

LETTER

Intraspecific diversity and dominant genotypes resist plant invasions

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Abstract

Numerous studies have asked whether communities with many species deter invasions more so than do species-poor communities or whether dominant species deter invasion by colonizing species. However, little is known about whether high intraspecific diversity can deter biological invasions or whether particular genotypes might deter invasions. In this study, we present experimental evidence that intraspecific diversity and particular genotypes of tall goldenrod, *Solidago altissima*, can act as a barrier to colonization by new species. We found that biomass of colonizing species was negatively correlated with genotypic diversity, and particular genotypes affected the richness, cover, and biomass of colonizing species. Stem density of *S. altissima* increased with genotypic diversity and varied among genotypes, suggesting that stem density is a key mechanism in limiting colonization dynamics in this system. Our results indicate that the loss of intraspecific diversity within a dominant plant species can increase susceptibility to plant invasions.

Keywords

Biodiversity, community genetics, ecological resistance, ecosystem function, genotypic diversity, invasive species, old field, *Solidago altissima*.

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INTRODUCTION

Biological invasions threaten native biodiversity, alter the functioning of ecosystems, and cause substantial economic impacts (Vitousek *et al.* 1997; Mack *et al.* 2000; Lockwood 2006). Thus, it is critical to understand which species are likely to invade and which communities are likely to be invaded. One hypothesis, first formalized by Elton (1958), is that communities with more species should be more resistant to invasive species than are species-poor communities. Elton's diversity-resistance hypothesis has been supported by a number of studies, especially at local scales (Levine *et al.* 2004; Hooper *et al.* 2005; Srivastava & Vellend 2005; Fridley *et al.* 2007a), while positive relationships between diversity and invasion have been found at larger spatial scales (Fridley *et al.* 2007a). Although the theory has advanced since first posited by Elton, the general idea is that competition among species intensifies as communities become more species rich, leaving fewer available resources for colonizing species. However, many biodiversity studies confound diversity effects with the identity and/or abundance of a particular species (Hooper *et al.* 2005). In fact,

the presence of competitively dominant species, rather than diversity *per se*, might be a key determinant of invasion resistance (Fridley 2001; Wardle 2001; Smith *et al.* 2004; Fargione & Tilman 2005).

Studies that link species diversity to invasion resistance are part of a larger body of work linking species diversity to the functioning of ecosystems (Hooper *et al.* 2005). A growing number of studies have shown that intraspecific diversity can also influence the structure of communities and the functioning of ecosystems (Hughes & Stachowicz 2004; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006; Whitham *et al.* 2006). Like diversity among species, diversity within species may play an important role in susceptibility or resistance to invasion, but this issue has been little explored (Weltzin *et al.* 2003; Hooper *et al.* 2005). For example, if genetic variation in the competitive ability of individuals within species occurs (Taylor & Aarssen 1990; Fridley *et al.* 2007b), then the colonization success of an invader may depend on both the genotypic and species identities of resident individuals (Vellend 2006). Therefore, the level of genotypic diversity within resident populations might ultimately determine species diversity, coexistence,

and susceptibility to invasion within a community (Booth & Grime 2003; Vellend 2006; Whitham *et al.* 2006).

In this study, we ask whether local populations of a dominant species with higher genotypic diversity are more resistant to invasion than are those with lower genotypic diversity, and whether particular genotypes are more resistant to invaders than are others. We find that genotypic diversity and particular genotypes within populations deter biological invasion, much like species diversity and dominant species do.

METHODS

Study site and natural history

We began this research in Spring of 2005 in an old-field site at Freel's Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park near Oak Ridge, Tennessee (35°58'N, 84°12'W). The site was abandoned from agricultural use in 1943. Plant community composition in the old fields surrounding the experimental area is typical of other old fields in east Tennessee. Besides *Solidago altissima*, common native plant species include *Verbesina occidentalis* L. (yellow crownbeard), *V. virginica* L. (white crownbeard), and *Rubus* spp. (blackberry). Out of the *c.* 100 total plant species in neighboring fields, *c.* 25% are exotic and invasive. Common invasive plant species at and near the experimental garden include *Microstegium vimineum*, *Lonicera japonica*, *Ligustrum sinense*, *Pueraria lobata*, *Rosa multiflora*, and *Lespedeza cuneata*.

Solidago altissima is a rhizomatous, out-crossing, perennial species that dominates old fields throughout eastern North America during the first 15–20 years following abandonment (Werner *et al.* 1980). Local populations of *S. altissima* can contain just a few to thousands of ramets, and densities of genotypes can vary from 1 to > 12 genotypes m⁻², creating a natural mosaic of single-genotype and mixed-genotype patches of plants, depending on how long an area has been left undisturbed (Maddox *et al.* 1989). Clones within a local area can exhibit considerable interclonal genetic variation in many plant traits, including those that might influence competitive ability, such as resistance to herbivores or biomass production (Crutsinger *et al.* 2006; Wise *et al.* 2006). In east Tennessee, *S. altissima* makes up, on average, 20% (range = 5–47%) of the aboveground biomass and 0–43% of total plant cover in old-field ecosystems (L. Souza, unpublished data).

Experimental garden

In 2005, we collected 21 *S. altissima* ramets from local *S. altissima* patches growing 50–150 m apart in old fields near the experimental garden. Each ramet was identified as a

unique genotype by means of amplified fragment length polymorphisms (AFLPs). All 21 genotypes were approximately equally related (Crutsinger *et al.* 2006). We propagated ramets for this experiment from rhizome cuttings grown in a greenhouse in the early spring of 2005.

In May 2005, we established 63 1-m² experimental plots in a 15 × 20-m grid in the experimental garden. We cut 6 × 30 cm trenches around each of the experimental plots and lined them with heavy plastic to prevent spread of ramets among plots. Three weeks prior to planting the ramets, we sprayed all of plots with herbicide to eliminate previously established species. A 3-m tall fence was constructed around the experiment to exclude deer.

Each 1-m² experimental plot contained 12 *S. altissima* ramets and was randomly assigned to contain 1, 3, 6, or 12 genotypes, mimicking natural densities of genotypes (Maddox *et al.* 1989). We created genotypic mixtures by randomly sampling from the pool of 21 genotypes with the constraint that no two patches in a treatment could have identical composition. There were seven replicates for the 3-, 6-, and 12-genotype treatments and two replicates of each of the 21 1-genotype treatments. For further details on the establishment of the experimental garden see Crutsinger *et al.* 2006.

Invasion experiment

From spring of 2005 to the peak of the growing season in 2006, we hand-weeded each of the plots bi-monthly to exclude all other plant species, along with any *S. altissima* stems that might have colonized the plots from the seed bank. We were able to distinguish *S. altissima* seedlings from new ramets because seedlings are much smaller than new stems produced from rhizomes. In July 2006, we stopped weeding and allowed plant species to colonize the experimental plots, either from the seed bank or via dispersal from adjacent old fields into the plots for 9 months, a duration similar to other invasion studies (e.g. Stachowicz *et al.* 1999; Levine 2000). Because of the initial treatments to the plots (e.g. spraying with herbicide and hand weeding the plots for 2 years), we are confident that most of the species that colonized the plots were derived from newly arriving seeds from adjacent old fields. Proximity to source pools of seeds should not affect our results because treatments were placed randomly within the experimental garden. We are confident of minimal disturbance effects of weeding because generally only small seedlings were removed and we did not weed the plots for 3 and 9 months prior to observations of colonists.

To test whether intraspecific diversity increased invasion resistance, we examined how variation in the number of genotypes of *S. altissima* affected the establishment and success of colonizing plant species in each of the 63 1-m² plots. We use 'colonists' and 'colonizing species' to refer to

both native and non-native taxa that colonized the plots. In October of 2006 and April 2007, 3 and 9 months after we terminated weeding, we recorded (i) richness and percent cover of exotic species, (ii) richness and percent cover of native species, (iii) richness and percent cover of all colonists, (iv) the biomass of colonists (April only), and (v) the number of *S. altissima* stems in each plot. To estimate percent cover, we overlaid a 20-cell grid (50 cm² per cell in a 4 × 5 grid or 5% cover for each square) over each plot and tallied the number of grid cells occupied by native and exotic species. High stem density and cover of *S. altissima* in many of the plots prevented us from using a higher resolution grid (e.g. a 100-cell grid). However, in a subset of the plots we were able to compare the results from 20- and 100-cell grids, and the results were not qualitatively different. *Solidago altissima* was excluded from all cover and biomass estimates. We estimated biomass of the colonizing species by harvesting all aboveground biomass of non-*S. altissima* species in each plot in April 2007. Plants were oven-dried at 60° C for 72 h and weighed to the nearest 0.01 g. We estimated plot-level *S. altissima* stem density at each time period by counting the total number of stems in each plot. We focused specifically on *S. altissima* stem density because it is positively and significantly correlated ($P < 0.001$ for all cases) with the aboveground biomass ($r = 0.54$), leaf area index ($r = 0.60$), and Normalized Difference Vegetation Index ($r = 0.60$) of *S. altissima*. Though other morphological characteristics that we did not measure could be important, we felt *S. altissima* stem density, or correlated traits, adequately represent competitive abilities of *S. altissima* genotypes and genotypic mixtures for abiotic resources (light, water, and nutrients) and space.

Statistical analyses

We used Pearson correlation coefficients to examine the relationships between genotypic diversity, stem density and each of the following response variables: native cover, exotic cover, the cover of all colonizing species (native + exotic), native species richness, exotic species richness, the richness of all colonizing species (native + exotic) in both October 2006 (3 months since weeding stopped) and April 2007 (9 months since weeding stopped), along with the biomass of colonizing species (native + exotic species biomass) in April (Table S1). In addition, we used an all-possible regressions approach to model the relative effects of genotypic diversity and stem density on the variables listed above in both October 2006 and April 2007. We used Akaike's Information Criterion (AIC) to identify the best model.

To examine the effect of *S. altissima* genotype identity (in the monoculture plots) on the richness and percent cover of total, native, and exotic species, along with total colonizer

biomass, we used separate ANCOVA models with genotype identity as the main effect in the model and stem density as the covariate. For all analyses, we analyzed the October and April data separately because the composition of the colonizing fauna differed substantially between October 2006 and April 2007 (data not shown). In all analyses, cover estimates were log-transformed prior to analysis to improve normality. However, for clarity, we show the untransformed values in all of the figures. We did not use Bonferroni corrections for any of the analyses because this would inflate the probability of committing type II errors (Gotelli & Ellison 2004).

RESULTS AND DISCUSSION

In both October and April, genotypic diversity was not related to the richness or cover of colonizing plant species ($P > 0.23$ for total, exotic, or native richness and cover). However, genotypic diversity was negatively correlated with the biomass of colonizing plant species in April, 9 months after the experiment was initiated ($r = -0.25$, $n = 63$, $P = 0.04$; Fig. 1a). Biomass of colonizing plants was 32%

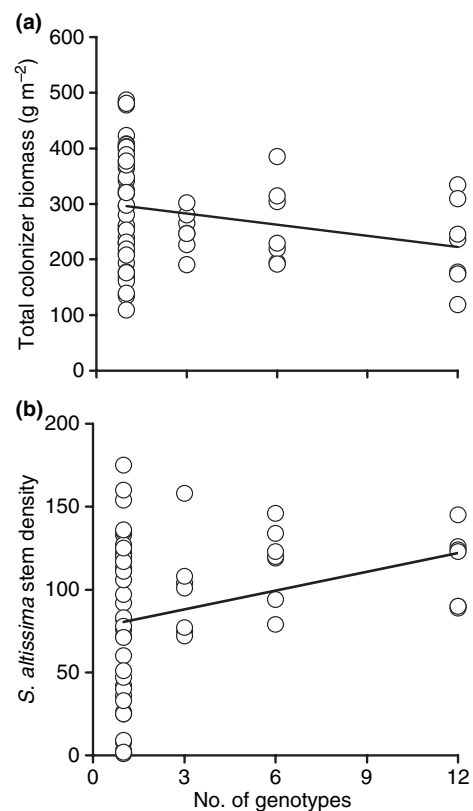


Figure 1 The relationships between the number of *Solidago altissima* genotypes in 63 1-m² plots and the total aboveground biomass of colonizing plant species (a) and *S. altissima* stem density (b).

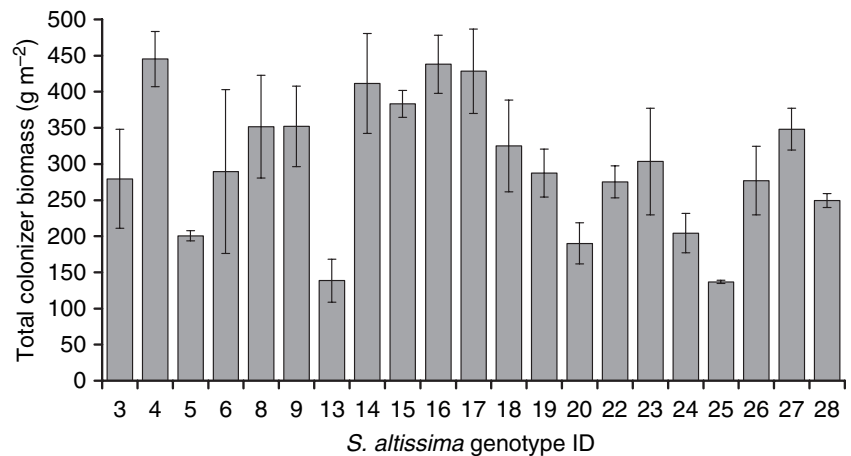


Figure 2 The relationship between total aboveground biomass of all colonizing plant species (native + exotic species) and genotype identity of *Solidago altissima*. Bars represent mean (\pm SEM) biomass (g m^{-2}).

lower in 12-genotype plots relative to 1-genotype plots. In addition, total biomass (native + exotic species) of colonizing species in polyculture plots (those with at least three genotypes) was 17% lower than total biomass of colonizing species in 1-genotype plots. These results support Elton's (1958) original hypothesis that diversity deters invasions and agree with a growing list of empirical studies indicating that among species diversity can deter invasions at neighborhood scales (Levine *et al.* 2004; Fridley *et al.* 2007a). However, our results extend these studies by demonstrating that within species diversity can also deter plant invasions.

One criticism of many biodiversity studies is that they often confound diversity with the presence of a particular dominant species (Hooper *et al.* 2005). Indeed, many studies have shown that the presence of competitively dominant species, rather than diversity *per se*, can deter plant invasions (Crawley *et al.* 1999; Smith & Knapp 1999; Dukes 2002; Smith *et al.* 2004; Wilsey & Polley 2002; Emery & Gross 2006, 2007). Here, we found that particular genotypes of *S. altissima* limited colonization. In October, total richness of colonizing species (native + exotic species richness; $F_{20,21} = 2.14$, $P = 0.04$) and native richness ($F_{20,21} = 2.45$, $P = 0.04$), along with total cover (native + exotic species cover; $F_{20,21} = 3.61$, $P = 0.002$), varied by over twofold among *S. altissima* genotypes. There was no effect of *S. altissima* genotype identity on exotic richness ($F_{20,21} = 1.08$, $P = 0.42$), and only marginal effects on native ($F_{20,21} = 1.84$, $P = 0.08$) and exotic cover ($F_{20,21} = 1.87$, $P = 0.08$). By April, after 9 months of colonization, there was no longer any difference in the richness of colonizing species among genotypes ($P > 0.45$ for total, native, and exotic richness). However, particular genotypes still limited total cover of colonizing species (native + exotic) ($F_{20,21} = 2.51$, $P = 0.02$) and the cover of exotic species ($F_{20,21} = 2.44$, $P = 0.02$), but not native cover ($F_{20,21} = 2.51$, $P = 0.24$). Total cover differed by 14% and exotic cover differed by 25% among genotypes. In

April, there were also strong effects of *S. altissima* genotype identity on total biomass of colonizing species: total biomass ranged from 136 to 445 g m^{-2} among genotypes ($F_{20,21} = 3.347$, $P = 0.004$; Fig. 2).

The majority of colonizing plant species in both October (29 of 34 species) and April (21 of 38) were perennial species. While we did not separate colonizer biomass into native and exotic species, of the 38 species that colonized the experimental plots, 14 are exotic species (<http://www.tneppc.org>), and nine are considered invasive in Tennessee (Table S2). Of the 10 most common species that colonized our plots, seven are invasive species. Therefore, we are confident that our results reflect the potential role of intraspecific diversity in determining invasion dynamics of exotic and invasive species in this system. In biodiversity studies, it is often challenging to grow every genotype/species in monoculture that occurs in mixture plots while still obtaining high levels of replication. In this study, individual genotypes had only two replicate plots. Though we observed strong effects of genotypic identity on colonizing plant species, the results should be interpreted cautiously because of the low replication.

The effects of both genotypic diversity and genotype identity on invasion resistance are likely mediated by the effects of genotypic diversity and genetic identity on stem density. Stem density increased with genotypic diversity ($r = 0.29$, $n = 63$, $P = 0.02$; Fig. 1b) and was 45% greater in 12-genotype plots than in 1-genotype plots. In addition, stem density was 40% greater in plots with at least three genotypes relative to plots with only one genotype. Stem density varied by over 10 orders of magnitude among genotypes ($F_{20,21} = 5.39$, $P = 0.0002$; Fig. S1). The number of *S. altissima* stems was negatively correlated with total cover ($r = -0.30$, $n = 63$, $P = 0.02$; Fig. 3a), native cover ($r = -0.38$, $n = 63$, $P = 0.002$), exotic cover ($r = -0.31$, $n = 63$, $P = 0.01$), and total biomass ($r = -0.78$, $n = 63$,

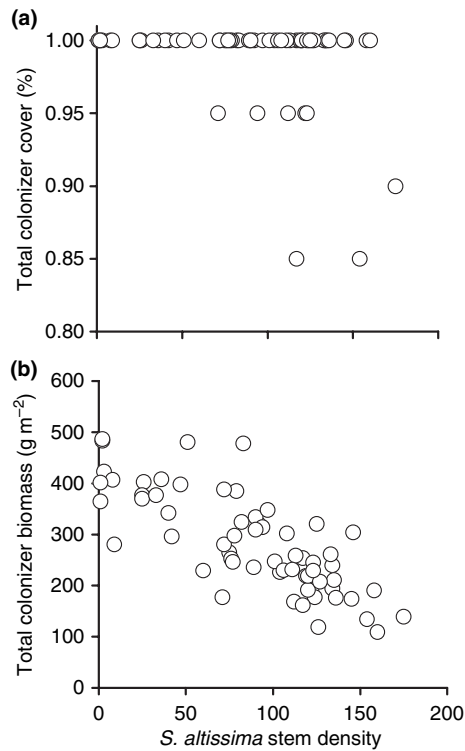


Figure 3 The relationship between *Solidago altissima* stem density and total cover (a) and total biomass (b) of colonizing plant species.

$P < 0.0001$; Fig. 3b) of colonizing plant species. All possible regressions indicated that stem density, rather than genotypic diversity, best predicted resistance to invasion in both October 2006 and April 2007 (Table 1). Similarly, stem density, rather than genotype identity, limited the total biomass of colonizing species in the monoculture plots (Table 2).

All of the experimental plots began with twelve stems. Our results suggest that stem density increased with genotypic diversity and that some genotypes produced more stems than did others. As a result, as stem density increased, space available for the establishment of colonizing species decreased. Increasing stem density may also lead

Table 1 All possible regression models using *Solidago altissima* stem density and genotypic diversity as predictors of total cover, exotic cover, and native cover of invading plant species for October 2006 and April 2007

	Parameter	<i>P</i> -value	AIC	<i>r</i> ²
<i>October 2006</i>				
Total cover				
Stem density	-0.004	< 0.0001	-203.72	0.31
Exotic cover				
Stem density	-0.067	0.003	208.39	0.13
Native cover				
Stem density	-0.0812	< 0.0001	178.99	0.27
Total richness				
Stem density	-0.021	0.01	85.89	0.10
Exotic richness				
	-	-	-	-
Native richness				
Stem density	-0.01	0.02	43.90	0.09
<i>April 2007</i>				
Total cover				
Stem density	-0.0002	0.008	-439.34	0.11
Exotic cover				
Stem density	-0.0004	0.01	-368.12	0.09
Native cover				
Stem density	-0.002	0.002	-224.10	0.14
Total richness				
Stem density	-0.01	0.06	99.00	0.06
Exotic richness				
	-	-	-	-
Native richness				
Stem density	-0.01	0.008	48.84	0.11
Biomass				
Stem density	-1.62	< 0.0001	519.08	0.61

Only models that were significant and with lowest AIC are presented.

to more intense competition between resident plants and colonizing individuals, thereby reducing the probability of their establishment and growth. For example, we observed no difference in the cover of colonizing species among genotypic diversity treatments. However, there was an effect of the treatments on the biomass of colonizing species,

Table 2 Results from ANCOVA with *Solidago altissima* genotype identity as the main effect and stem density as the covariate

	Total richness	Exotic richness	Native richness	Total cover	Exotic cover	Native cover	Total biomass
<i>October 2006</i>							
Genotype identity	1.68(0.13)	1.10(0.42)	1.63(0.14)	1.67(0.13)	1.14(0.39)	0.64(0.84)	
Stem density	1.04(0.32)	1.35(0.26)	0.08 (0.78)	1.65(0.21)	0.01(0.95)	4.56(0.04)	
<i>April 2007</i>							
Genotype identity	0.75(0.74)	1.16(0.37)	0.86(0.63)	1.95(0.07)	1.81(0.10)	1.14(0.38)	1.44(0.21)
Stem density	4.1(0.05)	2.02(0.17)	1.14(0.30)	0.66(0.43)	0.41(0.53)	1.70(0.21)	10.9(0.004)

Shown are the *F*- and *P*-values in parentheses.

indicating that the species that have established in diverse plots are not as productive. Interestingly, our results agree with other studies that have examined the relationships among species diversity, space use, and invasion success in plant communities (Knops *et al.* 1999; Levine 2000; Hector *et al.* 2001; Kennedy *et al.* 2002) and marine sessile invertebrate communities (Stachowicz *et al.* 1999, 2002). For example, at Cedar Creek in Minnesota, USA, Knops *et al.* (1999) found that total biomass of invaders was *c.* 50% lower in plots with 12 species relative to plots with only one species. In a similar study at Cedar Creek, Kennedy *et al.* (2002) found a 94% reduction in the cover of invading plant species in plots with 12 species relative to monoculture plots. In addition, Hector *et al.* (2001) found that there was no effect of species richness (ranging from 1 to 12 species) on invader biomass during the first year the BIODEPTH experiment, but biomass of invading species and species richness were negatively correlated in later years. Of course, these studies all assessed the effects of interspecific diversity, whereas our focus is on intraspecific diversity. Thus, it is perhaps not surprising that the effects of intraspecific diversity are generally weaker than the effects interspecific diversity on invasibility. Nevertheless, our results indicate that plant invasions can be constrained by within-species diversity.

Several mechanisms might explain why stem density increased with genotypic diversity, thereby deterring invaders. First, sampling effects, a contentious issue in biodiversity studies, might occur because high diversity plots have a greater chance of containing more productive genotypes (Huston 1997; Hooper *et al.* 2005). Indeed, genotypes were highly variable in stem production and the most productive mixture was never greater than the most productive monoculture. Second, positive interactions, such as niche complementarity or facilitation, might occur among genotypes, resulting in greater stem production in mixtures relative to monocultures (i.e. interactive or non-additive effects). Disentangling sampling effects from non-additive effects requires comparing stem density of individual genotypes when growing in mixtures to the same genotypes growing in monocultures (Trenbath 1974). We grew all 21 genotypes that occur in mixtures in replicate monocultures, but could not confidently sample the same genotypes in mixtures after the first year of the experiment because of high levels of interdigitation among ramets within plots. Determining the identity of each ramet would require genotyping hundreds of ramets growing in individual mixtures, which was beyond the scope of this project. However, a previous study in this system (Crutsinger *et al.* 2006) indicated that positive interactions among genotypes in mixtures led to increased relative aboveground primary productivity (i.e. overyielding) during the first year of the study. In addition, other

studies have also found support for positive interactions among genotypes leading to increased plant performance in mixtures (Reusch *et al.* 2005; Johnson *et al.* 2006). However, we did examine relative stem production from the first year of the study, when stems could still be assigned to particular genotypes. There were *c.* 19% more ramets produced in 12-genotype plots than the number predicted from component genotypes grown in monoculture (Fig. S2; for additive partitioning methods see Supplemental 3). Our results are limited to only the early dynamics of plant colonization into the experimental plots, and determining whether this mechanism and general patterns are consistent over multiple years requires further experimentation. But we conclude from the results from the first year that it is possible for facilitation or niche complementarity among genotypes, rather than sampling effects alone, to result in higher stem density in genotypically diverse plots.

Numerous studies have shown that *among*-species diversity and particular dominant species can limit biological invasions at small spatial scales (Fridley *et al.* 2007a). In a greenhouse study, Weltzin *et al.* (2003) found that the number of *Arabidopsis thaliana* genotypes did not affect emergence, survivorship, biomass, rosette area, or reproductive potential of the congener they introduced, *Arabidopsis suecica*. However, similar to our results, the density of *A. thaliana* had strong and negative effects on *A. suecica*. Collectively, our results demonstrate that *within*-species diversity and the identity of particular genotypes can reduce susceptibility to biological invasions. These results, in conjunction with a growing body of research (Wimp *et al.* 2005; Reusch *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006; Whitham *et al.* 2006), illustrate that intraspecific diversity can affect ecosystem processes and susceptibility to invasion. This suggests that the loss of intraspecific diversity could further exacerbate the impact of biological invaders on native biodiversity and ecosystems.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 The relationship between stem density and genotype identity of *Solidago altissima* after two years.

Figure S2 Non-additive responses of plot-level stem density in mixtures of 3, 6, or 12 genotypes of *Solidago altissima*.

Supplemental 3 Methods for additive partitioning of *Solidago altissima* stems.

Table S1 Correlation matrix of response variables for (a) October 2006 and (b) April 2007 datasets.

Table S2 Listed are the 38 species encountered in the experimental plots, whether they are native or exotic to east

Tennessee, their invasion status, and the number of plots out of 63 in which the species was detected.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01118.x>.

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