

# Competitive effects of non-native plants are lowest in native plant communities that are most vulnerable to invasion

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**Abstract** Despite widespread acknowledgment that disturbance favors invasion, a hypothesis that has received little attention is whether non-native invaders have greater competitive effects on native plants in undisturbed habitats than in disturbed habitats. This hypothesis derives from the assumption that competitive interactions are more persistent in habitats that have not been recently disturbed. Another hypothesis that has received little attention is whether the effects of non-native plants on native plants vary among habitats that differ in soil fertility. We documented habitat occurrences of 27 non-native plant species and 377 native plant species encountered in numerous study plots in a broad sample of ecosystems in MS (USA). We then reviewed experimental and regression-based field studies in the scientific literature that specifically examined potential competitive (or facilitative) effects of these non-native species on native species and characterized the habitats in which effects were the greatest. As expected, the non-native species examined here in general were more likely to be

associated with severely disturbed habitats than were the native species as a group. In contrast, we found that non-native species with competitive effects on natives were more likely to be associated with undisturbed habitats than with disturbed habitats. When longer term studies involving more resident species were given more weight in the analysis, competitive effects appeared to be the greatest in undisturbed habitats with low soil fertility. These results reinforce the notion that invasion is not synonymous with impact. The environmental conditions that promote invasion may limit competitive effects of invaders on native plant communities following invasion.

**Keywords** Competition · Disturbance · Impact · Invasive Species · Invasibility · Resources · Soil Fertility

## Introduction

The conditions that promote invasion and exacerbate the competitive effects of non-native species on native species are of great interest to ecologists and conservationists. Most ecologists agree that given an adequate supply of propagules, disturbances that cause or coincide with increases in resource availability tend to promote invasion (Hobbs and Huenneke 1992; Burke and Grime 1996; Davis et al. 2000; Stohlgren et al. 2001; Huston 2004; Stachowicz and Tilman 2005). A generally accepted explanation for such an association

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is that disturbances (events that cause the partial or complete destruction of biomass; Grime 1979) release resources that are often limiting but necessary for the establishment of non-resident species in a community (Burke and Grime 1996; Davis et al. 2000; Huston 2004; Stachowicz and Tilman 2005). Severe disturbances (e.g., those that cause substantial mortality such as soil disturbances or herbicide application) are especially effective at promoting the establishment of non-resident species in ecosystems with high site productivity (e.g., high soil fertility; high light availability; Davis et al. 2000).

Although severe disturbances may favor invasion by non-native species, not all non-native species require severe disturbance to invade natural communities. Resource availability alone can promote invasion by non-native species. For example, some species have been shown to invade undisturbed habitats with fertile soils (Huenneke et al. 1990). Furthermore, in some unproductive ecosystems, weak competitive interactions may permit invasions of non-native species that are themselves weak competitors (Huston 2004). Some non-native species may benefit from empty niches made available when species are lost due to processes unrelated to disturbance (Levine 2000). On the other hand, provided that there is an adequate supply of propagules, neither disturbances nor species losses may be necessary for an invader to ultimately dominate the community (Levine 2000; Von Holle and Simberloff 2005). Finally, and perhaps most relevant to biodiversity conservation, neither disturbances nor reduced competition may be necessary for dominance when the potential invader is competitively superior to the natives (Levine and D'Antonio 1999; Brewer 2008).

Although the competitive effects of invaders have received an increasing amount of attention over the past decade (Gurevitch and Padilla 2004; Huston 2004; Ricciardi and Cohen 2007; Hejda et al. 2009; Powell et al. 2011; references herein), how environmental factors influence effects on native species have received relatively less attention. In general, the conditions that favor invasion may not predict competitive effects of invaders (Ricciardi and Cohen 2007). In some instances, invaders may become numerically dominant within communities without displacing native species (Brewer 2011). Invasion may represent an opportunistic response to disturbance, high resource availability, alterations in plant-

soil feedbacks, or reduced competition. If the invader is better able to take advantage of these conditions than are most native species in the system, then the invader may become numerically dominant within a community characterized by disturbance or high resource availability, regardless of whether there is significant interaction (negative or positive) between it and resident plant species (Gurevitch and Padilla 2004; MacDougall and Turkington 2005; Surratte and Brewer 2008; Brewer 2011). Once a non-native species has invaded a community, competitive displacement of native species may require that the community be free of significant disturbance (Huston 2004). If the non-native species requires disturbance to persist within the community, then a lack of disturbance will more likely result in its competitive displacement rather than the reverse.

Ideally, examination of the effects of severe disturbance, resources or other environmental variation on competitive effects of invaders on native species would be built into the design of a single experimental study (Alvarez and Cushman 2002); however, such experiments can be costly and logistically unfeasible. Given the increasing number of studies of competitive effects of invaders (Powell et al. 2011), another approach is to conduct a literature review of studies that quantify the per capita competitive effect of non-native species on native communities, and then examine relationships between the competitive effects of invaders and the environments in which the invaders occur. Some relevant questions that can be addressed using this method are: Do the conditions that typically promote invasion also exacerbate competitive effects of invaders? Or are the least invulnerable communities the most vulnerable to competition from invaders once invaded?

In this study, we examined both the community invasibility and the potential vulnerability to competition from non-native plants for different ecosystems. We documented habitat associations of native and non-native plant species and then reviewed correlative and experimental studies in the literature that specifically examined competitive and/or facilitative effects of the non-native species on native plant communities. With these results, we pursued two objectives. First, we examined how environment conditions (e.g., disturbance regimes, resource availability) associated with different plant communities influenced their invasibility. Second, we examined how the disturbance regimes and

resource availability associated with different plant communities potentially affected their vulnerability to competition from invaders after invasion had occurred. We hypothesized that the non-native species examined here, as a group, are more likely to be associated with disturbed and productive ecosystems than are the native species as a group. We also hypothesized, however, that those non-native species with the greatest competitive effects on native plant communities (in terms of abundance, biomass, and species diversity) are more likely to be associated with undisturbed habitats than are non-native species with relatively weak effects on native plant communities.

## Methods

### Community invasibility of non-native species

To quantify community invasibility and associated ecological conditions, we examined the ecological distributions of 377 native and 27 non-native species (listed in Electronic Appendix 1a—Habitat indication of 27 non-native species and 377 natives encountered in field plots throughout MS) in multivariate habitat space (habitats listed in Electronic Appendix 1b—Habitats described in regional flora manuals for 27 non-native and 377 natives encountered throughout MS; described below). We assumed that the most invulnerable communities were those in which non-native species as a group most frequently occurred. We tabulated habitat occurrence (presence/absence) of all non-native and native species encountered and identified in field study plots across a wide range of wildland habitats in MS. The field study plots that provided the species list upon which habitat association analyses were based were located in natural communities encompassing a broad range of soil fertilities (e.g., from acidic pine savannas dominated by carnivorous plants to rich, silt-loam floodplains, loess-capped terraces, and nutrient-rich marshes), light regimes (open savannas and marshes to closed-canopy forests), and disturbance regimes (e.g., soils disturbed by logging or flooding, mowed roadsides and powerline clearings, fire-maintained savannas, and undisturbed forests). The following habitats in MS were sampled: upland mature hardwood forests with silt-loam soils in north MS, including mature stands and disturbed roadsides (Surrette and Brewer 2008;

Brewer and Menzel 2009), upland *Quercus L./Pinus echinata* Mill./*Carya* Nutt. forests with loamy sandy soils in north MS, including mature stands, stands recently damaged by a tornado, and stands damaged by a tornado and subsequently salvage-logged (Surrette and Brewer 2008; Brewer et al. 2012), mature and recently disturbed mesic and floodplain forests in north MS (Brewer 2011), mesic *Pinus palustris* L. flatwoods and hydric *P. palustris/Pinus elliotii* Engelman. savannas in southern MS, including logging machinery ruts and herbicide patches within these habitats (Hinman and Brewer 2007; Brewer et al. 2011).

To statistically analyze habitat associations of native and non-native species, we did a principal coordinates analysis (PCO) ordination of all species in habitat space using Bray-Curtis similarities (which, when using presence/absence data, are equivalent to Sørensen's quotient of similarity). The similarity matrix included 149 habitats as identified from multiple regional flora manuals (Radford et al. 1968; Godfrey and Wooten 1979a, b; Clewell 1985; Jones 2005; Electronic Appendices 1a and 1b). Statistically significant differences in the average locations of native and nonnative species in habitat space were compared using permutation MANOVA (Anderson 2001) using similarities among species in habitat space. We used a permutation-based multivariate dispersion test to test for differences in dispersion among native and non-native species in habitat space (Permdisp: Anderson 2006). The superimposing of habitat centroids on the ordination of species in turn enabled us to contrast the habitats with which non-native and native species were associated, and thus aided in interpretation of permutation MANOVA and Permdisp results. Centroids of weighted averages of species ordination scores for PCO axes one and two were calculated for the following six general habitat categories: disturbed habitats, open habitats with fertile soils, infertile (i.e., nutrient-poor) soils, shady habitats, shady habitats with fertile soils, and other habitats (i.e., habitats that could not be readily classified in terms of light, soil fertility, or disturbance). Together, perMANOVA, permdisp, and the ordination enabled us to determine the extent to which non-native species were associated with a certain subset of habitat types (e.g., disturbed areas) occupied by native species.

All but two of the 27 non-native species analyzed were encountered in the field plots. We added two other species: *Lythrum salicaria* L. and *Alliaria*

*petiolata* (M. Bieb.) Cavara and Grande. *L. salicaria* occurs in MS (Wielund et al. 2003) but is largely found in freshwater marshes, a community that is common in MS, but not sampled here. *A. petiolata* is not known to occur in MS, but it does occur in nearby Tennessee, Alabama, and Arkansas in hardwood forests similar to those our group has studied in northern MS. Both *A. petiolata* and *L. salicaria* have been studied extensively in eastern North America, thereby adding significantly to the number of competition studies that could be reviewed. The resulting list of 27 non-native species included high-profile invaders of natural and disturbed areas in eastern North America (e.g., *A. petiolata*, *L. salicaria*, *Microstegium vimineum* (Trin.) A. Camus, *Pueraria montana* (Lour.) Merr. var. *lobata* (Willd.) Maesen and S. Almeida, and *Imperata cylindrica* (L.) Beauv. and several lower-profile invaders (e.g., *Digitaria sanguinalis* L. Scop., *Cyperus iria* L., *Rumex crispus* L.). The 27 non-native species (in 18 families) examined here represented approximately 4 % of non-native species and 16 % of the families of non-native species in MS (Wielund et al. 2003). Six of the ten “worst weeds” in MS (as proposed by the MS Exotic Pest Plant Council; i.e., *I. cylindrica*, *Ligustrum sinsense*, *Lonicera japonica*, *L. salicaria*, *P. montana*, and *Triadica sebifera*) were included in our study.

To quantify habitat indication for each native and non-native species, we used an objective method that we developed in previous studies of effects of invasions, land management practices, or environmental conditions on plant species composition in a variety of ecosystems in MS (Brewer 2008; Brewer and Menzel 2009; Brewer 2011; Brewer et al. 2012). Detailed descriptions of the methods can be found in those studies, but an overview of the method is provided here. The binary, presence/absence matrix of 27 non-native species and 377 native species in 149 habitats described in regional flora manuals (mentioned above) was used to calculate habitat indicator scores for each species associated with each of the six general habitat categories of interest (Electronic Appendix 1a). This was done separately for each general habitat category by first pooling all specific habitats into a single pooled category (e.g., all habitats with nutrient-poor soils into a pooled general category called “infertile soils”). This pooled category was then treated as a specific habitat, and presence–absence within that pooled habitat was re-tabulated

for each species. We then calculated Bray-Curtis similarities between this pooled habitat and all the remaining specific habitats. The resulting similarity coefficients were then re-inserted into the matrix (replacing the 1’s), and weighted averages of occurrence in the pooled habitat category were calculated for each species. These species scores represented proportional indication of the pooled habitat category. The process was repeated for the remaining five general habitat categories. Hence, each species had an indication score for disturbed habitats, open habitats with fertile soils, infertile soils, shady habitats, shady habitats with fertile soils, and other habitats (Electronic Appendix 1a).

#### Quantifying competitive effects of non-native species

We reviewed correlative and experimental field studies in the literature that specifically examined effects of the 27 non-native species on native species or relationships between non-native and native species and characterized the habitats in which competitive effects were the greatest. In November 2011, we initiated targeted searches of all 27 non-native species from studies available from the entire electronic databases of the following ecological journals: *Biological Invasions*, *Biological Conservation*, *Conservation Biology*, *Ecology*, *Ecological Applications*, *Journal of Ecology*, *Plant Ecology*, *Journal of Applied Ecology*, *Natural Areas Journal*, and *Applied Vegetation Science*. In addition to these journals, we used search engines (BioOne, ISI Web of Science, and Google Scholar) and citations from the results of the targeted searches to locate studies of effects for these species in other journals, which included: *Invasive Plant Science and Management*, *Diversity and Distributions*, *Journal of the Torrey Botanical Society*, *American Midland Naturalist*, and *Northeastern Naturalist*. We defined effect to mean a per capita competitive or facilitative effect of the non-native plant on native plants (Parker et al. 1999). To demonstrate an effect, the study had to either (1) investigate a correlation in abundance, cover, or occurrence in space (regression) or time (repeated measures; observation before and after invasion) between the non-native species and one or more native species or (2) investigate the response of one or more native species to the experimental removal or

addition of the non-native species in question (or the experimental addition of native species to areas occupied by the non-native species). Because a primary objective of this study was to relate competitive effects to resource availability and disturbance regimes that naturally occurred in the field, we excluded from consideration all laboratory and greenhouse studies and included only field studies that specifically examined effects on or correlative relationships with resident vegetation. Artificial field (i.e., garden studies) studies were included, as long as they were conducted in soil types or disturbance regimes comparable to those associated with the habitats for which inferences were made.

To ensure an adequate sample size of studies investigating effects, we included a wide variety of response variables and methods and approaches for measuring effects. As a result, it was not possible to differentially weight studies according to effect size and do a meta-analysis. Instead, we categorized a non-native species' competitive or facilitative effect using ordered integers (−2, −1, 0, 1, 2) and then weighted the effect according to the methodology used in the study to quantify effects (weighting factor; see Electronic Appendix 2—List of studies, methodological weighting criteria and scores, and effects). The ordered categories of effects included: strongly negative (−2; a large fraction of studied species negatively affected in terms of biomass, cover, abundance, or occurrence; percent affected >25 % or  $r^2$  for correlation >0.25), weakly negative (−1; <25 % of studied species negatively affected), neutral (0; no significant positive or negative effects for any species studied), weakly positive (1, <25 % of studied species positively affected), and strongly positive (2; >25 % studied species positively affected). In cases in which both positive and negative effects were recorded, the net difference was categorized.

Because not all studies were based on long-term experiments involving numerous species, the validity of our conclusions regarding the effects of non-native species may depend on the methodological rigor of the studies sampled. To explore the influence of methodology, we conducted two sets of analyses with the data: one in which each study was weighted by the methodological approach used to assess effects; and one in which effects were not weighted by methodology. We chose two easily-defensible criteria to weight the effect of the non-native species for each

study: Study duration and the number of resident species potentially affected (Electronic Appendix 2). Longer duration studies (>3 years) were assigned a higher score (1) than studies of shorter duration (0.5), based on the empirically-supported contention that competitive effects (especially among perennial plants) may require several years to be adequately measured (Dybzinski and Tilman 2007). In addition, most long-term studies were experimental or quasi-experimental (i.e., before and after observation). Studies that involved several (>3) species were assigned a higher score (1) than studies investigating only a few species (0.5), consistent with the notion that evaluating community-level effects (e.g., effects on species diversity) require examining effects on numerous species. Some studies used more than one methodological approach or repeated the analysis in more than one resource/disturbance-level block or group. In those cases, the weighting factor was calculated or repeated for each approach or block/group. We avoided sampling multiple studies from a single researcher or research laboratory, unless the different studies examined different non-native species, different resident communities, or used different methodological approaches to measure effects.

The methodological weighting factor for each study was obtained by taking the product of the scores for both weighting criteria. Each study's methodological weighting factor potentially ranged from a low of 0.25 [e.g., for a short-term study involving few species ( $0.5 \times 0.5$ )] to a maximum of 1 [e.g., for a long-term study involving observation of many species ( $1 \times 1$ )]. Calculations are in Electronic Appendix 2.

#### Relationship between effects of invaders and soil fertility, light availability, and disturbance

The relationship of the effect of a non-native species with the habitat with which it was associated was examined in two different ways. First, we regressed effect values (with and without weights for study duration and the number of species) averaged across all studies for each non-native species against multiple predictors (habitat indication scores). Specifically, we examined relationships with the indication of disturbed habitats, open habitats with fertile soils, shady habitats with fertile soils, and infertile soils. Because we were only able to find published data on 11 of the 27 non-native species (in 43 studies/study locations),

we added more species to the analysis by considering anecdotal information available through the I-Ranking of species by NatureServe Explorer. Specifically, we considered NatureServe's assessment of the species' impact on community composition and disregarded other I-Rank criteria. Of the 16 species for which we could find no quantitative data on effects, NatureServe assigned rankings on impact on community composition for nine species, based on descriptive scientific reviews. To include these nine species in the weighted analysis, however, we assigned them a low weighting factor (0.25; equivalent to a short-term study involving few species). We assigned an effect value of 0 (neutral effect) to the seven species that were described as having weak or insignificant effects and  $-2$  to the two species that were described as high negative effects on community composition [*P. montana* (kudzu) and *Albizia julibrissin* Durazz (mimosa)]. No ranking was available for seven other species, and we excluded these species from all analyses of effects. Weighting the regression in terms of methodological strength was accomplished by multiplying the z-transformed effect value for each study by the weighting factor, yielding a weighted effect (see Electronic Appendix 2). The best habitat predictors of weighted (or unweighted) effect were chosen using Akaike's Information Criterion corrected for small sample sizes (AICc). To determine the influence of including anecdotal reviews, we did a second analysis excluding the nine species for which there were no quantitative data. Because the assumptions of linear regression were violated using these data, *P*-values associated with the multiple regression were obtained using permutation-based Euclidean distance-based linear modeling (McArdle and Anderson 2001).

A second set of analyses was done to examine the relationship between weighted effect and soil fertilities of the study sites at which the studies were conducted. Soil fertility was categorized for each site subjectively, as inferred from the study site description (Electronic Appendix 3). For example, a glade with rocky and thin soils received a soil fertility score of 0, whereas a floodplain forest with silt-loam soils received a fertility score of 1, and an upland forest on sandy-loam soils received an intermediate soil fertility score of 0.5. We made no attempt to distinguish soil fertility among sites within the same habitat type. We averaged both weighted effect and soil fertility across all studies/groups per species and

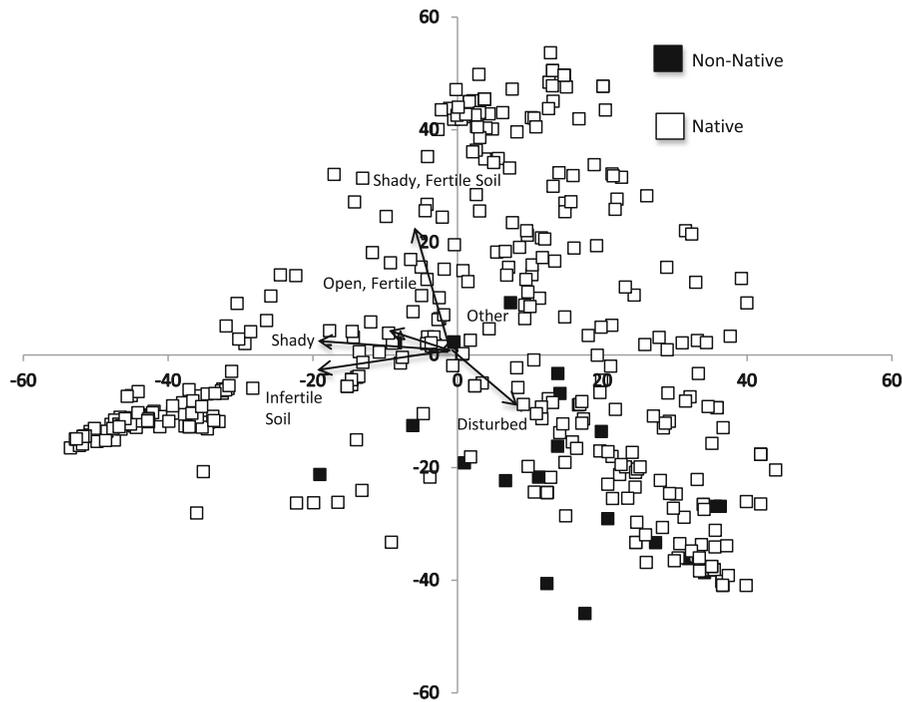
habitat type. We included only those 11 species for which quantitative data were available. Because the assumptions of linear regression were violated using these data, *P*-values associated with the regression were obtained using permutation-based Euclidean distance-based linear modeling. All multivariate and permutation-based univariate analyses were done using Primer v. 6+ PerMANOVA.

## Results

### Community invasibility

As expected, results indicated that the non-native species examined here, as a group, were more likely to be restricted to severely disturbed habitats than were the native species as a group (Fig. 1). PCO Axis 1 (which explained 18 % of variation in habitat association among species) reveals a soil fertility gradient (low to high, left to right), whereas PCO Axis 2 (which explained 14 % of the variation in habitat association among species) reveals a light gradient (low to high, upper to lower). A gradient of disturbance intensity occurs along a diagonal from little or low-intensity disturbance (upper left corner of the ordination) to high-intensity disturbance (lower right corner of the ordination), and non-native species are for the most part clustered in the lower right corner of the ordination (Fig. 1). Permutation MANOVA showed significant differences in habitat associations between non-native and native species (Pseudo- $F_{1, 402} = 9.61$ ;  $P < 0.001$ ). However, the permutation MANOVA assumption of homogeneous multivariate dispersion was violated ( $F_{1, 402} = 137.2$ ;  $P < 0.001$ ). Native species as a group occupied a greater variety of habitats (Fig. 1). Average deviation from the centroid was greater for native species than for non-native species ( $63.9 \pm 0.2$  vs.  $49.9 \pm 2.9$ , respectively).

Despite non-native species as a group being more strongly associated with severely disturbed habitats than native species as a group, there was nonetheless variation among non-native species in terms of their association with habitats that differed with respect to severe disturbance, light, and soil resource availability (Table 1). Whereas some non-native species were largely restricted to severe anthropogenic disturbance (*Abutilon theophrasti* Medik., *Allium vineale* L., *Cynodon dactylon* (L.) Pers., *D. sanguinalis*, *P.*



**Fig. 1** Principal coordinates analysis ordination of 377 native and 22 non-native species in habitat space, based on Bray–Curtis similarities of occurrence. *Axis 1* explains 18 % of the variation in habitat association and *axis 2* explains 14.7 % of the variation

in habitat association. Vectors are associated with centroids (averages of weighted averages of species scores) of six general habitat categories

*notatum* Flueggé, *Ipomoea purpurea* (L.) Roth, *Setaria pumila* (Poir.) Roem. and Schult.), others were not restricted to disturbed habitats (e.g., *A. petiolata*, *I. cylindrica*, *Lespedeza cuneata* (Dum. Cours.) G. Don, *M. vimineum*, *L. salicaria*, *Ligustrum sinense* Lour.). Of the group of non-natives that were not restricted to severely disturbed habitats, some were more strongly associated with infertile soils (e.g., *I. cylindrica*, *L. japonicum*, *L. cuneata*) than were other non-native species. Other non-native species were more associated with shady habitats with fertile soils (e.g., *A. petiolata*) or open habitats with fertile soils (e.g., *L. salicaria*) than were other non-native species.

#### Competitive effects of non-native species

Most studies with quantitative data found that effects were either strongly negative, weakly negative, or neutral (Table 2; Electronic Appendix 2—average effect =  $-1.06$ ). Only one study (a regression-based study of *L. salicaria*) revealed a positive effect (Hager and Vinebrooke 2004). Hence, most of the variation in

effects among studies and/or species reflected the magnitude in competitive effects. Observed weighting factors ranged between 0.25 and 1 (Table 2 and Electronic Appendix 2). Most species that had strongly competitive effects were represented by quantitative studies in support of such effects (but two exceptions were *P. montana* var. *lobata* and *A. julibrissin*).

Competitive effects of non-native species in relation to soil fertility, light availability, and severe disturbance

The regression of effect per species (unweighted by study duration or species number) and the habitat indication scores of 20 non-native species revealed that competitive effects were most associated with indication of undisturbed habitats. The model with the lowest AICc contained only severe disturbance indication (Table 3). The relationship between effect and indication of severe disturbance was positive and statistically significant at the 0.05 level (Table 3).

**Table 1** Regional habitat indication for 25 non-native species encountered in field plots in various habitats throughout MS and for two additional non-native species, *L. salicaria* and *A. petiolata*

Species	Disturbed <sup>a</sup>	Open, fertile soils	Nutrient-poor soils	Shady	Shady fertile	Other
<i>Abutilon theophrasti</i>	1.00	0.19	0.23	0.22	0.15	0.37
<i>Albizia julibrissin</i>	0.47	0.09	0.09	0.17	0.15	0.56
<i>Alliaria petiolata</i>	0.35	0.15	0.14	0.24	0.51	0.39
<i>Allium vineale</i>	1.00	0.12	0.09	0.11	0.09	0.16
<i>Cerastium fontanum</i> Baumg. ssp. <i>vulgare</i> (Hartm.) Greuter and Burdet	1.00	0.15	0.16	0.17	0.13	0.26
<i>Cynodon dactylon</i>	1.00	0.15	0.18	0.17	0.12	0.29
<i>Cyperus iria</i>	0.59	0.53	0.15	0.18	0.13	0.23
<i>Digitaria sanguinalis</i>	1.00	0.13	0.15	0.14	0.10	0.24
<i>Hedera helix</i>	1.00	0.20	0.15	0.19	0.15	0.30
<i>Imperata cylindrica</i>	0.38	0.11	0.30	0.15	0.10	0.31
<i>Ipomoea purpurea</i>	1.00	0.20	0.15	0.19	0.15	0.30
<i>Lespedeza cuneata</i>	0.69	0.17	0.24	0.20	0.14	0.53
<i>Ligustrum sinense</i>	0.28	0.30	0.13	0.28	0.28	0.38
<i>Lonicera japonica</i> Thunb.	0.53	0.16	0.18	0.31	0.18	0.39
<i>Lygodium japonicum</i>	0.31	0.17	0.37	0.39	0.29	0.20
<i>Lythrum salicaria</i>	0.34	0.40	0.07	0.07	0.08	0.35
<i>Microstegium vimineum</i>	0.41	0.39	0.20	0.41	0.23	0.28
<i>Nandina domestica</i> Thunb.	0.33	0.20	0.26	1.00	0.38	0.32
<i>Paspalum boschianum</i> Flueggé	1.00	0.29	0.15	0.19	0.13	0.25
<i>Paspalum notatum</i>	1.00	0.18	0.20	0.20	0.13	0.33
<i>Poncirus trifoliata</i> L. (Raf.)	0.63	0.06	0.06	0.12	0.11	0.50
<i>Pueraria montana</i> var. <i>lobata</i>	0.53	0.15	0.18	0.32	0.18	0.41
<i>Rumex crispus</i>	0.39	0.37	0.13	0.15	0.12	0.37
<i>Setaria pumila</i>	1.00	0.19	0.23	0.22	0.15	0.37
<i>Sonchus asper</i> (L.) Hill	1.00	0.18	0.20	0.20	0.14	0.33
<i>Triadica sebifera</i>	0.28	0.32	0.18	0.32	0.27	0.33
<i>Trifolium dubium</i> Sibth.	1.00	0.15	0.30	0.18	0.12	0.29

<sup>a</sup> Habitat indication scores for the 377 native species used in the calculation of scores are available in Appendix 1

Note that because positive effects were apparent in only one study, a positive correlation between effect and disturbance indication means that the effects of invaders were least negative in severely disturbed habitats. The model with the second lowest AICc contained indication of severe disturbance and indication of open habitats with fertile soils (Table 3), and the relationship between effect and indication of open habitats with fertile soils was positive, but not statistically significant (Table 3).

The regression of average effect per species (weighted by study duration and species number) and the habitat indication scores of 20 non-native species revealed that competitive effects were most

associated with indication of undisturbed habitats with infertile soils. The model with the lowest AICc value only included indication of infertile soils (Table 3). The relationship between weighted effect and infertile soil indication was negative and significant (Table 3). The model with the second lowest AICc contained both indication of infertile soils and indication of severe disturbance (Table 3). In this two-predictor model, the relationship between weighted effect and indication of infertile soils was, again, negative and statistically significant at the 0.05 level (Table 3). The relationship between weighted effect and indication of severe disturbance was positive, but was not statistically significant at the 0.05 level (Table 3). Note that a

**Table 2** Effect and methodological weighting factor averaged across studies for each species

Species	Average effect	Average methodological weighting factor	Weighted effect <sup>a</sup>
<i>Abutilon theophrasti</i>	0	0.25	0.26
<i>Albizia julibrissin</i>	−2	0.25	−0.24
<i>Alliaria petiolata</i>	−0.86	0.57	0.18
<i>Allium vineale</i>	0	0.25	0.26
<i>Cerastium vulgatum</i>	N/A	N/A	N/A
<i>Cynodon dactylon</i>	−0.5	0.5	0.28
<i>Cyperus iria</i>	N/A	N/A	N/A
<i>Digitaria sanguinalis</i>	0	0.25	0.26
<i>Hedera helix</i>	−2	0.5	−0.47
<i>Imperata cylindrica</i>	−2	1	−0.94
<i>Ipomoea purpurea</i>	N/A	N/A	N/A
<i>Lespedeza cuneata</i>	−2	0.5	−0.47
<i>Ligustrum sinense</i>	−1.8	0.6	−0.47
<i>Lonicera japonica</i>	−0.75	0.56	−0.03
<i>Lygodium japonicum</i>	−2	0.5	−0.47
<i>Lythrum salicaria</i>	−0.78	0.56	0.09
<i>Microstegium vimineum</i>	−1.36	0.39	−0.14
<i>Nandina domestica</i>	0	0.25	0.26
<i>Paspalum boschianum</i>	N/A	N/A	N/A
<i>Paspalum notatum</i>	0	0.25	0.26
<i>Poncirus trifoliata</i>	N/A	N/A	N/A
<i>Pueraria montana</i>	−2	0.25	−0.24
<i>Rumex crispus</i>	0	0.25	0.26
<i>Setariapumila</i>	0	0.25	0.26
<i>Sonchus asper</i>	N/A	N/A	N/A
<i>Triadica sebifera</i>	−2	1	−0.94
<i>Trifolium dubium</i>	N/A	N/A	N/A
Grand average <sup>b</sup>	−1.06	0.48	−0.06

<sup>a</sup> Obtained by z-transforming effect and multiplying by the methodological weighting factor

<sup>b</sup> Averaged over all studies

**Table 3** Regressions of unweighted and weighted effect against habitat indication for 20 non-native species, showing the best one- and two-predictor models based on AICc corrected for small sample sizes

Regression	AICc	r <sup>2</sup>	Strength of relationship	Error df
Unweighted effect versus severe disturbance	−6	0.23	$r_{\text{disturb}} = 0.48$ ; $P = 0.03$ ; Pseudo- $F = 5.3$	18
Unweighted effect versus severe disturbance and open habitats with fertile soils	−4.79	0.29	Partial $r_{\text{open fertile}} = 0.24$ ; $P = 0.23$ ; Pseudo- $F = 1.4$	17
Weighted effect versus infertile soils	−38.2	0.27	$r_{\text{infertile}} = -0.52$ ; $P = 0.02$ ; Pseudo- $F = 6.62$	18
Weighted effect versus nutrient-poor soils and severe disturbance	−37.3	0.33	Partial $r_{\text{infertile}} = -0.49$ ; $P = 0.03$ ; Pseudo- $F = 6.09$ Partial $r_{\text{disturb}} = 0.25$ ; $P = 0.22$ ; Pseudo- $F = 1.66$	17

negative correlation between effect and infertile soil indication means that effects were most negative in infertile soils. When the nine species for which no quantitative data were available were excluded from

the analysis, the best single-predictor model of weighted effect of the eleven remaining species contained indication of infertile soils (AICc = −20.3; Pseudo- $F_{1,9} = 5.91$ ;  $P = 0.04$ ;  $r = -0.63$ ).

**Table 4** Weighted effect and study site environments averaged across studies for each studied species/soil fertility combination

Species code/site fertility	Ave. weighted effect	Ave. light	Ave. soil fertility	Ave. soil disturbance
<i>Allpet</i> /high fert	0.02	0.00	1.00	0.13
<i>Allpet</i> /mod fert	0.54	0.00	0.50	0.00
<i>Cyndac</i> /mod fert	0.28	1.00	0.50	0.50
<i>Hedhel</i> /mod fert	−0.47	0.00	0.50	0.50
<i>Impcyl</i> /low fert	−0.94	1.00	0.00	0.00
<i>Lescun</i> /mod fert	−0.47	1.00	0.00	0.50
<i>Ligsin</i> /high fert	−0.31	0.00	1.00	0.00
<i>Ligsin</i> /mod fert	−0.47	0.00	0.50	0.00
<i>Ligsin</i> /low fert	−0.94	1.00	0.00	0.00
<i>Lonjap</i> /high fert	0.26	0.00	1.00	0.00
<i>Lonjap</i> /mod fert	−0.13	0.33	0.50	0.17
<i>Lygjap</i> /low fert	−0.47	1.00	0.00	0.50
<i>Lytsal</i> /high fert	0.09	1.00	1.00	0.00
<i>Micvim</i> /high fert	−0.18	0.44	1.00	0.19
<i>Micvim</i> /mod high fert	−0.31	0.00	0.75	0.00
<i>Micvim</i> /mod fert	0.26	0.00	0.50	0.00
<i>Triseb</i> /mod fert	−0.94	1.00	0.50	0.00
Grand average	−0.25	0.48	0.76	0.10

Ordered environmental conditions scaled from 0 to 1 were inferred from study site descriptions. In regards to soil fertility, study sites described as having sandy, acidic, and/or thin soils were assigned soil fertility values of 0, whereas study sites with alluvial soils (e.g., floodplain forest), mesic silt-loam soils, circumneutral (e.g., limestone-based) soils, loessal soils, or mucky soils (e.g., marshes) were assigned soil fertility values of 1. Study sites with intermediate soils (e.g., dry-mesic soils of upland hardwood forests, prairies) were generally assigned values of 0.5. See Electronic Appendix 3 for abbreviated study site descriptions for each study

The second best single-predictor model of weighted effect contained indication of disturbance, but it was not statistically significant (AICc = −17.0; Pseudo- $F_{1,9} = 2.11$ ;  $P = 0.18$ ;  $r = 0.43$ ). A regression of weighted effect versus the product of severe disturbance indication and the inverse of indication of nutrient-poor soils revealed no significant interaction between severe disturbance and soil fertility (Pseudo- $F = 0.29$ ;  $P = 0.60$ ;  $r = -0.13$ ). The regression of weighted effect against study site soil fertility averaged over all studies per species/habitat type combination revealed that the competitive effects were most associated with study sites with low soil fertilities (Pseudo- $F_{1,15} = 4.87$ ;  $P = 0.06$ ;  $r = 0.49$  for weighted effect vs. soil fertility; Table 4).

## Discussion

The 27 non-native species examined here, as a group, appeared to be associated with a disturbance-prone subset of habitats occupied by 377 native species

encountered in a wide range of habitats in MS (USA). This association of non-native species with disturbed habitats agrees with the findings of previous studies (Lozon and MacIsaac 1997; Davis et al. 2000; Huston 2004). Despite non-native species as a group being more strongly associated with disturbed habitats than native species as a group, there was nonetheless modest variation among non-native species in terms of their association with habitats that differed with respect to disturbance, light, and soil resource availability, indicating that not all non-native species encountered in this study were restricted to disturbed habitats (Table 2).

Negative effects of the non-native species examined in this study were most associated with undisturbed habitats. The non-native species that had the weakest effects on native plant communities were mostly annual ruderals, and thus were likely poor competitors relative to native species. Because disturbances can simultaneously favor invasion and reduce competition, ecologists should not assume that the same factors that promote invasion also result in

competitive displacement of native species (Huston 2004; Brewer 2011). Disturbances that are of sufficiently high intensity may both favor non-native and directly reduce native plant diversity (Brewer 2010), which could lead observers to incorrectly attribute disturbance-mediated reductions in native plant species diversity to competitive displacement by invaders.

When we gave greater weight to studies of longer duration and that involved more species, competitive effects of the non-native species examined in this study were most associated with undisturbed habitats with infertile soils. Examples included a >80 % reduction in groundcover plant species richness in just three years by *I. cylindrica* in a *P. palustris* flatwoods ecosystem with sandy, acidic, nutrient-poor soils (Brewer 2008), a significant reduction in plant species richness in 2 years by *L. japonicum* (Thunb.) Sw. in a moderately disturbed *P. palustris* flatwoods ecosystem (Bohn et al. 2011), a 35–100 % reduction in the density of indicative plant species over 13 years caused at least in part by *L. sinense* in xeric glades with thin, rocky soils (Sutter et al. 1993), and a reduction in percent cover of graminoids from 62 to 29 % 5–10 years after initiation of stands of *T. sebifera* L. (Small) invasion in coastal prairies with heavy, poorly-drained soils (Bruce et al. 1995).

Why competitive effects of invaders would be greater in soils of low fertility than in rich soils is not obvious nor necessarily expected (Blumenthal et al. 2003). Growth and reproduction are often favored in nutrient-rich soils (Grime 1979). To the extent that non-native species have a growth advantage over native species (perhaps due to their escaping enemies or negative soil feedbacks; Blossey and Notzold 1995; Klironomos 2002), one might expect competitive effects of non-native species on native species to be greater in those habitats in which high growth rates are most likely to confer a competitive advantage (Grime 1979; Blumenthal et al. 2003). Although we cannot rule out the influence of publication bias, one possible ecological explanation for our results is that greater size asymmetry between non-natives and natives in infertile soils gave rise to greater competitive asymmetry. *I. cylindrica*, *L. sinense*, and *T. sebifera* were all long lived and significantly taller than the majority of native species in the communities they invaded and affected, most of the latter being herbaceous plants associated with infertile or moderately low fertility

soils (Bruce et al. 1995; Brewer 2008; Sutter et al. 2011). In contrast, many of invaders of fertile soils were small and short-lived herbs (e.g., *A. petiolata*, *M. vimineum*, *L. salicaria*). These observations suggest that size asymmetry and/or life history might be important mechanisms of competitive suppression in plant communities in habitats with nutrient-poor soils (Hejda et al. 2009).

Although the current study builds upon the general consensus that severe disturbances that cause or coincide with increases in resource availability are important drivers of invasion, we also find the environmental conditions that promote invasion are not the same as those that maximize the competitive effect of non-native species on native species following invasion. A complete understanding of the effects of invasions on native species diversity requires that the environmental drivers of competitive effects be given just as much attention as the environmental drivers of invasion.

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