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Small-scale genotypic richness stabilizes plot biomass and increases phenotypic variance in the invasive grass *Phalaris arundinacea*

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Abstract

Aims

We aim to understand how small-scale genotypic richness and genotypic interactions influence the biomass and potential invasiveness of the invasive grass, *Phalaris arundinacea* under two different disturbance treatments: intact plots and disturbed plots, where all the native vegetation has been removed. Specifically, we address the following questions (i) Does genotypic richness increase biomass production? (ii) Do genotypic interactions promote or reduce biomass production? (iii) Does the effect of genotypic richness and genotypic interactions differ in different disturbance treatments? Finally (iv) Is phenotypic variation greater as genotypic richness increases?

Methods

We conducted a 2-year common garden experiment in which we manipulated genotype richness using eight genotypes planted under both intact and disturbed conditions in a wetland in Burlington, Vermont (44°27′23″N, 73°11′29″W). The experiment consisted of a randomized complete block design of three blocks, each containing 20 plots (0.5 m^2) per disturbed treatment. We calculated total plot biomass and partitioned the net biodiversity effect into three components: dominance effect, trait-dependent complementarity and trait-independent complementarity. We calculated the phenotypic variance for each different genotype richness treatment under the two disturbance treatments.

Important Findings

Our results indicate that local genotypic richness does not increase total biomass production of the invasive grass *P. arundinacea* in either intact or disturbed treatments. However, genotypic interactions underlying the responses showed very different patterns in response to increasing genotypic richness. In the intact treatment, genotypic interactions resulted in the observed biomass being greater than the predicted biomass from monoculture plots (e.g., overyielding) and this was driven by facilitation. However, facilitation was reduced as genotypic richness increased. In the disturbed treatment, genotypic interactions resulted in underyielding with observed biomass being slightly less than expected from the performance of genotypes in monocultures; however, underyielding was reduced as genotypic richness increased. Thus, in both treatments, higher genotypic richness resulted in plot biomass nearing the additive biomass from individual monocultures. In general, higher genotypic richness buffered populations against interactions that would have reduced biomass and potentially spread. Phenotypic variance also had contrasting patterns in intact and disturbed treatments. In the intact treatment, phenotypic variance was low across all genotypic richness levels, while in the disturbed treatment, phenotypic variance estimates increased as genotypic richness increased. Thus, under the disturbed treatment, plots with higher genotypic richness had a greater potential response to selection. Therefore, limiting the introduction of new genotypes, even if existing genotypes of the invasive species are already present, should be considered a desirable management strategy to limit the invasive behavior of alien species.

Keywords: invasive grass, genotypic diversity, *Phalaris arundinacea*, tripartite method, phenotypic variance

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INTRODUCTION

Species diversity at small scales can have a large influence on ecosystem processes (Barton *et al.* 2015; Hooper *et al.* 2005; Schöb *et al.* 2015; Srivastava and Vellend 2005). Similarly, intraspecific diversity within populations can influence both the structure and functioning ecosystems (Booth and Grime 2003; Crutsinger *et al.* 2006; Fridley and Grime 2010; Hughes *et al.* 2008; Johnson *et al.* 2006; Reusch *et al.* 2005; Whitham *et al.* 2006). Intraspecific plant diversity has been shown to influence plant productivity (Crawford and Rudgers 2012; Crutsinger *et al.* 2006; Dudley and File 2007; Kotowska *et al.* 2010; Schöb *et al.* 2015), resistance to stress (Hughes and Stachowicz 2011; Reusch *et al.* 2005), the diversity of higher trophic levels, particularly insects (Barton *et al.* 2015; Crutsinger *et al.* 2006; Johnson *et al.* 2006), and ecosystem processes such as total biomass and water quality (Tomimatsu *et al.* 2014). Furthermore, greater intraspecific diversity has been shown to decrease the susceptibility of a plant community to plant invasions by increasing productivity (Crutsinger *et al.* 2008). Yet, few studies have examined how genotypic diversity promotes invasiveness of an alien species in novel environments (but see Vellend *et al.* 2010; Weltzin *et al.* 2003). While high species diversity within communities has been posited to reduce the invasability of a community through biotic resistance (Kennedy *et al.* 2002; Richardson *et al.* 2000; Elton 1958), high genotypic diversity of the introduced species may increase the chance of a successful establishment of a plant species and ultimately its invasive potential (Lavergne and Molofsky 2007). Genotypic diversity is predicted to have larger ecological and evolutionary effects when a community is dominated by one or a few primary species (Hughes *et al.* 2008; Whitham *et al.* 2006). Thus, invasive species provide an excellent opportunity to examine whether genotypic diversity enhances the spread of an invasive species.

Determining the mechanistic underpinning of how genotypic or species diversity affects community and ecosystem processes has been the subject of several studies (Fox 2005; Loreau 2000; Loreau and Hector 2001). Loreau and Hector (2001) proposed two main mechanisms that separate the components of the diversity relationships that are responsible for community patterns: (i) complementarity effects, whereby diverse communities have collective effects such as niche complementarity, which results in more diverse communities achieving higher overall productivity in the form of greater biomass production than less diverse communities (Loreau 2000; Loreau and Hector 2001) and/or (ii) selection effects, whereby diverse communities have a higher probability of containing an individual that has an inherently higher growth rate and hence results in the plot having high productivity based on the performance of a superior individual (Aarssen 1997; Huston 1997). An alternative approach for understanding the role of biodiversity in experimental systems is to use the tripartite partition method (Fox 2005), which partitions the selection effect into two separate biodiversity effects (Saleem *et al.* 2012; Siebenkäs *et al.* 2016). This method comprises three additive effects: the 'dominance effect', 'trait-dependent complementarity effect', and the 'trait-independent complementarity effect'. The dominance effect occurs when certain genotypes have high values of a phenotypic trait such as biomass in monocultures and also produce similarly high values of biomass in mixtures; hence, they dominate the community and can lead to competitive exclusion of other individuals. The 'trait-dependent complementarity' effect occurs when a given genotype grown in mixture performs better than when grown in monoculture but does not depress other genotypes. In other words, how a genotype performs in mixture depends on its environment where the environment of the genotype is defined by the neighboring genotypes. The sum of the dominance effect and trait-dependent complementarity effect is equivalent to the selection effect sensu Loreau and Hector (2001). Fox (2005) claims that partitioning selection into its component parts allows isolation of dominance from trait-dependent complementarity effects and, that dominance effects are analogous to natural selection in evolution (Price 1972, 1995).

The 'trait-independent complementarity' effect occurs when all genotypes overyield or underyield when grown in mixture and is equivalent to the complementarity effect sensu Loreau and Hector (2001). Positive values indicate that genotypes produce more biomass in mixture than would be predicted from the sum of their biomass in monocultures, suggesting niche complementarity. Negative values indicate that genotypes produce less biomass in mixtures than expected, indicating competition.

The extent to which genotypic interactions increase or decrease invasive potential may depend on environmental conditions (Drummond and Vellend 2012). Yet, how environmental conditions influence genotypic interactions may be difficult to predict a priori (Drummond and Vellend 2012).

The ability of alien species to respond to different selection pressures and thus, evolve depends upon the phenotypic differences that exist among individuals and the genetic basis of the phenotypic differences (Sakai *et al.* 2001). In some invasive plant populations, the phenotypic traits have an underlying genetic basis such that there is a direct link between phenotypic expression and the populations response to selection (Lavergne and Molofsky 2007; Reusch *et al.* 2005 but see Dlugosch and Parker 2008). Understanding how phenotypic variance changes as a function of small-scale genotypic composition and the interactions among neighboring genotypes provides further insights into the mechanisms regulating the invasion process for particular species (Keller and Taylor 2008).

Here, we examine how small-scale genotypic richness influences biomass production and variance in the invasive grass, *Phalaris arundinacea*, which is known to form monospecific stands in North American wetlands (Lavergne and Molofsky 2004). Multiple introductions from the native range have been documented and have been shown to increase

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the genotypic diversity of invasive populations (Lavergne and Molofsky 2007). In this study, we address the following questions: (i) Does genotypic richness increase biomass production? (ii) Do genotypic interactions promote or reduce biomass production? (iii) Does the effect of genotypic richness and genotypic interactions differ in different disturbance treatments? Finally (iv) Is phenotypic variation greater as genotypic richness increases?

All experiments were conducted in both intact and disturbed treatments to determine whether the effect of genotypic richness changed under different disturbance treatments. We predicted that genotypically diverse communities would have greater biomass production than monocultures under both disturbance treatments but the diversity effect would be enhanced under the disturbed treatment because of more favorable growing conditions (Drummond and Vellend 2012).

MATERIALS AND METHODS

Study species

Phalaris arundinacea (reed canary grass) is a cool season perennial C_3 grass that is native to temperate zones of the northern hemisphere and is widely distributed throughout Eurasia (Lavergne and Molofsky 2004). This species reproduces both sexually by seed and vegetatively through a dense network of underground rhizomes (Lavergne and Molofsky 2004). It is a good study species for experiments on genotypic differences because individuals can be easily genotyped through allozyme screening (Lavergne and Molofsky 2007) and rapidly cloned through repeated vegetative tillering. Clonal spread through tiller fragmentation is an important mechanism of spread in *P. arundinacea* (Lavergne and Molofsky 2004). Previous collections of genotypes of *P. arundinacea* showed that genotypic differences amongst plants translate into differences in physiological and morphological characteristics (Brodersen *et al.* 2008; Morrison and Molofsky 1999) and differences in competitive ability and survival (Morrison and Molofsky 1998, 1999).

Study design

The experiment was conducted at the Biological Research Complex (BRC, Burlington, Vermont (44°27′23″N, 73°11′29″W). Plots were established in the 250 × 100 m lowland area of the research complex. The site was an open wetland with no canopy. The soils were of alluvial deposit (Udifluvents (Great Group), Fluvent (Suborder) and Entisol (Order)) and mean temperatures during the growing season (May–September) ranged between 13°C and 22°C. The site was dominated by several wetland indicator species including: *Typha latifolia*, *Phragmites australis*, *Verbena hastata*, *Equisetum fluviatile* and several *Juncus* species. There were also pre-existing populations of *P. arundinacea* close by so we were confident that the site was an area where *P. arundinacea* could become invasive.

We conducted a 2-year common garden experiment in which we manipulated genotype richness using eight genotypes planted under both intact and disturbed treatments. The eight genotypes used in our experiment had been collected from three populations in Vermont (Shelburne Bay [44°23′57″N, 73°14′5″W], Gavin Hill [44°35′8″N, 73°8′59″W] and Ethan Allen Homestead [44°30′18″N, 73°13′47″W]), and were distinguished as unique genotypes using 12 allozyme markers: DIA-1, DIA-2, TPI-1, TPI-2, PGI-2, PGM-1, PGM-2, UGPP-1, UGPP-2, IDH-1, MDH-1 and MDH-2 (see Lavergne and Molofsky 2007).

For all experiments, *P. arundinacea* genotypes were grown in the greenhouse through repeated vegetative tillering from one stock pot of each genotype. Before transplantation, all tillers were standardized to have two green leaves, 10 cm of stem, 5 cm of roots, 2 cm of rhizome, and one rhizome-1growing tip. Each genotype was tagged at the base of the stem with a color-coded pipe cleaner to allow for easy recognition, and subsequent tillers were tagged as they emerged. The genotype identity of new tillers was determined by pulling gently on the original planting and observing which new tillers moved. Once the plants were harvested at the end of the experiment the identity of each tiller was double checked.

To examine whether there were any inherent growth differences among genotypes when planted in the absence of intraspecific competitors, we planted each genotype (labeled *a*–*h*) alone in 0.5 m^2 plots, where the native community was either left intact or disturbed at the time of planting. To examine how genotypic richness influenced the total biomass production of *P. arundinacea*, we manipulated genotype richness using the same eight genotypes (*a*–*h*) as above and planted them under both treatments.

The experiment was planted on 5 May 2007 and consisted of a randomized complete block design of three blocks, each with 20 plots (0.5 m^2) running pair-wise with an identical disturbed treatment for a total of 40 plots per block (120 plots total). Disturbed plots had all native vegetation removed and the top 10 cm of turned over prior to planting. Disturbed plots were weeded bi-weekly. Therefore, plants were planted into homogeneous backgrounds that had decreased competition and increased availability of soil nutrients and light. All intact plots left the native community undisturbed.

Each plot was planted with eight *P. arundinacea* tillers with treatments of increasing genotype richness of 1, 2, 4, or 8 genotypes. The 20 plots in each block consisted of: 8 × 1-genotype monocultures, 4 × 2-genotype plots, 4 × 4-genotype plots and 4 × 8-genotype plots. Genotype combinations were chosen at random from a pool of eight genotypes with the constraint that no two 2-genotype and 4-genotype plots could have the same genotype composition. Density was kept constant such that a plot with two genotypes (*a* and *b*) would have four tillers of genotype *a* and 4 tillers of genotype *b*. The eight individuals in each plot were planted at a 5-cm planting density in a 3 × 2 × 3 grid using a plexi-glass template. We chose a 5-cm planting density as prior density experiments did not

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show any competitive effect of neighbors at 10-cm and 30-cm planting densities (Collins, unpublished data) and by measuring the mean plant density under field conditions. Growth measures of stem height, leaf number and tiller number were collected for each plant on a bi-weekly basis for the 2007 and 2008 field seasons (May–September). Stem height, tiller number and total biomass are all useful proxies for *P. arundinacea* fitness. *P. arundinacea* often needs to meet a critical threshold stem height prior to setting seed (~30 cm; Collins, personal observation) and tiller production can facilitate local spread. We harvested above- and below-ground biomass on 15 September 2008. We were able to collect the above- and below-ground biomass of each genotype in each plot by digging up the edge of the 0.5 m^2 plot and loosening the soil. Individual genotypes could be located using the colored pipe cleaners used in the initial tagging and then could be pulled apart from the other genotypes. This method enabled us to successfully separate each genotype however we did lose most of the fine root mass. Thus, our measure of below-ground biomass only included coarse roots and rhizomes. Below-ground biomass was washed by hand and above- and below-ground biomass was dried at 60°C for 48 hours before being weighed.

All three fitness proxies that we measured (stem height, tiller number and total biomass) were significantly positively correlated (correlation coefficients 0.7 or above). Thus, we only used the response variable of total biomass because it offered an integrated measure for overall plant fitness in a clonally spreading species. Total biomass was log transformed to meet assumption of normality.

Statistical analysis

We analyzed the biodiversity effects using the tripartite partitioning method presented in Fox (2005). This methodology calculates the ΔY, which represents the difference between the observed total yield and expected total yield in mixture under the null hypothesis that all intra- and inter-genotypic interactions are identical. This method partitions the ΔY into three components, a product of expectations and two covariance terms:

$$\Delta Y = N\,E(M)E(\Delta RY) + N\,Cov\left(M, \frac{RY_o}{RYT_o} - RY_o\right) + N\,Cov\left(M, RY_o - \frac{RY_o}{RYT_o}\right) \quad (1)$$

where, RY_o is a vector of observed relative species yields where component i is given by $RY_{oi} = \frac{Y_{oi}}{M_i}$ where Y_{oi} is the of observed relative yield species i in mixture and M_i is the species yield in monoculture. RYT_o is the sum of the vector of observed relative species yields for a plot. The expected relative yield of species is analogous to the observed relative species yield except for the fact that it is based on expectations from the biomass of genotypes in monoculture and the initial mixture of genotypes. ΔRY is the difference in the expected and observed relative yields. We refer the reader to Fox (2005) for more details and explanation of these terms.

To understand the relationship between the response of genotypes in monoculture to their response in mixture, we partitioned the difference between the observed and expected yields in mixture (ΔY) into its component parts (dominance effect, trait-dependent complementarity, trait-independent complementarity) following Fox (2005). In the partitioning of our data, we treated plant mortality (i.e. zero yields) as missing values, but used the original genotype richness of our treatments in our figures and analysis. All analyses were performed using R (R Core team 2014).

We describe the three components of biodiversity effects in order of occurrence in the partitioning Equation (1): Trait-independent complementarity, the dominance effect, and the trait-dependent complementarity. The trait-independent complementarity effect indicates the positive or negative effect of being in mixture on all genotypes. This is often referred to as the complementary effect (e.g., Loreau and Hector 2001). A positive or negative value may indicate niche complementarity through facilitation or underyielding through competition. The dominance effect indicates how a genotypes's monoculture performance determines its performance in mixture. A positive dominance effect, for instance, indicates that a genotype with a high biomass in monoculture also dominates in mixture at the expense of other genotypes. Trait-dependent complementarity signifies the extent to which a given genotype produces greater than expected yields in mixture relative to expectations without influencing other genotype yields. The sum of dominance effect and trait-dependent complementarity is equivalent to selection effect (Loreau and Hector 2001).

We also analyzed phenotypic variance in the genotypic richness treatments to determine how small-scale genotypic neighborhood influenced biomass of individuals in disturbed and intact treatments. Phenotypic variance is measured as the trait variation as a result of genotypic sources (V_G) and environmental sources (V_E) (Falconer and Mackay 1996). Phenotypic variance was calculated for each of the four genotypic richness treatments (1, 2, 4, 8 genotypes) by partitioning the genetic (V_G) and environmental (V_E) variance components and using the following equation:

$$V_P = V_G + V_E \quad (2)$$

The variation in the trait measured represents the influence of environmental variation and genetic variation. We calculated the phenotypic variance separately for the intact and disturbed treatments so that the environmental variance only accounts for the environmental factors occurring at small scales such as differences in soil nutritional factors or soil moisture levels. We estimated the phenotypic variance for total biomass by estimating variance components with a REML model with random effects using the PROC MIXED procedure in SAS (SAS 9.1.3). The data were bootstrapped 1000 times to achieve 95% confidence intervals for all estimates. Our bootstrap program was stratified such

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that each bootstrap sampled one individual randomly from each plot with the same genotype richness with replacement to have bootstrapped sample of eight plants per plot. The phenotypic variance was then calculated for each genotypic richness treatment and significant differences between genotypic richness treatments were determined using Bonferroni's multiple comparison test. Thus, the phenotypic variance for the monoculture plots calculated the phenotypic variance of all genotypes grown under monoculture. As phenotypic variance is a measure of the potential response to selection for a population, here, we refer to each plot of eight genotypes as a 'population' of genotypes.

RESULTS

Plant biomass in the disturbed treatment was greater than biomass in the intact treatment (Fig. 1) but total biomass per plot was not affected by genotypic richness treatment (Fig. 1). In the plots where the genotypes were grown alone, there was no significant difference in the total biomass produced among the eight genotypes after 5 months of growth ($F_7 = 1.43$; P = NS). However, there was a highly significant treatment effect. Plants in the disturbed treatment produced 85% greater total biomass than those in the intact treatment ($F_1 = 100.9$; $P < 0.001$). There was no significant genotype × treatment interaction ($F_7 = 1.2$; P = NS), indicating that there were no inherent biomass differences between the eight genotypes in the absence of intraspecific competitors over one growing season.

Our analysis of the relationship between genotypes in monoculture compared to their response in mixture highlighted different trends (Fig. 2). None of these relationships were statistically significant, but had some support based on delta Akaike information criterion values (suggesting low statistical power). We therefore discuss general trends in our data.

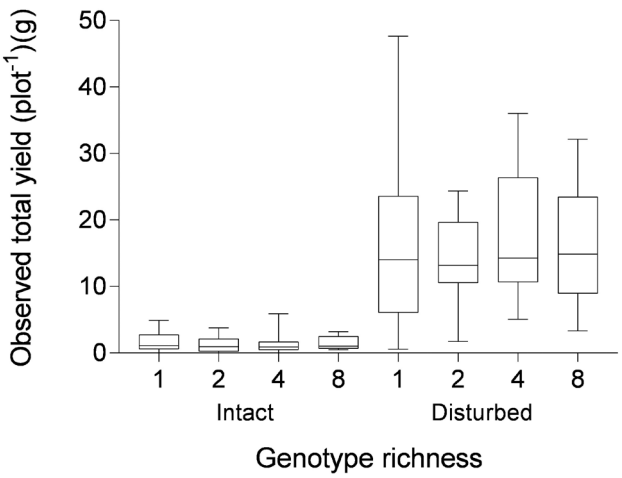


Figure 1: boxplots of observed yield per plot when *Phalaris arundinacea* genotypes were planted in 1, 2, 4, or 8 genotype plots (density kept constant at eight plants per plot) under both intact and disturbed treatments.

First, the treatments indicated very different patterns in response to genotypic richness. In the intact treatment ΔY, i.e. the difference between the observed and predicted yield, was positive (>0) indicating overyielding, but declined with increasing genotypic richness (negative slope). In the disturbed treatment, ΔY was negative (<0) at low genotypic richness but increased with genotypic richness (positive slope), approaching 0 at our most diverse genotype level.

In the intact treatment, trait-dependent complementarity was negative but had a positive slope, e.g., less negative as genotypic richness increased (Fig. 2). For the disturbed treatment, trait-dependent complementarity was also negative but became more negative with increasing genotypic richness.

Trait-independent complementarity also had opposite slopes in the intact and disturbed treatments. In the intact treatment, trait-independent complementarity was positive but became less positive with increasing genotypic richness. In the disturbed treatment, trait-independent complementarity was negative at low genotypic richness but became less negative with increasing richness. The dominance effect was close to 0 in both the intact and disturbed treatments.

In both treatments, ΔY was therefore dominated by contrasting trends in trait-independent and trait-dependent complementarity, and furthermore, the trends switched with treatment (Fig. 2).

When we examined phenotypic variance in biomass, we found contrasting patterns in the intact and disturbed treatments. In the intact treatment, phenotypic variances did not differ among genotype richness treatments (Fig. 3). In the disturbed treatment, the phenotypic variances of the monoculture plots, which consisted of eight different genotypes grown in monoculture, were significantly lower than the phenotypic variances in the 2- and 4-genotype plots which were significantly lower than the phenotypic variances in the 8-genotype plots (Fig. 3). Moreover, phenotypic variances of plants in 8-genotype plots were more than 10 times higher than when they were grown in monoculture.

DISCUSSION

While the overall effect of genotypic richness on plot biomass was minimal, tripartite analysis revealed different underlying mechanisms produced final biomass in intact and disturbed treatments. In the intact treatment, genotypes grown together produced more biomass than expected from their monoculture yield. In contrast, in the disturbed treatment, genotypes grown in mixture produced less biomass than the predicted yield in monoculture.

Further partitioning the observed yield into three components provided a more mechanistic understanding of how genotypic interactions occurred. In the intact treatment, overyielding was primarily due to positive trait-independent complementarity indicating niche complementarity. In contrast, trait-dependent complementarity was negative indicating that genotype–genotype interactions were negatively

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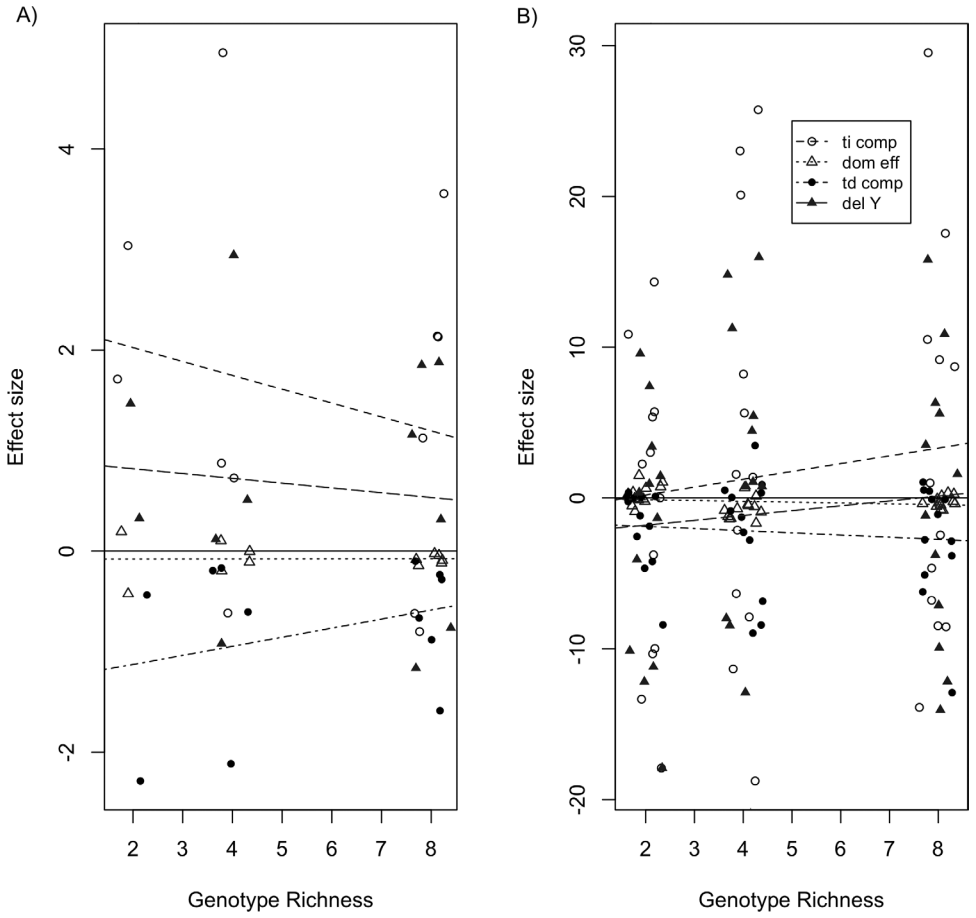


Figure 2: values of delta Y (closed triangle), dominance effect (open triangle), trait-dependent complementarity (closed circle), and trait-independent (open circle) effects as functions of genotype richness for both the (**a**) intact and (**b**) disturbed treatments. Lines are slopes of the multiple regression model including plot and genotype richness.

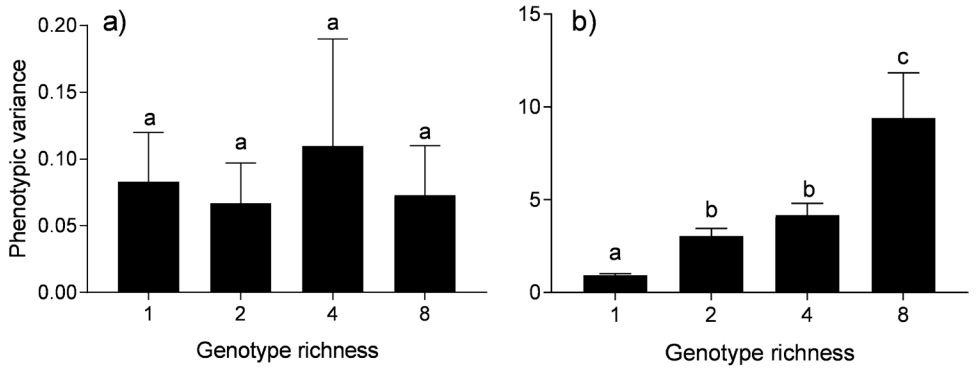


Figure 3: estimates of phenotypic variance for genotypes grown under (**a**) intact and (**b**) disturbed treatments with 1, 2, 4, or 8 genotypes. Different letters indicate significant differences among treatments within each community type. Error bars represent the 95% confidence interval for each estimate.

affecting plot biomass. The net result of these two counteracting processes resulted in intact treatment plots overyielding relative to predicted monoculture yields. Yet, the effects of trait-independent complementarity and trait-dependent complementarity were reduced at higher genotypic richness. Specifically, trait-independent complementarity became less positive and trait-dependent complementarity became less negative.

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In the disturbed treatment, underyielding was the result of negative trait-dependent complementarity and trait-independent complementarity. Interestingly, trait-dependent complementarity became more negative at higher genotypic richness treatments. This means that at higher genotypic richness, genotype-by-genotype interactions resulted in lower relative performance of each genotype relative to the monoculture yield. The opposite pattern was found for trait-independent complementarity. In this case, higher genotypic richness resulted in less underyielding. In other words, for higher genotypic richness, individual genotypes were less negatively affected by surrounding genotypes allowing their growth to be similar to their growth in monocultures. The net result of these complex interactions between genotypes resulted in final biomass in high genotypic richness plots approaching that produced in monocultures. Thus, in both treatments, as the number of genotypes within a plot increased, the complexity of interactions among genotypes increased. The final result was that plots with higher genotypic richness had observed biomass that was similar to predicted biomass. Therefore, genotypic diversity appeared to promote stable biomass within plots. Our results on genotypic diversity and plot biomass are similar to the theoretical results found for the relationship between species diversity and biomass (Hughes and Roughgarden 2000).

Conclusions from other studies that have manipulated genotypic richness in small plots have been equivocal. Huber *et al.* (2016) studying the clonal herb *Trifolium repens* found that genotypic richness had no effect on plot biomass. In contrast, Crutsinger *et al.* (2006) studying *Solidago altissima* and Drummond and Vellend (2012) studying *Taraxacum officinale* found increased plot biomass with higher genotypic richness. In perennial species, the results may depend upon the length of the study. In a study on eelgrass, Hughes and Stachowicz (2011) found that plots with higher genotypic richness recovered from a planned experimental disturbance faster and had higher total biomass after 2 years.

Identifying the underlying processes that are responsible for overall patterns between genotypic diversity and plot biomass may depend upon which analyses are performed (Fox 2005; Loreau and Hector 2001). For example, dominance effects have not been reported in genotypic diversity studies but studies have reported significant selection effects (Crawford and Whitney 2010; Drummond and Vellend 2012; Hughes and Stachowicz 2011). Yet, selection includes both dominance and trait-dependent complementarity (Fox 2005). In our study, we found significant negative trait-dependent complementarity which would have resulted in a significant negative selection effect using Loreau and Hector (2001). Negative selection effects have been reported for studies manipulating species diversity (Engelhardt and Ritchie 2002; Hooper and Vitousek 1997; Jiang *et al.* 2008; Troumbis *et al.* 2000) and in one genotypic study (Stuefer *et al.* 2009). In experimental plant studies, positive selection effects have been more frequently reported (Crawford and Whitney 2010; Drummond and Vellend 2012; Hughes and Stachowicz 2011). Selection effects may become apparent at longer time scales. Stuefer *et al.* (2009) planted genotype mixtures and followed them over 5 years and found that specific genotypes became more dominant over time.

Understanding why the intact treatment and disturbed treatment produced contrasting results require further investigation. In the disturbed treatment, we found plants underyielded in mixture, suggesting intraspecific competition had a negative effect on plant growth. In this treatment, the plants grew large enough to interfere with each other through above-ground competition. In the intact treatment, plants were small and interspersed with the native vegetation. Yet, there seemed to be niche complementarity between genotypes. Niche complementarity requires that individuals genotypes perform better than predicted in mixtures than monocultures, primarily because of ecological combining ability (Aarssen 1983). In our study, the mechanism for niche complementarity may be through below-ground interactions for shared soil resources (Ashton *et al.* 2010; van der Putten *et al.* 2013) as the plants in the intact treatment appeared too small to interact above-ground. Other studies on genotypic richness also report niche complementarity (Crawford and Whitney 2010; Drummond and Vellend 2012; Tomimatsu *et al.* 2014).

The genotypic composition of the plots can also influence the ability of a population to respond to selection (Lavergne and Molofsky 2007). In single genotype plots, if phenotypic variance is high, variation is due to phenotypic plasticity but in mixed genotype plots, the variation can be due to a combination of genotypic differences and phenotypic plasticity (Lynch and Walsh 1998). In the intact treatment, phenotypic variances were low across all genotypic richness treatments. In contrast, in the disturbed treatment, phenotypic variance was much higher in the more genotypically diverse plots. The low phenotypic variance in single genotype plots combined with much higher phenotypic variance for the highest diversity plots suggests that phenotypic differences have a strong genotypic component and that selection may alter genotypic composition over longer time scales. It is possible that our genotype richness treatments represent novel genotype combinations because we artificially created genotypic plots using a pool of genotypes collected in several locations around Vermont. Consequently, the chosen genotypes may have been adapted to different environmental conditions. As a result, we may have artificially inflated the expression of genotypic variance. Yet, this scenario may indeed be biologically realistic as genotypic diversity may be artificially inflated in invasive populations (Bossdorf *et al.* 2005; Ellstrand and Schierenbeck 2000; Kolbe *et al.* 2004; Lavergne and Molofsky 2007; Lockwood *et al.* 2005; Novak and Mack 2001) and may result in mixtures of unrelated genotypes at small spatial scales.

As evidence accumulates that genotype composition can have a large influence on diversity at higher trophic levels

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(Booth and Grime 2003; Kotowska *et al.* 2010; Schöb *et al.* 2015; Tomimatsu *et al.* 2014; Vellend and Geber 2005; Whitham *et al.* 2003), similar studies such as this one may be useful to understand the asymmetry and variability of within-species interactions as well as the resulting evolutionary response. Results from our experiments suggest that increased genotypic richness results in net population biomass approaching the sum of the individual genotype biomass in monocultures. Thus, genotypic richness functioned similarly to species diversity in that diversity-buffered plots against changes in total biomass (Hughes and Roughgarden 2000). Moreover, at least in the disturbed treatment, the increased genotypic richness enhanced phenotypic variance and the potential response of populations to environmental selection. Therefore, limiting the introduction of new genotypes even if existing genotypes of the invasive species are already present should be considered a desirable management strategy to limit the invasive behavior of alien species.

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