thousands of ramets per square meter (depending on ramet sizes). It simulates the spatially-explicit growth and clonal expansion of each genet together with explicit spatial competition for available N as a depletable resource. This highlights one of the key features of individual-based models, that the environment can be heterogeneous in resources and ecological interactions among individuals, and also that interacting organisms can produce heterogeneity in the environment (Huston et al., 1988). Each individual is located in a patch with local resource availability where it competes within a particular, time-varying neighborhood of other conspecific and interspecific individuals. At the population level, vegetative reproduction in genets produces new individuals and mortality removes individual ramets or even entire genets. Clonal reproduction is N-limited, thus connecting the population dynamics to

spatially-explicit competition for N among individuals in a patchy resource environment. At the third level of organization, the community, MONDRIAN is capable of producing species coexistence, changes in species diversity over time, and both successful and unsuccessful plant invasions into established communities. These community-level outcomes arise from individual and population-level interactions among 3–4 species simulated together.

At the ecosystem as a fourth level of organization in MONDRIAN, C and N cycles are produced as ecosystem-level phenomena as a result of individual, population, and community-level dynamics. As individuals grow, populations grow or decline, and community composition shifts, the drivers of system-level C and N cycling shift in response through community N uptake, community litter production, and litter N immobilization and mineralization. At the same time, these community and ecosystem-level effects on N availability strongly regulate individual plant growth and competition. Local N-cycling processes combine with N inflows and ecosystem N export to determine N availability to plants, which then strongly limits both the growth of individual ramets and clonal expansion over space. Wetland N retention arises as an emergent feature that is driven by internal cycling, biomass aggradation, and accretion of the litter layer. The model operates on a daily time step. It is formulated through a set of algorithms in an object-oriented programming language (Visual Basic.Net).

Cycling of C and N occur in a spatially heterogeneous way in equal-sized grid cells. Conceptually, the grid cells are similar in some respects to those of Loreau (1998): C and N accumulate in detrital pools specific to a grid cell, N mineralization occurs within each grid cell, and plants compete within a grid cell for uptake of cell-specific pools of available N (Fig. 1). Key differences in MONDRIAN, however, are that different species can compete directly within a grid cell, grid cells can differ in species composition, plant densities, and nutrient availability, and rhizomes can connect across the space from one grid cell to another. Shed litter (from both living and recently dead plants) produced in a given cell enters the litter C and N pools of the cell in which it was produced plus the 8 surrounding, adjacent cells. Decomposition loss of litter C mass in these grid cell pools is modeled with the single-exponential equation:

$$M(t) = M_0 e^{-kt} \quad (1)$$

where $M(t)$ is the C mass at time t , M_0 is initial litter C mass, t is the model time step (day) and k is the litter decay constant (day^{-1}) (Olson, 1963; Currie et al., 2010). As C is lost from decomposing litter, no exogenous N is immobilized; the N content in fresh litter concentrates until the litter reaches the critical C:N mass ratio (Table 1), at which point N mineralization occurs in stoichiometric proportion to C mineralization (Parton et al., 2007). A proportion of the litter C mass (Table 1) is transferred to sediment organic matter (SOM) pools, occurring at a C:N mass ratio specified as a parameter (Table 1; Melillo et al., 1989; Aber et al., 1990; Currie and Aber, 1997). SOM also loses C mass via slowed decomposition (Eq. (1), Table 1), mineralizing N at the same rate as C loss. Seasonal temperature effects are included on decomposition rates to simulate increased C and N mineralization in warmer months. To constrain model complexity, microbial biomass and activity are not explicitly included, but detrital N dynamics are modeled in this empirical manner, which has proven useful to represent the roles of detritus in ecosystem C and N dynamics in prior analytical models (Loreau, 1998) as well as numerous ecosystem simulation models (Running and Hunt, 1993; Currie et al., 1999; Whittinghill et al., 2012).

Nitrogen mineralized from litter and SOM enter a pool of available inorganic N specific to each grid cell (Fig. 1). Plants in each grid cell compete (described below) to take up available N from the available pool in a grid cell, which can be depleted at the scale of a grid cell (here 7.5 cm) and time scale of one day. MONDRIAN also

Table 1

Key MONDRIAN parameters and initial conditions used for ecosystem characteristics and biogeochemistry.

Parameter	Value
Length of growing season ^a	137 days
Mean annual temperature	20 °C
Initial litter layer dry mass ^b	180 g/m ²
Critical C:N mass ratio for mineralization of N from litter layer ^b	30:1
Proportion of litter layer mass exported from ecosystem ^g	0.05 y ⁻¹
Proportion of litter mass converted to SOM ^c	0.20
Initial SOC mass in surface sediments ^d	3859 g C/m ²
Initial C:N mass ratio of SOM and C:N ratio of SOM formation ^d	54:1
First-order decay constant (k) for SOM ^e	0.005 y ⁻¹
Proportion of regional N pool exported from ecosystem ^f	0.015 day ⁻¹

Notes: SOC = sediment organic carbon; SOM = sediment organic matter. Dry mass refers to material dried at 70 °C.

^a Average of 15 marshes across North America (Brinson et al., 1981).

^b Angeloni et al. (2006).

^c Aber et al. (1990).

^d Unpublished data, measured in Cheboygan marsh and Pointe Le Barb, Michigan, USA, assuming 15 cm depth of surface sediments.

^e Calibrated in MONDRIAN to produce steady-state SOM mass for native community.

^f Calibrated in MONDRIAN to produce steady-state N cycling in native community.

^g Arbitrary estimate.

^h Based on range of values for various marsh species incubated 1 year by Chimney and Pietro (2006).

includes a “regional” nutrient pool (Loreau, 1998), a single pool of available N the size of the entire modeled area. The regional pool conceptually represents N in standing water and mobile interstitial water; it receives inflows of available N to the wetland via precipitation and runoff (conceptually including river and groundwater inputs) and also exports available N from the wetland. Conceptually, ecosystem N exports (Fig. 1) include hydrologic flushing and denitrification, although at present, detailed processes controlling rates of hydrologic flushing (such as water level) or denitrification (such as the development of an anaerobic zone in sediments) are not included. The regional pool also exchanges N, via diffusion, with the pools of available N in each grid cell. As growing plants take up N and available N in grid cells is depleted, N moves from the regional pool into grid cells (or the reverse, if litter N mineralization exceeded plant uptake demand in grid cells), representing diffusion or other mixing against a concentration gradient. A portion of the litter layer can be lost from the ecosystem each year via hydrologic export, conceptually representing the combined export of litter (Bach et al., 1986; Loreau, 1998), particulate matter, and dissolved organic C and N (Heath, 1992; Wetzel, 1992).

2.2. Plant growth, translocation, and horizontal expansion in the model

MONDRIAN simulates key aspects of clonal growth and is designed, through changes of model parameters, to be applied to numerous types of herbaceous communities and research questions. For descriptive purposes we refer to individual aboveground stems as *stems*, individual below ground organs as *rhizome nodes*, a stem and its rhizome node together as a *ramet*, a connected series of stems and rhizomes as a *genet*, or *clone*. The model includes two-way internal translocations of C and N between individual stems and their rhizome nodes (described below) as well as horizontal, one-way C and N subsidies from parent to daughter individuals within each clone.

At the start of each growing season, no living stems are present in the simulated marsh but perennial rhizome nodes contain overwintered stores of C and N. Rhizome nodes compete for uptake of available N (described below). Once a rhizome node has enough C and N (which it can request as subsidies from parents, see below) it establishes a stem and translocates the needed C and N above

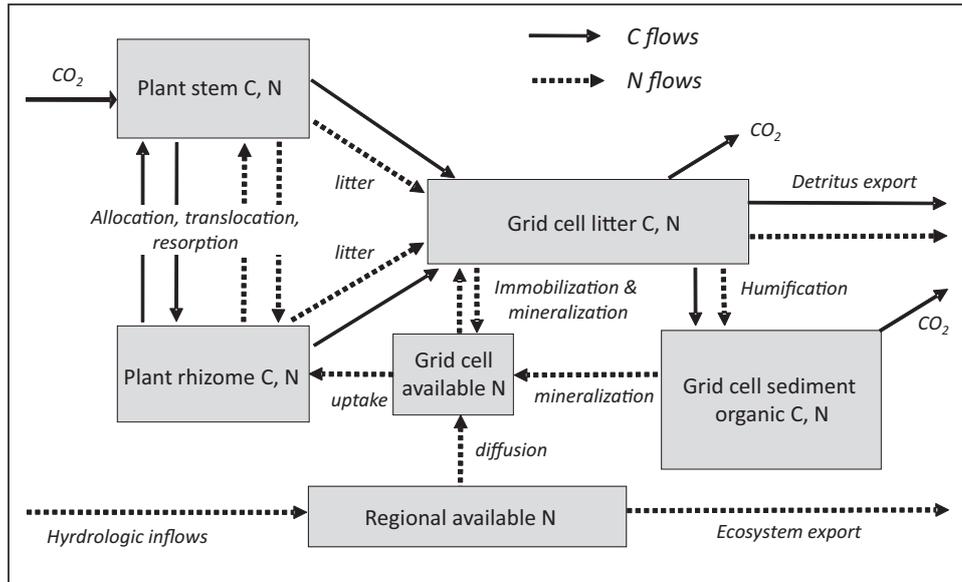


Fig. 1. Schematic diagram of pools and fluxes of C and N in the MONDRIAN model. Plant pools of C and N are specific to individuals; grid cell pools are specific to each spatially explicit cell (7.5 cm × 7.5 cm) within the modeled area, each containing numerous individual plants and allowing heterogeneous nutrient depletion; the regional nutrient pool is a single pool across the entire modeled area, akin to a pool of standing water. C flows are internally simulated in $\text{g cm}^{-2} \text{day}^{-1}$, N flows in $\text{g N m}^{-2} \text{day}^{-1}$.

ground. A stem, once established, then exerts a daily “demand” for N from its rhizome node, based on its current stem mass, its maximum relative growth rate (RGR), its target C:N stoichiometry for growth (Table 2), and maximum size by species (Table 3). Growth of each individual stem is limited by available N it is able to receive from its rhizome node. As they grow, stems translocate photosynthate C to rhizome nodes, which compete for N again in the next

Table 2
MONDRIAN plant parameters used that were independent of plant size or native v. invader status.

Parameter	Value
Maximum lifespan of rhizome nodes	4 y
Maximum relative growth rate ^a	$0.069 \text{ g g}^{-1} \text{ day}^{-1}$
Proportion of C from photosynthesis allocated belowground ^b	0.5
Ratio of maximum stem: maximum rhizome node mass for an individual ^b	1:1
Target C:N mass ratio for growth of aboveground stems ^b	18:1
Target C:N mass ratio for growth of rhizome nodes ^b	50:1
Proportion of green tissue N resorbed from senescing stems ^c	0.46
First-order decomposition (<i>k</i>) constant for litter ^d	0.8 y^{-1}
Proportion of maximum stem C that must be available for new stem allocation ^b	0.1
Maximum angle for directional rhizome growth ^a	43°
Internode distance ^e	4 cm

Notes:
^a Wildova et al. (2007).
^b D. Goldberg and K. Elgersma, unpublished data, samples collected in Cheboygan Marsh, Michigan, USA.
^c Sharma et al. (2006).
^d Calibrated to establish the approximately correct litter layer mass in native community (Table 4) under oligotrophic conditions.
^e Estimates based on typical values observed in Cheboygan Marsh, MI, USA.

Table 3
MONDRIAN maximum plant sizes used for natives and attempted invaders.

Maximum stem (aboveground) dry mass (g)	Natives			Invaders				
	0.053	0.17	0.53	0.053	0.17	0.53	1.7	5.3

daily time step based on current mass, maximum RGR, and target C:N ratio for growth (Table 2). The C:N ratios in living tissue are “targets” in the model because they drive uptake demand by setting the requirements for new tissue growth, but after rhizomes and stems are established, C:N ratios vary somewhat by individual as a result of C and N translocation within clones.

Competition arises mechanistically from aggregate demand (D_l) for N in each grid cell l :

$$D_l = \sum_{i=1}^4 \sum_{j=1}^{n_i} \frac{C_{ij} r_i}{\rho_i} \quad (2)$$

where i represents the plant species (four species were simulated in the present study), j represents the individual rhizome node within a species (where there are n individuals of species i in grid cell l), C_{ij} is the carbon mass (g) of the individual, ρ_i the target C:N mass ratio for new growth, and r_i the maximum RGR by species (both ρ_i and r_i are identical across species in the present analysis; Table 2). Uptake of N by each individual (U_{ij}) in grid cell l is then calculated as:

$$U_{ij} = \min \left[\frac{N_l}{D_l}, 1 \right] \frac{C_{ij} r_i}{\rho_i} \quad (3)$$

where \min denotes minimum and N_l is available inorganic N (g) in the grid cell prior to any plant uptake in a daily time step. In other words, the ratio of available N to aggregate N demand within a grid cell (when this ratio is <1) is used to scale back N uptake for each individual within the cell. This formulation allows competition to be highly dynamic in MONDRIAN as the numbers and sizes of neighbors change, for each of the thousands of simulated individuals, on a daily basis. When, as in the present analysis, values of maximum RGR (r_i) and target C:N ratios in new tissue (ρ_i) are equal across species, competition for N is directly proportional to size differences (perfectly size-symmetric; Schwinning and Weiner, 1998).

Table 4

Comparison of field data and MONDRIAN model results^e for key ecosystem and community characteristics. Some values are listed as mean (range). Where available, field data are from Cheboygan marsh, MI, USA.

	Native community		Community with largest invader	
	Field data	MONDRIAN	Field data (<i>Typha</i> stand)	MONDRIAN
Aboveground NPP ($\text{g m}^{-2} \text{y}^{-1}$)	351(117–473) ^a	138–331	527 ^a –1029 ^d	450–1597
Litter layer dry mass (g m^{-2})	188(40–357) ^a	161–396	2197(1857–2878) ^a	511–1880
C:N mass ratio in litter layer	13–61 ^b	46–61	27–61 ^b	34–60
C:N mass ratio in sediment organic matter	54 ^c	54	18 ^c	54

Notes: NPP = net primary production. Dry mass refers to 70 °C. For MONDRIAN simulations listed, ecosystem N inflows were 0.86–2.5 $\text{g N m}^{-2} \text{y}^{-1}$ (for native community) and 4.0–15.0 $\text{g N m}^{-2} \text{y}^{-1}$ (for community with largest invader).

^a Farrer et al. (*unpublished data*), measured in Cheboygan marsh on Lake Huron.

^b Based on aquatic macrophyte litter in the litter layer of a constructed wetlands in FL, USA, Chimney and Pietro (2006).

^c *Unpublished data*, measured in Cheboygan marsh and Pointe Le Barb, Michigan.

^d Fertilization experiment in Wisconsin (Woo and Zedler, 2002).

^e All model results listed here were not calibrated; these results arose from simulations. C:N mass ratio in sediment organic matter was initialized based on field data, and although this variable was dynamic, it changed little throughout the simulations.

Rhizome nodes are connected in series, which snake irregularly through the area (stochastically deviating from a straight line through a positive or negative angle limited by a maximum absolute value) but at present do not branch. In each genet, the newest rhizome node (after it has successfully established a stem) attempts throughout the growing season to expand horizontally by establishing a new daughter rhizome node. It can do so if it has enough C and N to establish the daughter rhizome node (via a parameter defined as a proportion of species maximum size; Table 2). Once established, a daughter competes on its own for uptake of available N within its grid cell. If a rhizome node lacks adequate N to establish a stem, it can obtain an N subsidy from up to 2 of its parents back within the clone. Parent individuals can translocate stored N to the daughter to help with new stem establishment. Because clones can be connected across grid cells, N can thus be translocated spatially from a grid cell in which a parent may dominate N uptake into an adjacent cell where a small-size daughter may face competition from either large-size plants or a high density of plants.

Given the model complexity, MONDRIAN includes extensive error-checking routines and mass-balance checks (Currie, 2007). It also includes extensive “bookkeeping” code that tracks the numbers and densities of living individuals, average individual masses, and average C:N stoichiometries by species, together with all C and N cycling pools and fluxes.

2.3. Model parameterization, tests, and simulations to address research questions

For the *in silico* experiments we report here, we constructed hypothetical clonal plants that were similar in all traits except plant size. We ran simulations in which potential invaders of a range of sizes were introduced, across a range of ecosystem N inflows, into established native communities. These included identical sets of simulations that either had (a) no effect of litter layer mass on stem emergence or (b) incorporated the potential suppression of new stem establishment as an exponential function of accumulated litter layer mass.

For species sizes, we used a series of 5 discrete values for maximum aboveground dry mass that ranged over a logarithmic scale from 0.053 g to 5.3 g (Table 3). (Because individuals in a species were heterogeneous and competition for N among neighbors controlled growth rates, the average stem sizes were below these maxima by ca. 25–40% in our simulations.) The 0.053, 0.17, and 0.53 g maximum sizes corresponded well with field-measured stem sizes of common native species in our study region, *Eleocharis smallii*, *Juncus balticus*, and *Schoenoplectus* spp., respectively, while the 5.3 g size corresponds well to *Typha x glauca*, a large-stature clonal plant that is invasive in the Great Lakes region. All other plant

traits were constant across all native and invader species, including internode distance, target C:N ratios for new tissue growth, maximum values of relative growth rate (RGR), lifespan, proportion of maximum size required to produce a new stem, and others. Parameter values came from our own field measurements or from the literature (Table 2).

Given that we used hypothetical species that differed only in maximum size, the application of MONDRIAN here is exploratory and theoretical. At the same time, MONDRIAN is an ecosystem–community model with mass balance in C and N cycling, key processes driven by C:N stoichiometry, and designed to reflect realism in community–ecosystem C and N cycling. In construction of species parameter sets, we ensured that under oligotrophic conditions (N inputs presumed below or equal to 2× rain-fed levels) the three “native species” were able to coexist throughout the full 40 y simulation period. We ensured that under oligotrophic conditions litter mass and community NPP corresponded reasonably well with that of field-measured values for native (uninvaded) communities in coastal marshes of northern Michigan (Table 4). Observational data were collected from coastal marshes on Lakes Huron and Michigan, USA, and from the literature, emphasizing coastal freshwater Great Lakes marshes (Tables 1–4). We also tested to ensure that the average dry masses of individual ramets, growth rates, numbers of stems, nutrient cycling rates, and litter production rates in the model were reasonably consistent with field-measured values for native communities (unpublished data) and calibrated the litter decomposition constant to produce the approximately correct litter layer mass in native communities under oligotrophic conditions. At the same time, we did not calibrate MONDRIAN to perfectly reproduce field-measured values of NPP, litter layer mass, and ramet densities for two reasons: first, we preferred to allow these to arise from fine-scale parameters and process interactions; second, each of these model outcomes varied dramatically over the range of nutrient inflows that we simulated.

We conducted sets of contrasting model runs, each run lasting 40 model years, with a fully factorial design of different invader sizes, levels of N inflow, and litter suppression of stem establishment *on* or *off* (described below). The 6 species combinations included the native community alone (0.053, 0.17, and 0.53 g size native plants together) and the 5 sizes of potential invaders each introduced into an established native community. (Model testing showed that each invader became well established when introduced in the absence of natives, so outcomes here depend on competition with natives. This will be explored more fully in a forthcoming paper.) Native species were established at intermediate densities in four cohorts of 65 genets per species in years 1, 3, 5, and 7, randomly distributed throughout the area. Subsequent growth in ramet densities and NPP were highly sensitive to N

inflows but at a given N inflow level, the native community was stable within 15 years. To allow the native community to first become well established, attempted invaders into native communities were introduced as partially grown individual ramets in two cohorts of 15 each, in years 15 and 20, randomly distributed spatially.

Each species combination was simulated at 8 different levels of ecosystem N inflows, ranging from $0.86 \text{ g N m}^{-2} \text{ y}^{-1}$ to $15.0 \text{ g N m}^{-2} \text{ y}^{-1}$. The lowest value represents northern Michigan present-day rain-fed N deposition on the wetland surface only: i.e., wet + dry inorganic N deposition plus atmospheric organic N deposition (NADP, 2009; Neff et al., 2002).

Finally, a simulated suppression of stem establishment through shading by accumulated litter was an additional factorial effect, set either to *off* (no effect) or *on*. When this factor was *on*, the more massive the litter layer, the more additional C and N was needed as a parental subsidy for new stem establishment, representing the additional shading of newly-emerging stems by a thick litter layer. We parameterized this effect to be greater on smaller-size species, requiring parent individuals of a smaller species to accumulate a larger amount of C and N, in proportion to the species' maximum size, before a daughter stem could be established via clonal subsidies. The parameterization of this function was based loosely on our field measurements of ramet sizes and litter mass.

The simulated area comprised 49 grid cells of $7.5 \times 7.5 \text{ cm}$ each, for a total extent of $52.5 \times 52.5 \text{ cm}$. To eliminate edge effects, the space was constructed as a torus: individuals moving off of any edge wrapped onto the opposite edge of the space. The 6 plant communities, 8 levels of exogenous N inflows, and 2 settings of the litter suppression factor produced 96 combinations of model settings; we ran each in 3 identical runs with stochastic differences (initial plant distributions and spatial movements during clonal reproduction).

In addition to the model runs described above, we performed a sensitivity analysis focused on model sensitivity and robustness related to N cycling. We selected 10 model parameters with the greatest influence on plant N uptake, N recycling, and wetland N retention. We perturbed each parameter independently, using a standard case for all: the largest size invader attempting to invade an established native community at an intermediate N inflow of $4.0 \text{ g N m}^{-2} \text{ y}^{-1}$. For each of the 10 parameters we conducted three stochastic model runs with the nominal parameter value, 3 stochastic runs each using 5 different, greater values of the parameter (+5%, +10%, +15%, +20%, +25%), and 3 stochastic runs each using 5 lower values of the parameter (−5% to −25%). This amounted to 330 additional model runs, 33 for each parameter perturbed over a range from +25% to −25%. For each parameter, over its set of 33 sensitivity runs we then tested two linear regressions for significance ($p < 0.05$): a regression of the 33 parameter values against total community NPP as the dependent variable and a regression of the 33 parameter values against ecosystem N retention as the dependent variable.

3. Results

3.1. Invasion success with invader size and rate of N inflow

In our simulations, attempted invasions went through a 10–20 year transition period to a stable community composition. The attempted invaders either failed to become established in the extant native community, became established and coexisted with natives, or came to dominate, in some cases displacing the natives (Fig. 2). When the largest size invader was not successful at dominating, the invader NPP rose in the first 10–15 years following introduction then declined as the native species regained a higher proportion of community NPP (Fig. 2a). Given the approximate stability in community composition reached after 20 y in our

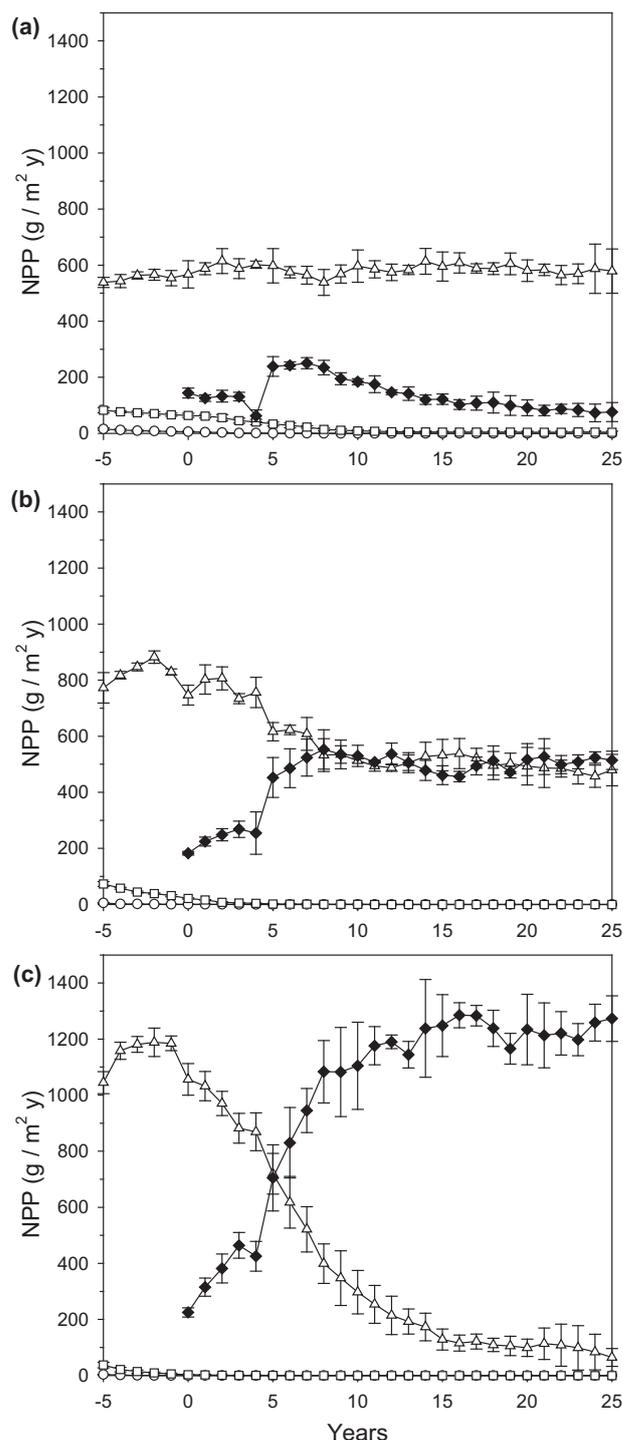


Fig. 2. MONDRIAN model results for time series of NPP (above + belowground) by species during attempted invasions of the largest invader. Open circles = native size 0.053 g; open squares = native size 0.17 g; open triangles = native size 0.53 g; Filled diamonds = invader size 5.3 g. Years since the beginning of attempted invasion are shown on the x axis. Each panel shows results from simulations using a different steady level of ecosystem N inflows: (a) $2.5 \text{ g N m}^{-2} \text{ y}^{-1}$, (b) $4.0 \text{ g N m}^{-2} \text{ y}^{-1}$ and (c) $6.0 \text{ g N m}^{-2} \text{ y}^{-1}$. Each symbol represents the mean (error bars SD) of 3 identical, stochastic model runs.

simulations, we used the mean annual NPP of each species from 21 to 25 years after attempted invasion as a measure of invasion success. NPP responses of invaders to N inflow depended on both invader size and litter suppression of new stems: in a three-way ANOVA all main effects, as well as all 2- and 3-way interactions

involving N inflow were highly significant ($p < 0.01$; data not shown). While the litter suppression factor was significant in controlling invader NPP, the general patterns of invader success as a function of invader size or N inflow were similar with this factor *on* or *off*. Therefore, in the results that follow, we consider the subset of model runs with this factor *on* (unless otherwise noted) because the overall patterns were similar and this assumption is more realistic (Farrer and Goldberg, 2009).

Invader size and success at various levels of N inflow showed a complex but systematic pattern. The smallest size invaders (0.053 and 0.17 g) were able to become established and coexist, exhibiting very low NPP, only at the low end of the N inflow gradient (Fig. 3a and b). This was similar to the patterns of coexistence of species of these identical sizes (Table 3) when introduced together in the native community (Section 3.2). The 0.53 g invader, which was the same size as the largest native, was able to become established and coexist with at least one of the native species throughout the entire N inflow gradient (Fig. 3c). At levels of N inflow $2.5 \text{ g N m}^{-2} \text{ y}^{-1}$ or greater, the 0.53 g invader dominated over the smallest and intermediate size native species, although it never came to dominate or even to equal the NPP of the largest size native (Fig. 3c). The 0.53 g invader and the largest native were identical in all respects, including size (Table 3), however the largest native benefited from being pre-established.

The 1.7 g and 5.3 g invader species, factors of 3 and 10 (respectively) larger in size than the largest native, exhibited dramatic switches in their invasion success along the gradient in N inflow (Fig. 3d and e). They were unsuccessful at low levels of N inflow, but came to dominate the community at high levels of N inflow. This switch was most dramatic in the case of the largest size invader. At the two lowest levels of N inflow ($0.83\text{--}1.5 \text{ g N m}^{-2} \text{ y}^{-1}$) it was either unable to become established or did so at a very low productivity ($< 1\%$ of community NPP). At intermediate levels of N inflow ($2.5\text{--}4.0 \text{ g N m}^{-2} \text{ y}^{-1}$) it coexisted with at least one other native species without dominating. At the high end of the N inflow gradient ($6.0\text{--}15.0 \text{ g N m}^{-2} \text{ y}^{-1}$) it dominated community NPP. This reversal of invasion success across the N inflow gradient indicates that the largest size invader, while able to thrive and dominate at high rates of N inflow, also required high rates of N inflow in order to become dominant and required at least intermediate rates of N inflow to remain in the community at more than 1% of community NPP.

3.2. Loss of native species with increasing N inflow and invasion

In the absence of any attempted invasions, the largest size native (0.53 g) persisted across all levels of N inflow, exhibiting greater NPP and N uptake with increasing N inflow (data not shown, but nearly identical to Fig. 3a). The larger size alone made the 0.53 g native a superior competitor at high N, completely excluding the smaller size species where N inflows were high. Only at low N inflows of $1.5 \text{ g N m}^{-2} \text{ y}^{-1}$ and below could all three native species coexist throughout the 40 y simulation period. (Recall that MONDRIAN was parameterized and tested to ensure such coexistence under oligotrophic conditions, consistent with field observations.)

With attempted invasions by invader species of increasing size, the small and intermediate sized natives showed patterns of persistence quite similar to those in the native community alone: the small and intermediate sized natives persisted at low levels of N inflow, but failed to persist at higher levels of N inflow. The losses of these natives from the community at intermediate levels of N inflow were accelerated by the attempted invasions of the largest size invaders (Fig. 3d and e). The largest size native, which persisted and thrived at all levels of N inflow in the absence of invasion, was also dominated over or driven out of the community by invader species of larger size. The largest size native coexisted at all levels

of N inflow with the 0.53 g invader, coexisted but at successively lower levels of NPP, under greater N inflow, with the 1.7 g invader, and was extirpated completely by the 5.3 g invader at intermediate and higher levels of N inflow (Fig. 3c–e). This aspect of our results differed slightly in simulations with the litter suppression factor *off*. When this factor was *off*, the largest size invader still dominated NPP at the high end of the nutrient gradient, but the intermediate and largest size native species continued to persist in the community (data not shown). This means that the mechanism of competition for N alone enabled the larger sized invaders to dominate over natives at high levels of N inflow, but in our simulations the suppression of reproduction by massive litter layers, at high N availability, was needed to fully drive natives from the community.

3.3. Ecosystem N cycling, feedback, lag times, and sensitivity

In our model results, ecosystem internal N cycling amplified the effects of the N inflow gradient. While the gradient represented a difference of $14.17 \text{ g N m}^{-2} \text{ y}^{-1}$ from the lowest to the highest rate of N inflow, and identical starting conditions were used for all simulations, by years 21–25 N uptake varied by up to $36 \text{ g N m}^{-2} \text{ y}^{-1}$ and N mineralization varied by up to $31 \text{ g N m}^{-2} \text{ y}^{-1}$ across the N inflow gradient (Fig. 3f–j). Ecosystem internal N cycling exhibited a positive feedback in plant uptake, litter production, and N mineralization over the 40 year period. This feedback amplified, by a factor of up to 2.5, the difference in N uptake over that of N inflow. This occurred in the native community alone (not shown, but similar to Fig. 3f) and was accentuated further by establishment of the largest-sized invaders. As invaders increased in size, the positive feedbacks leading to amplified N uptake and N mineralization increased substantially over the similar positive N-cycling feedback present in the native community (Fig. 3f–j).

A closer examination of temporal dynamics in the rise of invader NPP and rates of ecosystem N cycling, together with the accretion of the litter layer, provides further insight into the N-cycling feedbacks as affected by rates of N inflow and invader size. At two contrasting levels of N inflow, the intermediate-sized (0.53 g) invader rose to ca. 8% of community NPP (Fig. 4a and b) and produced no appreciable change in community N cycling through the 40 year period. The unchanged community N uptake is unsurprising because this invader was the same size as the largest native species; however its invasion serves as a baseline against which to contrast the effects of invasion by a species much larger in size than all of the native species. The largest-sized invader (5.3 g) had a strong effect on community N uptake. At two contrasting levels of N inflow, community N uptake rose in lock step with invader NPP. At the lower level of N inflow, community N uptake declined as invader NPP declined following the attempted invasion, but at the higher level of N inflow, community N uptake grew to 25% higher than the pre-invasion level and remained there, because the invader came to compose 100% of community NPP at the higher level of N inflow (Fig. 4c, d, g and h).

Did an ecosystem-level N-cycling feedback emerge (*sensu* Levin, 1998; Currie, 2011), in our simulations, that helped to maintain the higher level of N uptake by the largest invader and thus reinforce the successful invasion? A close look at differences in the accretion of litter layer mass indicates that this was so. While litter layer mass (averaged over the last 5 years of each simulation) showed a consistent increase along the N inflow gradient, the largest size invader produced a significantly more massive litter layer than either the native community alone or communities with smaller-sized invaders (Fig. 5). This resulted in increased N mineralization from litter in these cases (Fig. 3j) well over that of communities with only natives or with smaller invaders (Fig. 3f–h). Overall, it is clear that at high rates of N inflow, when the largest-sized invader

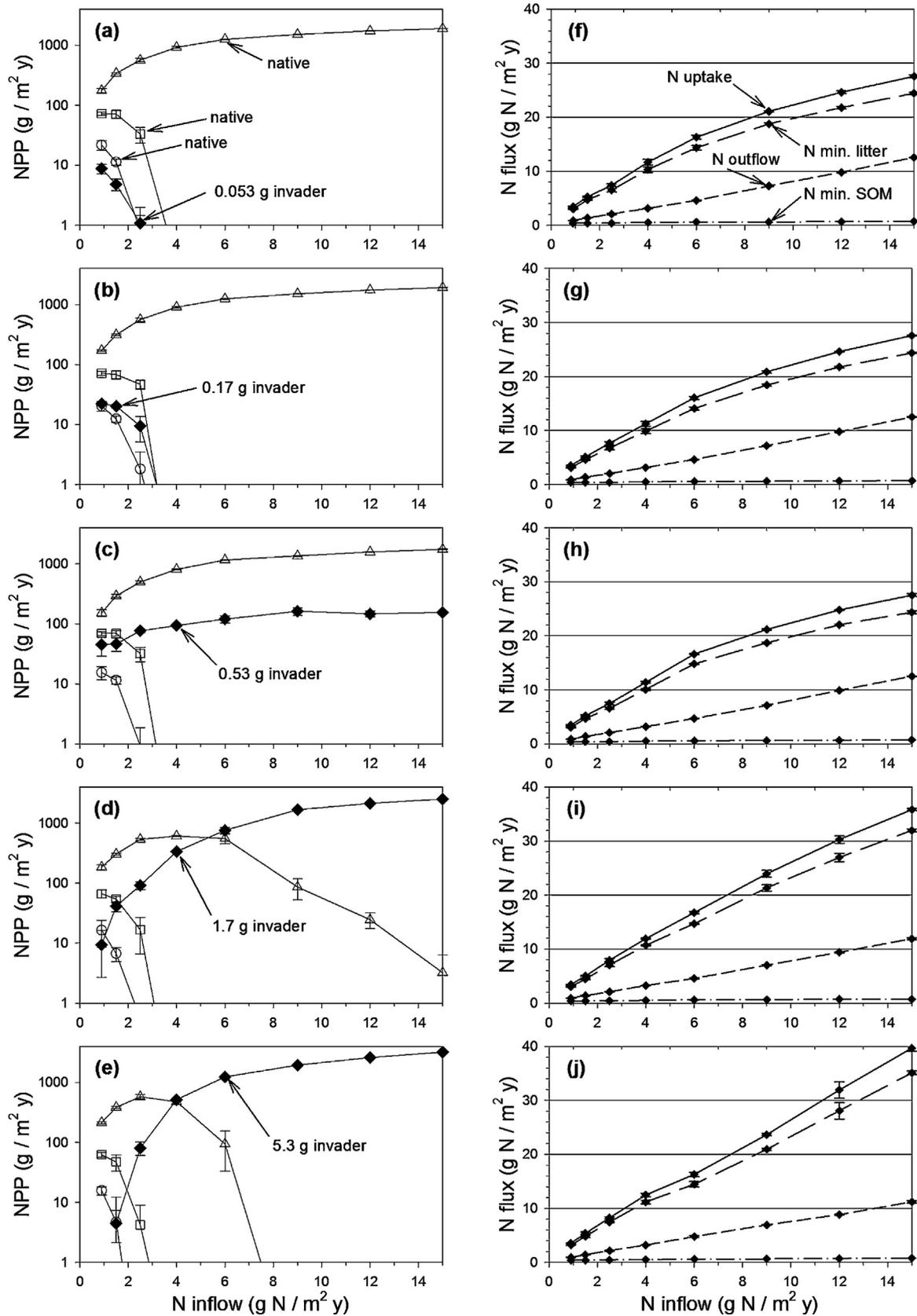


Fig. 3. MONDRIAN model results for attempted plant invasions into established native communities. Results here are averaged over the last 5 years of each model run for sets of model runs with different values of steady nutrient inflows and invader size. Panels (a) through (e) show NPP (above- plus below-ground dry mass) for each species; species symbols are as in Fig. 2. Invader sizes are as listed. Panels (f) through (j) show key fluxes of ecosystem N cycling in corresponding sets of simulations in (a) through (e). N min. litter = N mineralization from litter; N min. SOM = N mineralization from sediment organic matter. N uptake is aggregated for the entire plant community. N outflow represents ecosystem loss or export of N through hydrologic loss and denitrification.

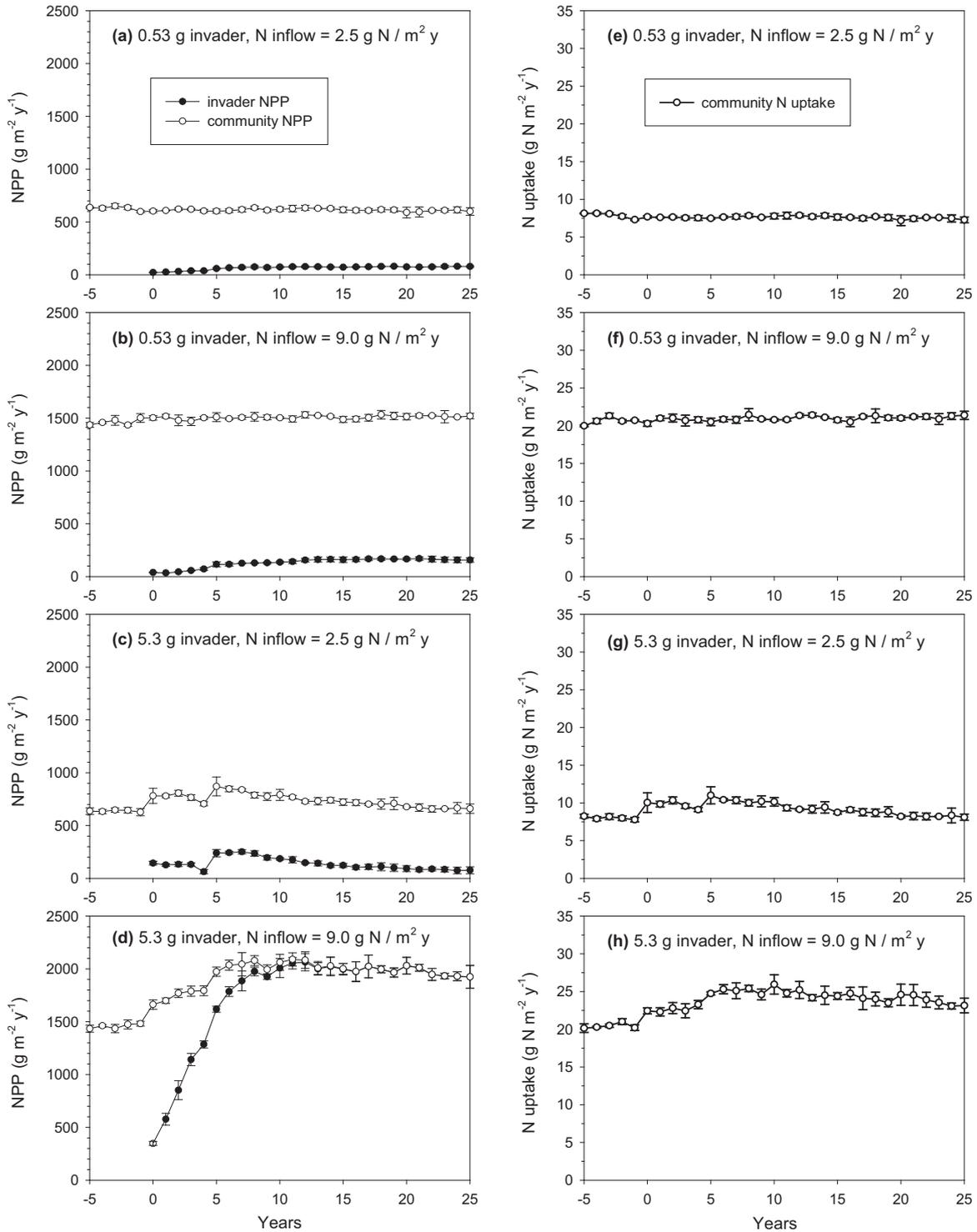


Fig. 4. MONDRIAN model results for time series of attempted invasions into established native communities over time, relative to start of attempted invasion (year 0). Two invader species sizes at two levels of N inflow are shown, as listed. Panels (a) through (d) show invader NPP (above- plus below-ground dry mass) (filled symbols) and community NPP (unfilled symbols); in panel (d), values for invader NPP and community NPP are nearly identical, 12+ years after invasion. Panels (e) through (h) show community N uptake in corresponding simulations shown in panels (a) through (d). Each symbol represents the mean (error bars SD) of 3 identical, stochastic model runs.

entered the established native community, NPP and N uptake rose rapidly over 7–10 years, a more massive litter layer formed with increased rates of N mineralization, and this worked to sustain the higher N uptake and NPP of the largest invader, thus reinforcing the invasion success.

Accretion of a more massive litter layer can also contribute to wetland N retention. MONDRIAN provides a useful approach to

examine the processes controlling wetland N retention because in the model it is not pre-specified, but instead it emerges as an ecosystem-level phenomenon from processes integrated over four levels of organization. In parameterizing MONDRIAN for the present analysis, including the initial conditions for C and N stocks in ecosystem pools, we calibrated ecosystem C cycling to be at equilibrium in the native community at an N inflow of $1.5 \text{ g N m}^{-2} \text{ y}^{-1}$,

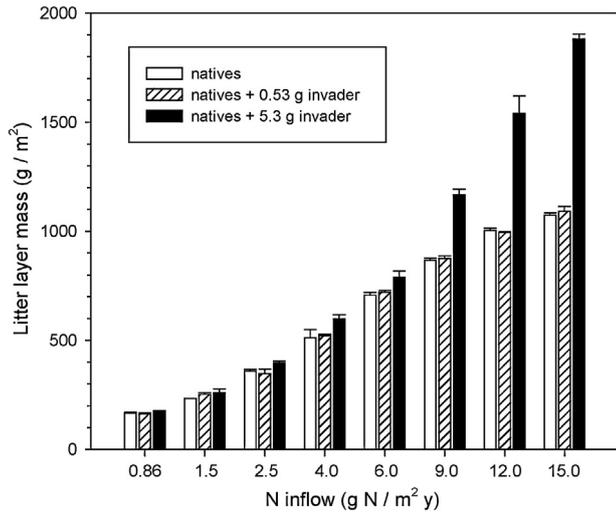


Fig. 5. MONDRIAN model results for litter layer mass in the native community alone and invaded by the mid-sized (0.53 g) and largest (5.3 g) invader, across the entire range of N inflows simulated. Results are averaged over the last 5 years of each model run. Each bar represents the mean (error bars sd) of 3 identical, stochastic model runs.

an estimate of relatively oligotrophic conditions. With no net gain or loss of litter or sediment organic matter (SOM), this meant the N inflows and outflows were in approximate equilibrium, with ecosystem N retention near zero at N inflow of 1.5 g N m⁻² y⁻¹ (Fig. 6). At higher rates of N inflow, the accumulation of N in living plants together with accretion of the litter layer and SOM caused simulated wetland N retention to rise to levels up to 15% in the native community (Fig. 6). Where the largest invader was successful, ecosystem N retention rose to 17%, slightly greater than that of the native community, consistent with the accretion of a more massive litter layer (Figs. 5 and 6).

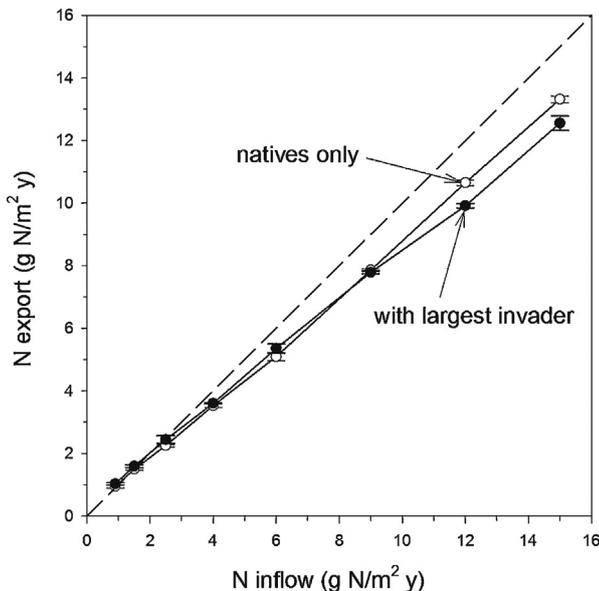


Fig. 6. MONDRIAN model results for wetland ecosystem N export versus N inflow. Model was calibrated to be in steady-state, with N export = N inflow, for native community at N inflow 1.5 g N m⁻² y⁻¹. Results here are averaged over the last 5 years of each model run, shown as means (error bars sd) of 3 stochastic model runs for each case. Open circles = native community. Filled circles = largest invader (5.3 g) into established native community. The dashed line is a 1:1 line shown for reference. Each symbol represents the mean (error bars sd) of 3 identical, stochastic model runs.

Table 5
Sensitivity analysis of model parameters related to N cycling.

Model parameter	Average relative sensitivity ^a	
	Total NPP ^b	Ecosystem N retention ^b
Rate of hydrologic flushing of N from regional nutrient pool	-0.51*	-1.29*
Rate of export of detritus from wetland	-0.08*	-0.76*
Decay rate of sediment organic matter	0.17*	-0.85*
C:N ratio below which N is released from decomposing litter	0.22*	0.48*
Plant relative growth rate	0.11*	0.17
C:N ratio for new plant tissue, aboveground	0.56*	0.73*
C:N ratio for new plant tissue, belowground	-0.02	-0.25*
Rate of N resorption from senescing stems	0.40*	0.25
Decay rate of litter	0.26*	1.25*
C and N needed to establish a new daughter rhizome	0.04	0.08

Notes:

^a Average relative sensitivity calculated as the average, over 33 model runs, of the percentage change in the response variable divided by the percentage change in the model parameter, where the model parameter was perturbed over the range of +25% to -25%. If the response variable changed by 10% following a 10% change in the model parameter, the relative sensitivity would be 1.0. (Positive and negative model responses to positive and negative parameter perturbations, respectively, do not cancel out but instead reinforce one another in our calculations of relative sensitivity.)

^b Bold and asterisk (*) values indicate that a regression of model response against parameter change, in a set of 33 model runs focusing on each parameter, was statistically significant ($p < 0.05$).

Our sensitivity analysis showed that modeled values of total community NPP and ecosystem N retention showed a range of sensitivities to parameters controlling N uptake and N cycling, when tested individually (Table 5). While 15 out of 20 regressions tested were significant, all but 2 of these had average relative sensitivities with absolute values below 1.0, indicating that interactions in the model tended to dampen out the effects of perturbations in a parameter value. One exception was a relative sensitivity of 1.25 for ecosystem N retention in response to perturbations in the decay rate of litter. This indicates that differences in wetland N retention tended to slightly magnify perturbations in the rate of litter decay. This finding is consistent with the ecosystem-level positive feedback involving litter decomposition and N cycling that we observed (Fig. 3f–j) as well as the importance of litter accretion to ecosystem N retention described above (Figs. 5 and 6). The second exception was a relative sensitivity of -1.29 for the response of N retention to changes in the rate of hydrologic flushing of N, also consistent with the existence of ecosystem feedbacks controlling wetland N retention in the model.

4. Discussion

4.1. Invasion success

MONDRIAN is a complex model that simulates competition for a depletable, limiting nutrient among continually shifting combinations of neighbors of the same and different species of clonal plants. We found that with all other plant traits equal, plant size made an important difference in invasion success along an N inflow gradient. With N demand formulated through a relative growth rate (RGR), the larger an individual grew, the greater N demand it had. Where the combined N demand among a group of neighbors exceeded availability, we used perfectly size-symmetric competition (Schwinning and Weiner, 1998) to apportion N among neighbors (Eqs. (2) and (3)). As a plant grew larger relative to its neighbors, it was thus able to gain a greater future apportion of

available N, creating a positive feedback in individual growth and a competitive advantage of size that is well documented (Weiner and Thomas, 1986; Keddy, 2001). Invasion success under high N inflows in our simulations was related to greater nutrient capture, not greater nitrogen use efficiency. This is consistent with other modeling work related to plant community development (Berendse, 1998) and empirical findings related to plant invasion (Ehrenfeld, 2003; Penuelas et al., 2009). Here it meant that simulated larger-size species, simply because their individuals could grow larger, came to dominate N uptake and NPP where N availability was great enough. Our simulations exhibited this phenomenon not only with large invaders but also among the natives themselves, with natives dropping out in order of their size in simulations with increasing rates of N inflow.

Nutrient translocation in clones contributed to a positive feedback in N acquisition at the population level, but only where N was plentiful enough to allow continued clonal expansion for the species. This illustrates a tradeoff related to plant size: while the largest size invader could acquire the bulk of the N resource at high N availability, it could not acquire enough N to reproduce clonally at low N availability. Small species, in contrast, were able to accumulate enough N to expand horizontally under low N availability. This modeling result suggests that small size per se may be an adaptive trait in clonal species in nutrient-poor habitats, while large size may be adaptive for invaders in eutrophic habitats.

4.2. Plant traits and ecosystem N-cycling feedbacks

The positive feedback in plant–litter–soil N cycling that occurred in our simulated ecosystems meant that N availability itself was controlled by a combination of plant- and decomposer-driven processes (Daufresne and Hedin, 2005). By accentuating this positive feedback, the two largest invaders drove N availability higher as they came to dominate community NPP. This is consistent with field observations comparing native and *Typha*-invaded patches in our study system (Angeloni et al., 2006; Farrer and Goldberg, 2009). At the same time, in our simulations the positive feedback also occurred in the native community; only with high N inflow and large invaders was it augmented by the invasive species. The augmentation of positive feedbacks here was due only to direct and indirect effects of size. In reality, natives and invasives in various communities have additional trait differences that could either strengthen or diminish the positive feedback (Miki and Kondoh, 2002).

In a meta-analysis of 94 experimental studies of plant invasions, Liao et al. (2008) found that invaders tended to have 40% higher N concentrations in plant tissues and more rapid litter decomposition. Each of these phenomena could be related to plant traits and has the potential to strengthen a positive feedback in ecosystem N cycling under high nutrient inflows. At the same time, our results suggest that a requirement of higher N concentration in plant tissues could make it more difficult for a large-size invader to reproduce clonally at low N availability, consistent with the idea that low nutrient-use efficiency would limit population success at low N availability (Tilman, 1990). If this trait also strengthened the positive feedback at high N availability, it would create a sharper switch in invasion success with N inflows. This would be a useful area for further research with the MONDRIAN model.

Feedbacks involving decomposition and the litter layer could be complex and we only investigated a small number of factors here. At high levels of N inflow, our litter suppression factor determined whether native species either persisted in the community at very low NPP or were completely excluded by the largest size invader. Even so, MONDRIAN under-predicted field-observed differences in litter layer mass between native and large-invader dominated communities (Table 4). Our hypothetical plant species differed only in

maximum size and had the same, somewhat rapid decomposition rate constant for all plant species (Table 2). If litter decomposition rates differed among species, this could significantly affect the mediation of ecosystem nutrient cycling (Miki and Kondoh, 2002; Daufresne and Hedin, 2005; Liao et al., 2008). Faster litter decay could mean a less massive litter layer and a shorter lag time between increased NPP and increased N mineralization, while a slower rate of litter decay could result in greater litter accretion and litter N storage, with a much longer lag time in the rise of N mineralization.

Additional complexities in litter-layer mediation of nutrient cycling arise from litter layer thickness, water depth, litter fragmentation, and storms. *Typha* spp. produce rigid stems that suspend some litter above the water level where it dries out, impeding decomposition. At the same time, partially decomposed litter may become waterlogged and buried as peat or muck. Burial of N-rich litter below water level could significantly impede decomposition and N release; this is used as a management strategy to retain nutrients in Florida (Chimney and Pietro, 2006). Such burial of litter and peat accretion is not currently included in MONDRIAN, but is being developed in a future version of the model. Another complication is that litter can fragment and be swept out of wetlands during storm events (Bach et al., 1986). Such an export of litter N from the wetland, particularly if the litter were from an N-rich species or had immobilized N prior to its export, could work to mitigate N-cycling feedbacks. If there were a difference among species in rates of litter fragmentation or in how tightly litter was held in place (e.g., in dense *Typha* stands with stems that persist through winter), these could be important species-specific effects on litter accretion and ecosystem nutrient cycling.

4.3. Wetland N retention

Human-driven production of biologically reactive forms of N and their losses to the environment are increasing worldwide, while we still have much to learn about the fates and impacts of elevated N inputs in ecosystems (Galloway et al., 2008). N retention in wetlands is a valuable ecosystem service because it lowers the fluxes of N that reach aquatic ecosystems (Krieger, 2003; Jenkins et al., 2010; Simonit and Perrings, 2011). N retention also exerts long-term controls on community composition through nutrient cycling, as seen in our results and in previous modeling analyses (Pastor et al., 2002; Daufresne and Hedin, 2005).

Are our simulation results for rates of N retention (up to 17%) realistic? Across a range of natural and constructed wetlands, Hansson et al. (2005) summarized N retention that ranged widely, from –57% to 98%. In a one-year study of hydrogeochemical flows and retention in an embayment wetland in our region (Old Woman Creek, Ohio, which drains into Lake Erie), Krieger (2003) measured N retention of 21% for $\text{NO}_3\text{-N}$, –92% for $\text{NH}_3\text{-N}$ and –17% for dissolved organic N. Excluding the organic N and focusing on inorganic available N, the weighted N retention was 19%. Krieger (2003) focused on hydrologic N flows, omitting N fixation or denitrification, which would have lowered the calculated value of wetland N retention if denitrification were greater than N fixation. Krieger (2003) also omitted N in precipitation onto the wetland surface, which we included; including this would again have lowered Krieger's values of N retention. In another study in our region (Lost Creek Wetland, Wisconsin, which drains into Lake Superior), Morrice et al. (2004) measured N retention ranging seasonally from 11% to 94%. Arheimer and Wittgren (2002) modeled N removal by wetlands at the catchment scale in Sweden using a hydrogeochemical model parameterized with field data, with resulting average rates of N removal of 6%. A key factor controlling wetland N retention in both the field study of Morrice et al. (2004) and the modeling analysis of Arheimer and Wittgren (2002) was the residence time

of water in the wetland. Arheimer and Wittgren (2002) concluded that a water residence time of <2 days in a wetland worked against N retention because of rapid hydrologic flushing. In the study of Old Woman Creek wetland in our region, Krieger (2003) measured the residence time of water during 21 storm events, the vast majority of which had a water residence time of <2 days. Morrice et al. (2004), in Wisconsin, measured a water residence time that ranged from 1 day during snowmelt to 26 days in summer.

In MONDRIAN a parameter controls the rate of ecosystem N losses, which conceptually includes hydrologic N flushing and denitrification; changes in this parameter result in slightly different values of wetland N retention. Future model improvements may include more process-based treatment of hydrologic flushing, water level, anaerobic zones, and denitrification. Our current results for wetland N retention are thus highly uncertain but useful for gaining insight into the integration of community and ecosystem processes with realistic values of NPP, litter accumulation, and C:N ratios in plant tissues and detritus (Table 4).

In our results, the largest invader at high N inflows augmented wetland N retention, although our results probably underestimate differences that occur with invasion of large-size *Typha x glauca* in field settings. MONDRIAN underestimated both the increase in litter layer mass and the N concentration in SOM observed in a dense *T. x glauca* stand in the field (Table 4), both of which would cause greater N retention. In a mesocosm study of *Phalaris arundinacea* invasion in wet prairie, Herr-Turoff and Zedler (2005) found that N retention was no greater in invaded versus non-invaded treatments. However, these authors also did not observe any differences in NPP or plant N pools summed over the community in invaded versus non-invaded treatments. In our simulation results the largest size invader did cause a rise in community NPP at the high end of the N inflow gradient, facilitated by increased ecosystem N cycling, and therefore increased simulated N retention. In their meta-analysis of 94 experimental studies of plant invasions, Liao et al. (2008) found that NPP did significantly increase in invasion experiments overall.

4.4. N versus P limitation

Additional resources, including phosphorus, together with complex resource interactions and elemental stoichiometry in plant tissues are likely to play a role in determining invasion success in many wetlands. We focused our analysis of invasion success over an inflow gradient of a single depletable resource. In choosing a primary limiting nutrient, based on prior research there are good reasons to focus on N rather than P in the types of marshes we studied here. In a meta-analysis of nutrient enrichment experiments from a wide range of ecosystem types, Elser et al. (2007) found that wetland plants had a 2× greater response to N than to P, although the addition of both N and P produced the greatest response. A survey of North American temperate wetlands by Bedford et al. (1999) showed that marshes exhibited N:P ratios in live plant tissue and surface soils that suggested N limitation. Additionally, The general pattern of wetland plants responding more to N than to P was observed by Fraser and Feinstein (2005). There is extensive literature showing the positive growth response of wetland plant invaders such as *Phragmites australis*, *Typha* spp., and *P. arundinacea* to elevated soil-N levels. Escutia-Lara et al. (2009) found that the growth of *Typha domingensis*, a wetland invader similar to the largest invader in our study, responded to N loading but not P in an outdoor mesocosm experiment. The positive growth response of *P. arundinacea* to N has been well established (Green and Galatowitsch, 2001, 2002; Martina and Von Ende, 2012) and Perry et al. (2004) showed that when N was immobilized in C-amended soil the growth of *P. arundinacea* decreased and was outcompeted by a native wetland sedge, illustrating the importance

of N to invader success. Similarly, *P. australis*, a dominant invader throughout the Great Lakes area, greatly increased biomass production in N rich soil while *Spartina pectinata*, a native grass, did not (Rickey and Anderson, 2004). Romero et al. (1999) supplied N-enriched and/or P-enriched solution to seedlings of *P. australis* and found N enriched solution significantly increased the growth rate of *P. australis*, whereas P enriched solution had no effect.

Taken together, these studies suggest that it is plausible, if not probable, that N is more strongly limiting than P in the types of historically oligotrophic marshes that we model in the present paper, which are being invaded by *Typha* and *Phragmites* species in our region. At the same time, we recognize the importance of P limitation generally and its interactions with N limitation. We are currently working to develop P cycling and P limitation in a future version of the MONDRIAN model and plan to explore the interactions of N and P limitation across different types of wetlands in future modeling work.

4.5. Integrative community–ecosystem modeling and future research

An important current direction in plant community ecology is to understand feedbacks between community change and ecosystem processes to gain increased understanding of both natural system functioning and system responses to global change (Daufresne and Hedin, 2005; Cleland, 2011). Incorporating plant–plant interactions into this understanding is also an important direction of current research (Brooker, 2006). Our results show that a useful modeling approach is to conduct a large set of simulations with complex interactions across levels of organization, while exploring a simplified difference in plant species traits across a gradient in an environmental driver. This allowed us to explore mechanisms with a specificity not possible in field studies. For example, by isolating the effects of plant size on invasion ability in *in silico* experiments, we were able to identify important positive feedbacks and trade-offs quite differently at low and high levels of N inflow. At the same time, the complexity and biological realism of the model enables improvements in integrated understanding (Canham et al., 2003; Hastings et al., 2005; Clark et al., 2005). For example, although we did not focus on biodiversity *per se*, our results showed an integrated set of mechanistic processes whereby elevated N inflows produced a reduction in plant community diversity.

The present analysis is part of a larger research project that combines field experiments to test controls on plant invasions, remote sensing to identify wetland plant invasions throughout coastal Michigan, and modeling to integrate understanding and simulate scenarios of invasion risk. We recently constructed 100 wetland mesocosms in the field to test some of the model results given here regarding invasion success across a range of N inflows and plant species combinations. In future work with MONDRIAN we plan to investigate competitive mechanisms and effects more closely and to include other limiting resources in a future version of the model. Our finding that plant N uptake continued to increase as N inflow and N availability increased in MONDRIAN (Fig. 3) is predicated on the assumption that plant growth continued to be N-limited even at high rates of N inflow. With the inclusion of other limiting resources, a cap or ceiling on the positive feedback in N cycling could result.

Although our initial application of MONDRIAN here focuses on clonal wetland plants, we designed MONDRIAN to be more broadly applicable. The suite of physiological, population–community, and ecosystem processes represented in the model are likely to be applicable across a range of other terrestrial ecosystems, particularly herbaceous systems such as grasslands. Because numerous species parameters are read from an input file, the model can be used to explore the interactions of a large number of plant

traits and ecosystem processes. In addition to empirically testing key results shown here, we hope to further develop the model and work with collaborators to apply the model to a variety of ecosystems and a range of research questions.

Author contributions

WC and DG conceived and designed the study and new model; WC wrote the model code; WC and JM tested the model and conducted simulations, DG, RW, EF, JM, and KE conducted field research; WC, DG, RW, JM, EF, and KE analyzed results and wrote the paper.

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