

Effect of Invasive Plant Species on Temperate Wetland Plant Diversity

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Abstract: *Invasive species are a major threat to global biodiversity and an important cause of biotic homogenization of ecosystems. Exotic plants have been identified as a particular concern because of the widely held belief that they competitively exclude native plant species. We examined the correlation between native and invasive species richness in 58 Ontario inland wetlands. The relationship between exotic and native species richness was positive even when we controlled for important covarying factors. In addition, we examined the relationship between the abundance of four native species (Typha latifolia, T. angustifolia, Salix petiolaris, Nuphar variegatum) and four invasive species (Lythrum salicaria, Hydrocharis morsus-ranae, Phalaris arundinacea, Rhamnus frangula) that often dominate temperate wetlands and native and rare native species richness. Exotic species were no more likely to dominate a wetland than native species, and the proportion of dominant exotic species that had a significant negative effect on the native plant community was the same as the proportion of native species with a significant negative effect. We conclude that the key to conservation of inland wetland biodiversity is to discourage the spread of community dominants, regardless of geographical origin.*

Key Words: competitive exclusion, invasive species, *Lythrum salicaria*, species richness, wetlands

Efecto de Especies de Plantas Invasoras sobre la Diversidad de Plantas de Humedales Templados

Resumen: *Las especies invasoras son una amenaza mayor para la biodiversidad global y una causa importante de la homogenización biótica de ecosistemas. Las plantas exóticas son de particular preocupación por la amplia creencia de que excluyen competitivamente a especies de plantas nativas. Examinamos la correlación entre la riqueza de especies nativas e invasoras en 58 humedales interiores en Ontario. La relación entre riqueza de especies exóticas y nativas fue positiva aún cuando controlamos importantes factores covariantes. Adicionalmente, examinamos la relación entre la abundancia de cuatro especies nativas (Typha latifolia, T. angustifolia, Salix petiolaris, Nuphar variegatum) y cuatro exóticas (Lythrum salicaria, Hydrocharis morsus-ranae, Phalaris arundinacea, and Rhamnus frangula) que a menudo son dominantes en humedales templados y la riqueza de especies nativas y nativas raras. Las especies exóticas no tuvieron mayor probabilidad de dominar un humedal que las especies nativas y la proporción de especies exóticas dominantes que tuvieron efecto negativo significativo sobre la comunidad de plantas nativas fue la misma que la proporción de especies nativas con efecto negativo significativo. Concluimos que la clave para la conservación de la biodiversidad de humedales interiores es evitar la dispersión de dominantes en la comunidad, independientemente de su origen geográfico.*

Palabras Clave: especies invasoras, exclusión competitiva, humedales, *Lythrum salicaria*, riqueza de especies

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Introduction

Invasive species are one of our most pressing environmental concerns (Enserink 1999; Mack et al. 2000a), and humans have been identified as a major vector in the dispersal of exotic species throughout the world (Hodkinson & Thompson 1997; Palumbi 2001). This concern has led to the development of organizations both national (e.g., U.S. National Invasive Species Council) and international (e.g., World Conservation Union's Global Invasive Species Program) whose mandate is to combat invasive species and their deleterious effects. Many invasive species are plants, leading to widespread concern about the effects of exotic species on native plant species (Mack et al. 2000a), especially those already at risk (Wilcove et al. 1998). Wilcove et al. (1998) estimate that 57% of plant species identified by The Nature Conservancy as either "possibly extinct," "critically imperiled," or "imperiled" are threatened, at least in part, by predation or competition with exotic species. Moreover, exotic species can cause fundamental changes in ecosystem processes and community structure that may have disastrous economic consequences, including loss of crops, forests, fisheries, and grazing capacity (Pimental et al. 2000). Although there is unequivocal evidence of the negative effects of exotic species on native plant communities mediated through biological interactions such as predation or disease (e.g., chestnut blight [*Cryphonectria parasitica*], Dutch elm disease [*Ceratomyces ulmi*], gypsy moth [*Lymantria dispar*]) (Wallner 1996), there is considerably less evidence of competition from introduced exotic plants resulting in competitive exclusion of native plants from natural plant communities (Dukes 2002). What evidence exists is almost exclusively from small-scale (microcosm) competition experiments (Boyle et al. 1999; Carlsen et al. 2000); these results contrast with observational studies showing positive relationships between native and exotic species richness (Lonsdale 1999; Stohlgren et al. 1999; Levine 2000).

If exotic plant species tend to outcompete native species, we would predict (1) a negative relationship between exotic species richness and native plant species richness once covarying factors are controlled; (2) a greater likelihood of an exotic species becoming a community dominant; or (3) a greater negative effect of exotic community dominants on native plant species richness compared with the effect of native community dominants.

We tested the hypothesis that exotic plant species outcompete natives in 58 temperate wetlands, an important and endangered habitat that is considered particularly vulnerable to invasion by exotic plants (McIntyre et al. 1988; Deferrari & Naiman 1994; Knops et al. 1995).

Methods

We sampled 58 wetlands from southeastern Ontario between 44°12'N and 45°51'S and 74°34'E and 76°30'W.

This area is in the humid, high, cool, temperate climatic region of Canada and has a mean annual temperature of 4.2° C, a mean annual precipitation of approximately 800 mm, and an average of 117 frost-free days annually (Ecoregions Working Group 1989). About 60–70% of southeastern Ontario land area is covered in forest, and these forests are dominated by sugar maple (*Acer saccharum* L. Marsh.), yellow birch (*Betula lutea* Michx.), hemlock (*Tsuga canadensis* [L.] Carr.), and white pine (*Pinus strobes* L.). Almost all wetlands contained swamp and marsh habitat, and nine contained some fen and/or bog habitat. The dominant swamp plants in Ontario wetlands include silver maple (*Acer saccharinum* L.), cedar (*Thuja occidentalis* L.), dogwood (*Cornus* spp.), willows (*Salix* spp.), alder (*Alnus rugosa* [DuRoi] Spreng.), and ash (*Fraxinus* spp.). Dominant marsh plants include cattails (*Typha* spp.), purple loosestrife (*Lythrum salicaria* L.), aquatic macrophytes (*Hydrocharis morsus-ranae* L., *Nuphar* spp., *Nymphaea* spp., *Potamogeton* spp.), and grasses and sedges (*Calamagrostis Canadensis* [Michx.] Beauv., *Leersia oryzoides* [L.] Sw., *Phalaris arundinacea* L., *Carex* spp., *Scirpus* spp.). The bogs and fens are dominated by leatherleaf (*Chamaedaphne calyculata* [L.] Moench.), blueberries and cranberries (*Vaccinium* spp.), sedges (*Carex* spp.), and cottongrass (*Eriophorum* spp.). Most of the sampled wetlands were in the St. Lawrence lowlands and are underlain by Paleozoic rock, but several of the wetlands in the northwestern corner of the study area are at the edge of the highlands and have Precambrian metamorphic bedrock (Fulton et al. 1987). Mean wetland size was 66.7 ha; 44 wetlands were palustrine, 8 lacustrine, and 6 riverine. The wetlands occurred along a wide gradient of land-use intensity from urban wetlands (located near the heart of Ottawa, Canada) to relatively remote wetlands in the Pakenham Hills, approximately 80 km west of Ottawa).

We spent between 1.5 and 40 person-hours in each wetland, conducting daytime sight surveys, with search time increasing with the size of the wetland (\log_{10} effort = $0.39 + 0.52[\log_{10}$ area]). We visited each wetland three times (May or early June, mid-June or July, and August or early September) so as to sample early, middle, and late-flowering species. We used a modified Brown-Blanquet abundance-estimation method to score species abundance: 0, absent; 1, one to five individuals; 2, more than five individuals but never dominant plant cover; 3, many individuals with the species occasionally dominant over small areas <5% of total wetland area; 4, many individuals representing dominant plant cover over 5–20% of total wetland area; 5, many individuals and dominant over >20% of the total wetland area. To estimate the completeness of our species lists, we constructed collection curves for each visit for every wetland. Survey times were partitioned into six segments of equal duration (e.g., if the allocated time for a visit was 3 hours, the survey was broken into six 30-minute intervals), and the number of species

for each segment was recorded. We then constructed collection curves by plotting cumulative species richness over the six time segments. These curves showed that, in most surveys, more than 60% of species were found in the first time segment and 95–100% of all recorded species were found by the fifth segment.

We used Pearson correlation analysis to examine the bivariate relationship between exotic and native/rare native plant species. We previously developed models that predict native (S) and rare native plant species richness (S_r) (all native species found in three or fewer wetlands) based on wetland size; landscape attributes, such as the proportion of forest cover and road density on adjacent lands; and measures of water and sediment quality (a detailed description of land use and methods for sampling water and sediment quality is available from J.E.H.). We included exotic species richness (S_e) in these models to examine its effect when the effects of other important covarying wetland characteristics are statistically controlled.

We compared the proportion of native versus exotic species that dominate wetland plant communities with simple chi-square analysis. Species were classified as dominating a wetland if they were given an abundance score of 4 or 5. Finally, using generalized linear models, we examined the relationship between the abundance of the four exotic plant species—*Lythrum salicaria* L., *H. morsusranae*, *P. arundinacea*, and *R. bannus frangula* L. (Table 1)—that occasionally dominate wetland communities and S and S_r . Because dominant species are expected to show a negative effect on richness irrespective of their origin, we compared these results with those for four native species from matched functional groups—*Typha latifolia* L., *T. angustifolia* L., *S. petiolaris* Sm., and *N. variegatum* Engelm. (Table 1)—that occasionally dominate wetland communities.

Results

There was a positive relationship between S and S_e ($R = 0.405$, $t = 3.314$, $p = 0.002$; Fig. 1a) but no statistically significant relationship between S_r and S_e ($R = 0.005$,

$t = 1.133$, $p = 0.262$; Fig. 1b). For S , the best statistical model included wetland area (A), percent forest cover within 250 m of the wetland (F_{250}), minimum total Kjeldahl nitrogen present over the course of the growing season (TKN_{min}), and variation in water magnesium levels over the course of the season (MGV), whereas for S_r , the best model included A , road density within 200 m of the wetland (R_{200}), proportion of wetland that is bog or fen, and TKN_{min} over the course of the growing season. The models predicting S and S_r explained 76% and 57% of the variation in species richness, respectively. Controlling for these key variables did not eliminate the effect of S_e on S ($t = 2.095$, $p = 0.041$; Fig. 1b) and did not uncover any hidden effect on S_r ($t = 1.398$, $p = 0.168$; Fig. 1b).

We found that 5.5% (5/91) of exotic species were dominant (i.e., four or five in the abundance category) in at least one wetland, while 8% (48/600) of the native species were dominant in at least one wetland. The difference was not statistically significant ($\chi^2 = 0.700$, $p = 0.403$).

The S and S_r showed statistically significant negative bivariate relationships with the abundances of one (*P. arundinacea*) and three (*L. salicaria*, *P. arundinacea*, and *R. frangula*) exotic species, respectively. When other key predictor variables were included in the model, the relationship between S/S_r and *P. arundinacea* was still present, whereas the relationships between S_r and *L. salicaria* and *R. frangula* disappeared (Fig. 2). Thus, for these two species, the negative relationships can be explained by wetland characteristics (i.e., bog-fen communities are rare habitats that contain a large number of species found only in bogs and/or fens and tend to have low abundances of *L. salicaria* and *R. frangula*, likely because of acidic conditions common to bogs and fens), and invoking species interactions as an explanation for the relationships is unnecessary. Based on the estimated effect size, for each step up in abundance category by *P. arundinacea*, S_r declined by approximately 14%. Among the four native species, S and S_r showed significant negative bivariate relationships only with the abundance of *S. petiolaris*. These relationships persisted when other key variables were included in the model (Fig. 3). Based on the estimated effect size, each step up in abundance category by *S. petiolaris* was predicted to result in a decline in S_r by

Table 1. Geographic origin and life-history characteristics of four exotic and four native wetland species.

Species	Geographic origin*	Functional group	Height (cm)	Introduction date*
<i>Lythrum salicaria</i>	E	herbaceous perennial	100–200	mid-1800s
<i>Pbalaris arundinacea</i>	E	graminoid perennial	50–250	mid-1800s
<i>Rbannus frangula</i>	E	shrub perennial	600–750	early 1800s
<i>Hydrocharis morsusranae</i>	E	aquatic perennial	10–15	1932
<i>Typha angustifolia</i>	N	herbaceous perennial	100–250	n/a
<i>Typha latifolia</i>	N	herbaceous perennial	100–250	n/a
<i>Salix petiolaris</i>	N	shrub perennial	300–450	n/a
<i>Nupbar variegatum</i>	N	aquatic perennial	30–200	n/a

*Abbreviations: E, exotic; N, native; na, not available.

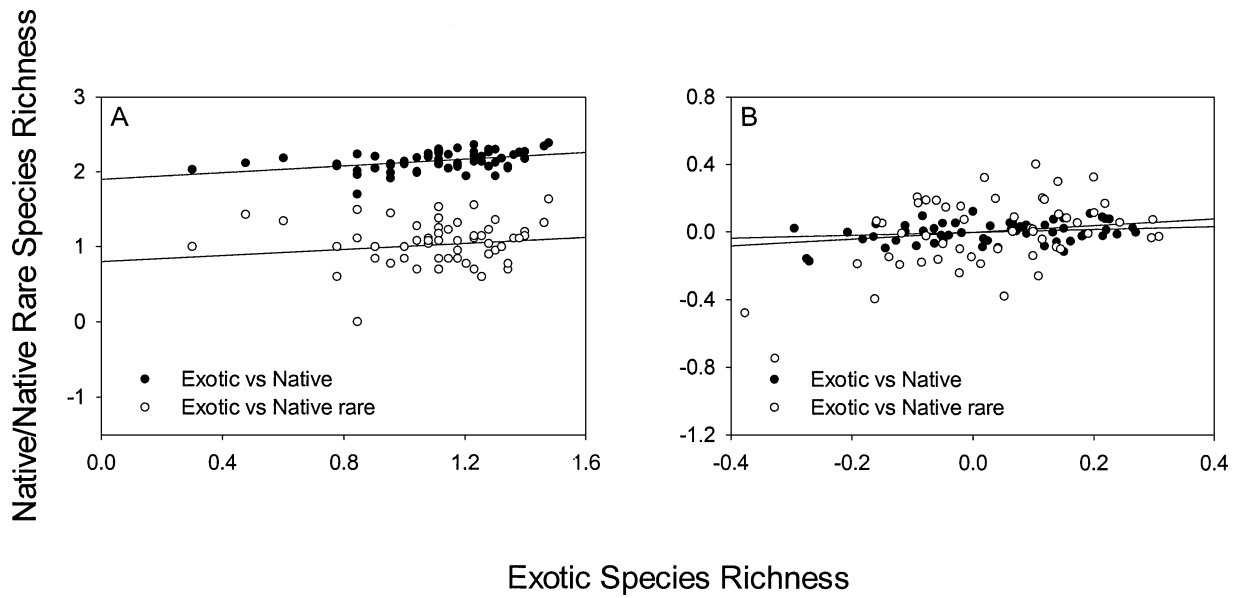


Figure 1. (a) Relationships between exotic species richness (\log_{10}) (S_e) and native (\log_{10}) (S) and rare native species richness (\log_{10}) (S_r) in 58 Ontario wetlands (without including key covarying factors). (b) Partial plots of the relationships between S_e and S and S_r (controlling for the effects of key covarying factors).

approximately 13.0%. Thus, wetlands where *S. petiolaris* or *P. arundinacea* are rare or absent would be predicted to have approximately twice as many rare native species as wetlands where they are dominant over >20% of the wetland.

Discussion

We found no evidence to support the hypothesis that in southeastern Ontario wetland exotic species competitively exclude native plant species. First, exotic and native

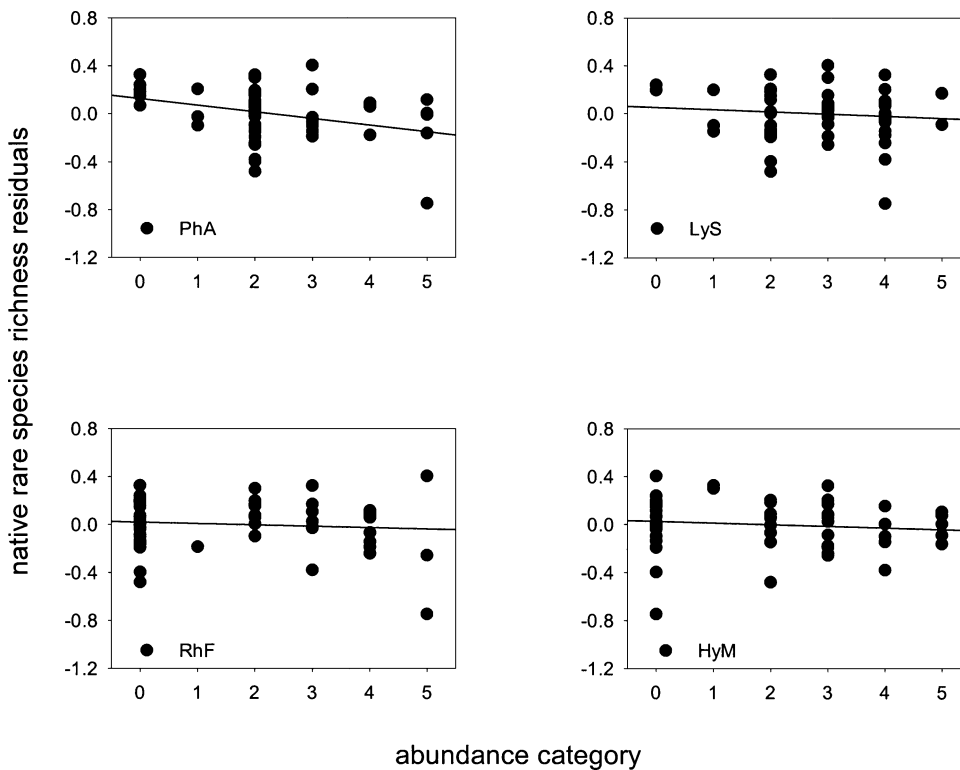


Figure 2. Relationship between the abundance of four exotic wetland species and rare native species richness (S_r) (*PhA*, Phalaris arundinacea; *LyS*, Lythrum salicaria; *RhF*, Rhamnus frangula; *HyM*, Hydrocharis morsus-ranae). Abundance categories are defined in the text (range is, absent at 0 to many individuals and dominant over >20% of area at 5).

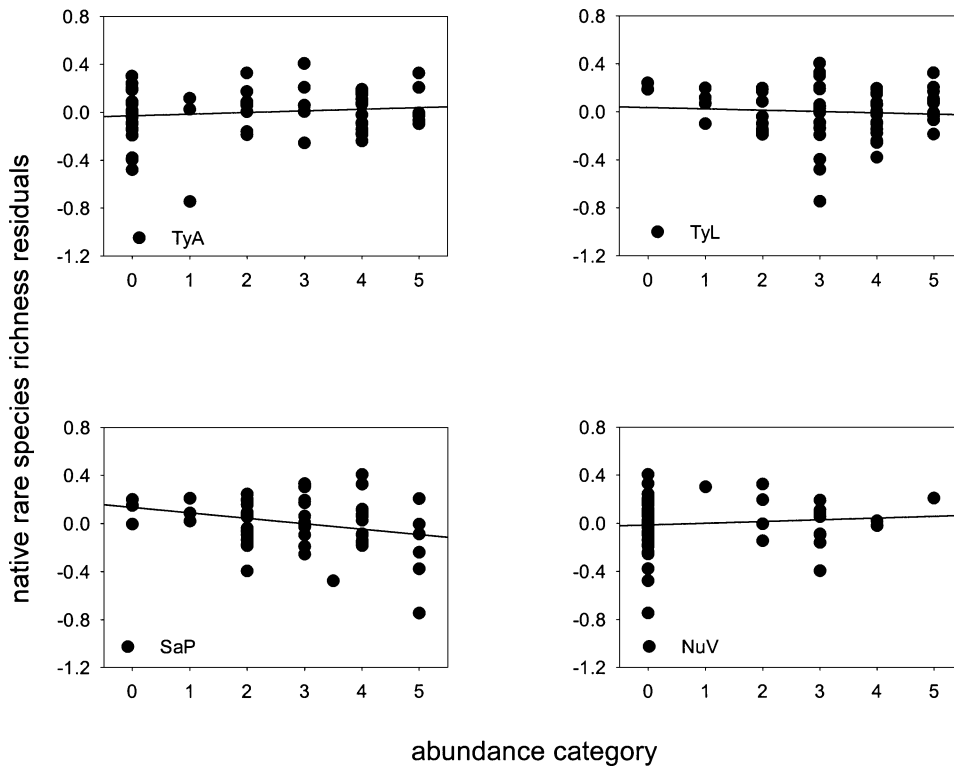


Figure 3. Relationship between the abundance of four native wetland species and rare native species richness (S_r) (TyA, *Typha angustifolia*; TyL, *Typha latifolia*; SaP, *Salix petiolaris*; NuV, *Nuphar variegatum*). See Fig. 2 legend for note on abundance categories.)

species richness were positively, not negatively, related. The positive relationship between native and exotic species richness was consistent with the results of most observational studies, but we also controlled for several key ecological variables and still found a positive relationship. The relationship was somewhat weaker, suggesting that part, but not all, of the explanation for the positive relationship is the similar response of exotic and native species to factors such as wetland size, nutrient status, and land use.

Second, exotic species were no more likely to be community dominants than native species. Approximately 6% of the 81 exotic species in our sample were dominant in at least one of the wetlands, which is somewhat lower than the 10% rule of thumb (Williamson 1996). There was no evidence to support the hypothesis that exotic species are more able to dominate invaded communities because they have fewer natural enemies than native plants (Cronk & Fuller 1995; Mack et al. 2000b).

Third, when the effects of other wetland characteristics were statistically controlled, the effect of exotic dominants on native species richness was indistinguishable from that of native dominants. Thus, it does not appear that exotic species invade and competitively exclude native species to a greater degree than do other native species.

Because these communities were only sampled in 1 year, we have no direct measure of changes in wetland plant species richness due to exotic species, but our results suggest that in southeastern Ontario wetlands, most exotic species pose little threat to native plant diversity.

Those that do appear to be no more threatening than native dominants.

In some cases, dominance by a single species was correlated with low species diversity. This may seem obvious, but there is little empirical data describing the relationship between dominance and species diversity. Ervin and Wetzel (2002) found that increased areal cover of *Juncus effusus* L. is correlated with lower species richness in the surrounding area, and Hurst and John (1999) concluded that there is a negative correlation between the abundance and species richness of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands. On the other hand, there is no evidence of a negative correlation between the percent cover of *L. salicaria* and native species richness (Treberg & Husband 1999). This conflicting evidence is consistent with our results that *some* dominant species competitively exclude others.

Our results suggest that *P. arundinacea* and *S. petiolaris* are capable of competitively excluding native species. It is notable that the effect of these dominants was strongest on rare native species. One explanation for rarity is poor competitive ability (Gaston 1994), and we predict that poor competitors will be more likely to be competitively excluded than good competitors. Thus, this result is consistent with the hypothesis that *P. arundinacea* and *S. petiolaris* competitively exclude some species when they occur at high densities. We conclude that the key to conserving wetland plant diversity is the control of those factors conducive to the spread of community dominants, irrespective of their geographical origins. There is some evidence that, in some ecosystems,

invasive species can fill an empty niche and dominate, but there is no evidence that this is occurring in Ontario wetlands.

The implications of unwarranted concern about the effects of exotic plants are not trivial. For example, the belief that purple loosestrife (*L. salicaria*) competitively excludes native species is firmly embedded in the ecological mainstream: "... purple loosestrife is an intensive competitor, choking out species in native American wetlands" (Stiling 2002); "... the highly competitive nature of purple loosestrife (*Lythrum salicaria*) has eliminated many species of wetland plants from marshes in eastern North America" (Bolen & Robinson 1999); "... purple loosestrife... has invaded prime wetlands throughout the temperate regions of United States and Canada. It replaces native wetland species..." (Smith & Smith 2001).

Because of these concerns, we have seen the use of biological pest control on purple loosestrife, namely the importation of alien weevils and beetles that are natural loosestrife predators in Europe and Asia (Stamm et al. 1999). The majority of results from empirical studies, however, show no effect of *L. salicaria* on native plant diversity (Anderson 1995; Hager & McCoy 1998; Farnsworth & Ellis 2001). This lack of empirical evidence extends beyond species-specific cases to the effects of exotic species in general (Slobodkin 2001). We are not suggesting that invasive species are not a problem. In fact, the empirical evidence that introduced predators and pathogens can have devastating impacts on native diversity is unequivocal. In addition, there is convincing evidence that plant invasions can have dramatic effects on ecosystem functions such as nutrient cycling (Mack et al. 2001; Blank & Young 2002) and fire regime (Platt & Gottschalk 2001). The evidence for the negative effects of introduced competitors on species richness is much less convincing, although there is some evidence of invasive effects in woodlands (Franks 2002) and grasslands (Meiners et al. 2001; Alvarez & Cushman 2002). Certainly, the verdict is not in and there is room for much more research on the effects of exotic plant species, but our work joins a growing amount of empirical research suggesting that exotic plant species are, by and large, a minor threat to native wetland plant diversity.

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