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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.

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. Interconnected 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