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ECOSPHERE

Plant genotype, nutrients, and G × E interactions structure floral visitor communities

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Abstract. Intraspecific variation in plants is driven by both genetic and environmental factors and has been shown to play an important role in determining assemblages of herbivores, predators, and pathogens. Yet, the consequences of genetic (G) and environmental (E) factors, as well as potential (G × E) interactions, for floral visitor communities remains poorly explored. In a common garden experiment, we compared the relative effects of host-plant genotype and genotypic diversity as well as soil nutrient enrichment on floral resource abundance and insect floral visitors associated with tall goldenrod, *Solidago altissima*. We found that the floral visitor community varied considerably among genotypes, driven predominantly by variation in floral phenology among *S. altissima* clones. Floral visitors also varied among nutrient treatments, though this response was much weaker than to different plant genotypes, and was likely driven by effects of floral rewards rather than of floral phenology. Importantly, we also detected several G × E interactions for both flowering and floral visitors. Taken together, our results suggest that the effects of host-plant genetic variation, and to a lesser extent G × E interactions, are key agents in structuring the diversity and composition of floral visitors.

Key words: arthropods; fertilization; honey bees; interspecific interactions; monoculture; nitrogen; non-additive effects; phosphorus; pollinators.

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INTRODUCTION

A growing focus in ecology has been on the role of intraspecific variation in determining community dynamics and ecosystem function (Bolnick et al. 2011, Violle et al. 2012). In particular, genetic variation (differences among genotypes) and levels of genotypic diversity (number of locally growing genotypes) within host plant species have been shown to have an important influence on associated species (e.g., Crutsinger et al. 2006, Johnson et al. 2006, Zytynska et al. 2011). Indeed, in a recent review, Whitham and colleagues (2012) found that some degree of preference by associated communities for different genotypes of host plants is a widespread phenomenon occurring across an array of study systems, from grasses to trees. Yet, the vast majority of studies on community-level consequences of plant genetic variation (e.g., genotype identity) and genotypic diversity have focused on herbivores, predators, and pathogens (e.g., Maddox and Root 1987, Johnson and Agrawal 2005, Tack and Roslin 2011), while

mutualistic interactions, such as pollination, have been relatively ignored (but see Genung et al. 2010).

Host-plant genotype identity and genotypic diversity account for some of the variance in the communities associated with them, but the relative importance of genetic variation and genotypic diversity compared to other ecological factors, such as environmental heterogeneity, is only beginning to be understood (Hughes et al. 2008, Hersch-Green et al. 2011). One key environmental factor for plants and their associated floral visitors is soil nutrient availability, as nutrients can vary considerably at a local level and are known to influence flower production and bloom duration (e.g., Campbell and Halama 1993, Asikainen and Mutikainen 2005, Munoz et al. 2005, Burkle and Irwin 2009*a*). In fact, pollination ecologists have documented the role of floral traits, such as floral display size (the number of open flowers) and flowering phenology (timing and duration of bloom period) in explaining pollinator preferences (e.g., Stang et al. 2006, Olesen et al. 2008, Burkle and Irwin 2009*b*). Yet, the degree to which the drivers of intraspecific variation in floral display and phenology are either genetically-based, the result of the environmental conditions, or a combination of both remains unclear for most host-plant systems. For instance, variation in soil nutrients can lead to shifts in flower production and the rates of floral visitors to plants (Burkle and Irwin 2010). Along with such direct effects, soil nutrient availability might also interact with plant genetic variation to influence floral traits, and it is ultimately these genotype by environment ($G \times E$) interactions that could shape the structure of associated communities (e.g., Johnson and Agrawal 2005, Tétard-Jones et al. 2007, Genung et al. 2012). To date, the role of $G \times E$ interactions for communities associated with floral resources and with floral visitors has been ignored.

In this study, we used a commonly distributed perennial host-plant species in eastern North America, tall goldenrod (*Solidago altissima*), to determine the influence of genetic variation, genotypic diversity, and soil nutrient availability for flowering, floral visitation and floral community structure and composition. Hereafter, we use the term 'floral visitors' rather than 'pollinators', since not all of the species associating with the reproductive parts of flowers were strictly pollinators, but are still important community members associated with floral resources. Using a factorial common garden experiment, we addressed the following three inter-related questions: (1) Does the identity or diversity of *S. altissima* genotypes influence floral resource production and floral visitor abundance, richness, and composition? (2) How do the effects of *S. altissima* genetic variation and genotypic diversity compare to those of soil nutrient enrichment? And (3) what is the role of $G \times E$ interactions in shaping floral visitor assemblages associated with *S. altissima*?

Materials and Methods

Tall goldenrod, *Solidago altissima*, is a dominant perennial forb that grows in old fields and roadsides throughout eastern North America (Semple and Cook 2006) and influences community dynamics and ecosystem processes (Crutsinger et al. 2006, Souza et al. 2011*b*). *Solidago altissima* is a self-incompatible, obligately-outcrossing plant species, rendering pollination by floral visitors critical for sexual reproduction and seed production (Gross and Werner 1983). Further, while local spread and maintenance of established *Solidago* populations is achieved by vegetative reproduction through the production of clonal rhizomes, creating patches ranging from individual clones to mixtures of genotypes (Gross and Werner 1983, Halverson et al. 2008), floral abundance and visitors promote seed production that is important for the colonization of new habitat patches (Meyer and Schmid 1999). Intraspecific genetic variation occurs in many *S. altissima* traits, such as flowering phenology and floral production, above- and belowground productivity, and tissue quality (Gross and Werner 1983, Crutsinger et al. 2006, Halverson et al. 2008, Breza et al. 2012, Genung et al. 2012). *Solidago altissima* genetic variation and genotypic diversity can also influence a diverse community of foliage herbivores (Maddox and Root 1987, 1990, Root and Cappuccino 1992, Crutsinger et al. 2006) and pollinators (Genung et al. 2010, 2012). The fact that *S. altissima* is a well-studied plant species that grows across a wide array of soil nutrient conditions and displays considerable clonal variation makes this species an ideal

study system to address our research questions.

Plant collections

In March 2009, we collected rhizomes from 20 distinct patches of *Solidago altissima* plants located in three adjacent old-field sites in Eastern Tennessee (near Oak Ridge, Tennessee; 35° 58′ N, 84°17′ W). Patches were located 50–120 m apart to ensure that the rhizomes collected were actually different individual genotypes (Maddox et al. 1989, Crutsinger et al. 2006). To create replicates of these 20 genotypes, we cut rhizomes into 3-cm sections and transplanted them into flats containing potting mix (Pro-Mix BX, Premier Brands, New Rochelle, NY) and a root stimulator (Roots 2, Roots Inc. OSIA Independence, MO). These plants were grown in a greenhouse environment (at 25°C) and fertilized twice during the period of 12 weeks. By June 2009, three *S. altissima* individuals from each genotype were transplanted into 76-L pots (n = 3) in a common environment at the University of Tennessee's Agricultural Experimental Station, Knoxville, TN (35°53′47.84″ N, 83°57′22.86″ W). We measured a variety of morphological and reproductive traits to quantify differences among genotypes. Morphological traits included height, stem diameter, leaf length, leaf width, leaf area, internode space, aboveground biomass (Appendix: Table A1) as well as herbivory (percent leaf damage and aphid density) (Appendix: Table A2). Reproductive traits included first day of flowering, last day of flowering, flowering duration, and inflorescence mass (Appendix: Table A3). Of these 20 original genotypes, we observed an eight-fold difference in inflorescence mass among clones (Appendix: Table A3). We then performed a principal component analysis including all plant traits across the 20 *S. altissima* genotypes and selected eight genotypes to be used in a field experiment that maximized trait variance across the first two principle component axes (Appendix: Fig. A1).

Study site and experimental design

In summer 2010, we initiated a common garden experiment (Fig. 1) at the University of Tennessee's Agricultural Experimental Station, Knoxville, Tennessee (35°53′47.84″ N, 83°57′22.86″ W). We established a grid of 76 1 × 1 m plots, spaced 1 m apart, in an existing mowed field surrounded by a 3-m tall fence to exclude deer. A weed cloth barrier was placed between plots to prevent other plants species from growing. We maintained experimental plots by hand weeding non-target individuals (e.g., non-*S. altissima* individuals) once per week.

To manipulate *S. altissima* genotype identity, we planted all eight genotypes in replicated monoculture plots (n = 8 per genotype, 64 total) with six individuals per plot, arrayed in a circle. To manipulate genotypic diversity, we established mixed genotype plots (n = 12 total) containing six individuals belonging to different *S. altissima* genotypes (1 individual per genotype in each mixture plot). Genotype mixtures were created by randomly drawing from the pool of eight genotypes. Six genotypes were chosen as the maximum diversity level per plot because prior work showed that *S. altissima* genotypic diversity effects on aboveground net primary productivity and herbivore communities tended to plateau at ca. six genotypes (Crutsinger et al. 2006). This level of genotypic diversity also falls within the range observed in natural communities (1–13 genotypes/m^2; Maddox et al. 1989).

To manipulate soil nutrient availability, we created four fertilization treatments: (1) control (no nutrient manipulation), (2) soil nitrogen (N) addition (10 g m^{-2} yr^{-1}), (3) soil phosphorus (P) addition (10 g m^{-2} yr^{-1}), and (4) soil P and N addition (P = 5 g m^{-2} yr^{-1} and N = 5 g m^{-2} yr^{-1}). We added fertilizer as dry, slow-release pellets (nitrogen was added in the form of urea, N_2H_4CO, and phosphorus was added as triple super phosphate, P_2O_5) which released nitrogen and phosphorus into the soil during rainfall events. These levels of enrichment have been shown to double nutrient availability in similar systems (Goldberg and Miller 1990, Sanders et al. 2007) and are comparable to several local old-field studies manipulating nutrients to examine effects on plant community dynamics (Sanders et al. 2007, Blue et al. 2011, Souza et al. 2011*a*,), as well as other studies examining nutrient enrichment effects on floral traits and pollinators (e.g., Campbell and Halama 1993, Asikainen and Mutikainen 2005, Munoz et al. 2005, Burkle and Irwin 2009*a*, Burkle and Irwin 2010). We crossed *Solidago altissima* genotype identity and genotypic diversity with these nutrient treatments such that there were two monoculture plots of each

Fig. 1. Common garden experimental set up at the University of Tennessee's Agricultural Experimental Station.

genotype for each nutrient treatment and three genotype mixture plots for each nutrient treatment. Plot treatment positions were arrayed randomly in the grid in the common garden.

Floral visitor and diversity responses

To assess floral visitation, we first visually estimated percent flowering (percent of the plot area containing flowers) for each of the 76 plots during peak *S. altissima* bloom (October 1–2, 2010; within the peak flowering period across plots: October 4 ± 4.5 days). Next, we observed each experimental plot for floral visitors for three 5-minute sessions, for a total of 15 minutes during peak insect activity (0930–1600) for each plot. To characterize the range of floral visitors throughout the day, all of the plots were observed once in the morning, mid-day, and afternoon. We identified the floral visitors to species or lowest taxonomic level possible in the field, and caught representative specimens to confirm identifications in the lab under a dissecting scope. For each plot, we quantified total floral visitor abundance, as well as calculating total richness, total abundance, rarefied richness, evenness, and community composition of floral visitors. Our sampling was a snapshot during the peak bloom period in old fields, which is likely the most important time for understanding floral visitor communities (Crutsinger et al. 2008, Genung et al. 2010).

Statistical analyses

Because our experimental plots were spaced 1m apart, we first tested for spatial correlation, or whether neighboring plots influenced the abundance of floral visitors visiting any given focal plot. We employed two tests for spatial autocorrelation that test for autocorrelation between neighboring plots at different spatial scales. First, for the smaller spatial scale, we calculated the average abundance of floral visitors on nearest-neighbor plots, which is any plot that shares a full edge border with the focal plot (i.e., plots which border each other at corners were not used, such that each focal plot could have a maximum of four nearest neighbors). Some plots had fewer than four nearest neighbors due to their location at the edge of the experiment. We then used a general linear model to test the relationship between focal plot floral visitor abundance and average nearest neighbor floral visitor abundance (Haddad et al. 2000, Genung et al. 2010). We repeated this analysis for floral visitor richness. We did not detect any neighbor effects for floral visitor abundance ($F_{1,86} = 0.11$, $P = 0.740$) or richness ($F_{1,86} = 0.43$, $P = 0.513$); one plot was excluded from tests for neighbor effects because it had only one neighbor. To test for spatial autocorrelation across all plots, we used a Mantel test (package "ade4" in R version 3.0.0). We found no correlation between plot location and floral visitor abundance ($P = 0.228$). We did detect a correlation between plot location and floral visitor richness ($P = 0.016$); however, this effect explained only 0.9% of the variation in floral visitor richness. We used t-tests to determine whether edge plots (those which had fewer than four nearest-neighbors) predictably received fewer or more visits than interior plots. We detected no location effects (i.e., edge vs. interior) for floral visitor abundance ($F_{1,87} = 1.77$, $P = 0.081$) or richness ($F_{1,87} = 1.33$, $P = 0.19$). We treat our plots as independent replicates henceforth.

In order to examine the main and interactive effects of genetic variation (i.e., genotype identity) and soil nutrients (control, N-addition, P-addition, or NP-addition) on the floral visitor community, we first used a MANOVA to test the independent factors on floral visitor abundance (square-root transformed), richness (log-transformed), rarefied richness, and Shannon's evenness. A significant MANOVA was followed by univariate, full-factorial ANOVAs for each response variable (Scheiner 1993). Given the strong influence of genotype identity (see *Results*), we repeated these tests including mean percent flowering of each plot (squared-transformed) as a covariate to identify whether percent flowering was driving the genotype effect. Percent flowering as a covariate in this MANCOVA model and in subsequent univariate ANCOVAs was not significant ($P > 0.19$ in all cases), and its inclusion did not qualitatively change our results. We report these results on the effects of genotype identity and nutrients including percent flowering as a covariate. Next, we examined the main and interactive effects of genotypic diversity (i.e., monoculture versus mixtures) and soil nutrients on the floral visitor community using a MANCOVA, with mean percent flowering of each plot (squared-transformed) as a covariate to determine whether genetic and nutrient effects on floral visitors remained when percent flowering held constant. When testing for the effects of genetic variation, we included only monoculture plots. Analyses were performed in JMP 10.0.2.

Next, we tested for whether the effects of genotypic diversity were the result of additive (i.e., sum of individual genotype effects) or non-additive (i.e., interactions of genotypes in mixtures lead to unpredictable outcomes) for percent flowering as well as floral visitor abundance, richness, and evenness. This was necessary because the genotypic composition of the mixed-genotype plots was determined randomly and, therefore, each genotype was not equally represented in the mixed-genotype treatment. To correct for this, we created a list of which genotypes were present, and how many times those genotypes occurred, in the mixed-genotype treatment. From the monoculture plots, we then resampled replicates to recreate the genotypic composition found in the mixed-genotype plots and determined a mean "expected" value. We repeated this process 1000 times using Monte Carlo simulations, and used the resulting data to obtain a boot-strapped mean and error term for the mixed-genotype plots. We repeated this process for all four traits (floral visitor abundance, richness, evenness, and percent flowering) and compared our observed values to the range of values given by the Monte Carlo simulations. When observed values fell in top or bottom 2.5

percentile of this range, we called the result non-additive (at $\alpha = 0.05$), meaning that ecologically important interactions between genotypes are occurring in mixture plots. Due to a limited number of replicates for a few genotype-nutrient treatment combinations, we were unable to use null models to assess the potential interaction of diversity and nutrient treatments.

To directly compare the relative responses of flowering and floral visitors to genetic variation, genotypic diversity and soil nutrients, we calculated the standard effect sizes for each treatment as log-response ratios (Hedges et al. 1999). For genetic variation, we compared the richness, abundance, rarefied richness, and evenness of floral visitors of each genotype to that of the genotype with the lowest percent flowering. For genotypic diversity, we compared mixtures to monoculture averages, and for soil nutrients we compared N, N + P, and P treatments to controls. We used a fixed-effects model to include nutrient treatments when investigating the main effects of genetic variation or genotypic diversity and vice versa. We calculated 95% confidence intervals with bias-corrected bootstrapping using MetaWin (Rosenberg et al. 2000). If the confidence intervals did not overlap zero, effect sizes were considered statistically significant (Gurevitch and Hedges 2001).

To determine the effects of genetic variation, genotypic diversity, nutrients and their interactions on floral visitor community composition, we conducted a permutational multivariate analysis of variance (PERMANOVA) using percent flower as a covariate, followed by pairwise Student t comparisons. The PERMANOVA approach tests whether the observed variability in species composition both within and across treatments differs from expected variability generated from permutational shuffling of species (10,000 iterations), generating a pseudo F-ratio. We performed PERMANOVA tests on Bray-Curtis similarity triangular matrices (Bray and Curtis 1957) generated from transformed (log x + 1) species-specific floral visitor abundance data. We then performed similarity percentage analyses (SIMPER) to determine the contribution of each floral visitor species to the community compositional differences between treatments. A significant pseudo F-ratio from a PERMANOVA may result from between-treatment differences in location of species composition and/or from within treatment differences in dispersion of species composition in multivariate space. As a result, we performed a permutational analysis of multivariate dispersions (PERMDISP) to test whether, in addition to differences in compositional location, there were any differences in community dispersion (i.e., variability) among treatments. We used PRIMER version 1.0.3 (Plymouth Marine Laboratory, UK) for these analyses.

Table 1. Univariate ANCOVA results testing for the main and interactive effects of genotype identity and nutrients on floral visitor abundance, richness, and evenness in *Solidago altissima*. Genotype identity influenced floral visitor abundance, richness, evenness, and rarefied richness. Nutrients affected floral visitor richness and evenness. In some cases, nutrients mediated the response of floral visitors to genotype identity (i.e., marginally significant G × E interaction for floral visitor evenness). P values in boldface are significant at $\alpha = 0.05$.

Source	df	F	P
Abundance			
Whole model	32, 31	9.18	**<0.0001**
Nutrients	3, 31	1.54	0.22
Genotype ID	7, 31	3.52	**0.0068**
Nutrients × genotype	21, 31	0.83	0.67
Percent flowering	1, 31	0.85	0.36
Richness			
Whole model	32, 31	4.22	**<0.0001**
Nutrients	3, 31	4.23	**0.013**
Genotype ID	7, 31	4.01	**0.025**
Nutrients × genotype	21, 31	1.05	0.44
Percent flowering	1, 31	0.74	0.40
Evenness			
Whole model	32, 31	8.20	**<0.0001**
Nutrients	3, 31	3.88	**0.018**
Genotype ID	7, 31	9.98	**<0.0001**
Nutrients × genotype	21, 31	1.90	0.052
Percent flowering	1, 31	1.82	0.19
Rarefied richness			
Whole model	32, 31	2.33	**0.013**
Nutrients	3, 31	2.22	0.10
Genotype ID	7, 31	3.13	**0.013**
Nutrients × genotype	21, 31	0.99	0.50
Percent flowering	1, 31	0.19	0.66

Results

Overall, genotype identity ($F_{21,87} = 7.60$, $P < 0.0001$), nutrients ($F_{9,73} = 2.08$, $P = 0.042$), and their interaction ($F_{63,90} = 1.70$, $P = 0.011$) influenced floral visitor abundance, richness, and evenness (Table 1; MANCOVA whole model:

Table 2. Univariate ANCOVA results testing for the effects of genotypic diversity and nutrients on floral visitors to *Solidago altissima*, with percent flowering as a covariate. Percent flowering influenced floral visitor abundance, richness, evenness, and rarefied richness. Additionally, there was a marginal effect of genotypic diversity on floral visitor evenness. P values in boldface are significant at $\alpha = 0.05$.

Source	df	F	P
Abundance			
Whole model	5, 81	29.52	**<0.0001**
Nutrients	3, 81	0.29	0.84
Diversity	1, 81	0.76	0.38
Percent flowering	1, 81	145.54	**<0.0001**
Richness			
Whole model	5, 81	17.42	**<0.0001**
Nutrients	3, 81	1.91	0.14
Diversity	1, 81	1.29	0.26
Percent flowering	1, 81	78.53	**<0.0001**
Evenness			
Whole model	5, 81	11.85	**<0.0001**
Nutrients	3, 81	0.86	0.47
Diversity	1, 81	3.82	0.054
Percent flowering	1, 81	54.73	**<0.0001**
Rarefied richness			
Whole model	5, 81	2.73	**0.025**
Nutrients	3, 81	0.53	0.66
Diversity	1, 81	0.64	0.42
Percent flowering	1, 81	11.93	**0.0009**

Wilks' $\lambda = 0.010$, $F_{93,91} = 3.51$, $P < 0.0001$; percent flowering covariate: $F_{4,21} = 0.42$, $P = 0.79$). We found that genotypic diversity ($F_{3,79} = 3.00$, $P = 0.035$) but not nutrients ($F_{9,192} = 0.96$, $P = 0.48$) influenced floral visitor abundance, richness, and evenness (Table 2; MANCOVA whole model: Wilks' $\lambda = 0.28$, $F_{15,218} = 8.44$, $P < 0.0001$; % flowering covariate: $F_{3,79} = 50.68$, $P < 0.0001$).

Plant genotype

We observed considerable variation among *S. altissima* genotypes in percent flowering during peak flowering in the common garden ($F_{7,32} = 111.58$, $P < 0.0001$; Fig. 2), ranging from an average of 28% to 96% of stems among the eight selected genotypes. Variation in percent flowering among *S. altissima* genotypes translated into variation in the richness, abundance, and evenness of floral visitors (Figs. 2 and 3, Table 1). Floral visitor abundance varied 25-fold among our eight genotypes growing in monoculture, while observed and rarefied richness varied by over 7-fold and 2-fold, respectively. Evenness also varied 2.5-fold among genotypes, suggesting that some genotypes contained communities

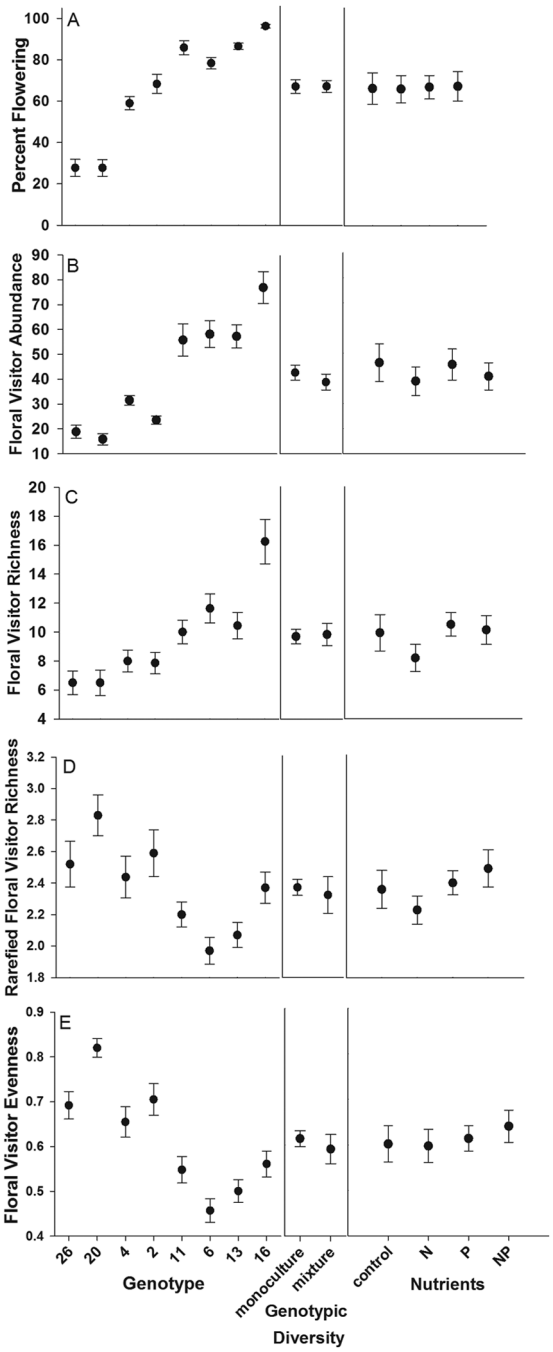

Fig. 2. Mean percent flowering (A) and floral visitor abundance (total number of individuals per 15 minute observation) (B), richness (total number of morphospecies per 15 minute observation) (C), rarefied richness (number of morphospecies) (D), and evenness (E) for genotypes, monocultures and mixtures, and nutrient treatments in 2010.

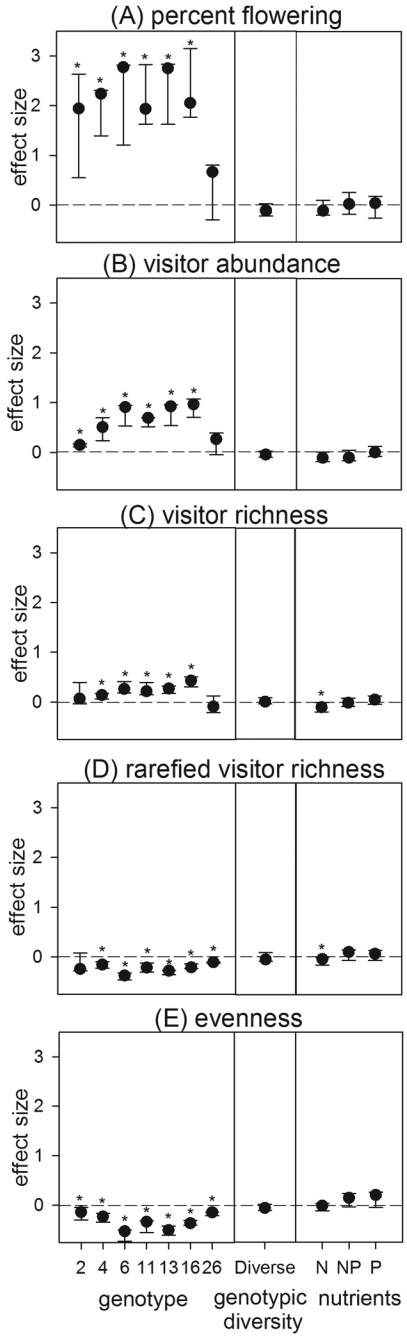

Fig. 3. Effect sizes of percent flowering (A) and floral visitor abundance (B), richness (C), richness (D), and evenness (E) among genotype identity, genotypic diversity, and nutrient treatments in 2010.

Table 3. Results shown are the main and interactive effects of genotypic identity and nutrients and percent flowering on floral visitor community composition (PERMANOVA) and dispersion (PERMDISP). Plant genotype and percent flowering altered floral visitor composition in *Solidago altissima*. Floral visitor assemblages did not differ in compositional variability (dispersion). P values in boldface are significant at $\alpha = 0.05$.

Source	df	F	P(perm)
Composition			
Genotype ID	7, 31	2.35	**0.0001**
Nutrients	3, 31	1.49	0.0680
Genotype × nutrients	21, 31	1.20	0.0760
Percent flowering	1, 31	14.72	**0.0001**
Dispersion			
Genotype ID	7, 56	2.21	0.0950
Nutrients	3, 60	1.28	0.3500

dominated by particular floral visitors while other genotypes had more even distribution of species. Floral visitor community composition was also influenced by plant genotype, with clones varying by up to 88% in community similarity. Many species contributed to these community differences, however the most dominant were *Apis mellifera* (honey bees; contributing 10%) and *Diabrotica undecimpunctata* (cucumber beetles; contributing 7%) (Appendix: Table A4). Floral visitor community variability (i.e., degree of dispersion) was marginally affected by genotype identity (Table 3).

Plant genotypic diversity

In contrast with variation in flowering among clones, we observed no differences in percent flowering when comparing monoculture versus mixture plots ($F_{1,74} = 0.38$, $P = 0.54$; Figs. 2 and 3). There were also no differences in floral visitor richness and abundance responses between monocultures and mixtures. Our null models, which accounted for the random genotype-compositions of mixture plots, provided similar results; the expected value for mixture plots did not differ from expectations for floral visitor abundance (observed 38.36; expected 39.07 with 95% CI of 35.46–41.76; $p = 0.586$) or floral visitor richness (observed 9.55; expected 9.52 with 95% CI of 9.00–10.13; $p = 0.880$), indicating the effects of genotypic diversity were additive. Based on our null models, percent flowering did not differ

Table 4. Results shown are the main and interactive effects of genotypic diversity and nutrients and percent flowering on floral visitor community composition (PERMANOVA) and dispersion (PERMDISP). Percent flowering influenced floral visitor composition while genotypic diversity altered floral visitor variability (dispersion) in *Solidago altissima*. P values in boldface are significant at $\alpha = 0.05$.

Source	df	Pseudo-F	P(perm)
Composition			
Diversity	1, 78	1.41	0.17
Nutrients	3, 78	1.32	0.11
Diversity × nutrients	3, 78	0.89	0.65
Percent flowering	1, 78	13.88	**0.0001**
Dispersion			
Diversity	1, 85	7.31	**0.021**
Nutrients	3, 83	2.78	0.068

from additive expectations (mixture observed 66.53; expected 65.35 with 95% CI of 63.43–67.35; $p = 0.252$). There was a marginal effect of genotypic diversity on visitor evenness (Table 2), with floral visitor communities being slightly more even (6%) in monocultures compared to mixtures. Mixture plots had higher levels of dominance by floral visitors, such as honey bees. Our null models confirmed this pattern, as evenness in mixture plots was lower than expected (i.e., non-additive) based on monoculture values (mixture observed 0.591; expected 0.632 with 95% CI of 0.613–0.649; $p < 0.001$). Genotypic diversity did not affect floral visitor community composition, but strongly influenced community dispersion (Table 4). Genotype monocultures exhibited 21% greater dispersion (i.e., had more variable floral visitor communities) than mixture plots. This pattern could be driven by variation among genotypes (e.g., large differences in percent flowering) that resulted in a wider range of floral visitors compared to mixtures. In addition, there were more monoculture plots compared to mixture plots, and mixture plots were more similar to one another in the composition of genotypes (i.e., similarity effects; Fukami et al. 2001).

Soil nutrients

There were no differences in percent flowering among soil nutrient treatments ($F_{3,32} = 0.63$, $P = 0.60$; Fig. 2). When we examined floral visitor responses to soil nutrient manipulation, we observed a relatively weak negative effect of nitrogen enrichment on visitor richness and rarefied richness compared to all other soil nutrient treatments (Fig. 3). Observed richness was 7% lower in the N treatment and 11% higher in P and N+P treatments compared to controls (Table 1). Floral visitor evenness was 3% lower in the N treatment and 6% higher evenness in N+P treatments compared to control (Table 1). That these effects occurred in the absence of any significant response of percent flowering to nutrient additions suggests that nitrogen and phosphorus addition may alter the quality of floral resources, such as nectar or pollen. Floral visitor community composition and dispersion was marginally influenced by nutrients (Tables 3 and 4). Composition differed by 37–52% among nutrient treatments (Appendix: Table A5), while control plots were 13–40% more dispersed (i.e., more variable) compared to P fertilized plots (e.g., P and NP plots) (Appendix: Fig. A2).

G × E interactions

We observed a significant interaction between *S. altissima* genotype identity and soil nutrients on percent flowering ($F_{21,32} = 3.10$, $P = 0.002$), which corresponded with a marginally significant interaction between genotype and nutrients for floral visitor evenness (Table 1). There was also a marginal interaction between genotype identity and nutrients for floral visitor composition (Table 3). For instance, floral visitor composition differed among genotypes in N fertilized plots (e.g., N and NP plots) but not in P or control plots (Appendix: Fig. A3).

Discussion

In this study, we compared the relative and interactive effects of genetic variation, genotypic diversity and nutrient enrichment on percent flowering and insect floral visitors associated with *Solidago altissima*. We found that the identity of different *S. altissima* clones had the strongest effect on floral visitors, followed by nutrient enrichment, and then genotypic diversity. A key mechanism underlying these effects was genetic variation in the timing of flowering. Individual genotypes varied considerably in when they flowered, which was influential in the attraction

of a suite of floral visitor species. The lack of significance of percent flowering in some analyses with genotype identity, however, indicates that there are additional traits that are influential in floral visitor attraction and lends support to the important role of genetic variation in shaping the floral visitor community. Importantly, we also observed several interactions between genotype and soil nutrients for both flowering and floral visitors; floral visitor responses to genetic variation depended on the level of soil nutrient availability. In sum, our results indicated that G $\times$ E interactions were capable of influencing floral visitors, but that these interactive effects tended to be weaker than the direct consequences of either genotype or soil nutrients.

Our results are consistent with prior work in this system showing that floral visitor richness and abundance are influenced by genetic variation in *S. altissima* (Genung et al. 2010), though we did not observe as strong of effects of genotypic diversity compared to other studies (Crutsinger et al. 2006, Johnson et al. 2006, Genung et al. 2010). Because we assessed the floral visitor community during peak-flower only, and did not repeatedly sample throughout the flowering season, the genotypes with high percent flowering during this period were clones that were highly attractive to floral visitors. As there was variation in flowering times among genotypes (e.g., early- versus late-flowering genotypes), we may have underestimated the benefit that mixtures may experience by blooming less intensely at any one point but flowering over a longer duration compared to the 'bloom and bust' of genotype monocultures.

In a recent review, Whitham et al. (2012) outlined how community-level genetic specificity results from individual genotypes or populations of plant species supporting different communities of organisms, particularly arthropods. Of the 29 systems reviewed, most focused on the role of leaf phytochemistry and herbivores, whereas only a few explored floral traits and floral visitors. Yet, a separate body of research has long been interested in variation in floral traits within and among plant populations and the response of pollinators (e.g., Waser and Price 1983, Schemske and Bradshaw 1999, Fenster et al. 2004). For example, floral traits such as color, nectar resources, and anther-stigma separation and protandry, have been shown to vary genetically and across environments (e.g., Holtsford and Ellstrand 1992, Young et al. 1994, Carroll et al. 2001). We did not distinguish between true pollinators and other species using *S. altissima* flowers as a resource, though certainly many of the species (e.g., bees) in our system were pollinators. Few studies have considered the role of genetic variation in floral phenology on pollinator assemblages, though, as evident from our results, genetic variation in flower timing is likely to be an important structuring agent. Moreover, we surveyed our plots during one sampling period at peak bloom, while *S. altissima* genotypes bloomed at different times during the flowering season. At peak bloom, there was variation in the degree to which different genotypes were flowering, and genotypes with more flowers attracted more individuals and species of floral visitors. Yet, genotypes also vary in their duration of flowering ($F = 19.7$, $P < 0.0001$; Appendix: Table A3), and matching floral visitor assemblages with genetic variation in floral phenology throughout an entire season is worthy of further study.

A key finding in our study was that the effect sizes of plant genetic variation were greater than the soil nutrient environment. In another G $\times$ E manipulation, Johnson and Agrawal (2005) found that genetic variation in Common Evening Primrose, *Oenothera biennis*, also accounted for more of the arthropod community than did environmental variation among microhabitats in which they were growing. As with our results, flowering phenology was one of the best predictors of arthropod community responses to different genotypes. Although nutrient enrichment did not influence percent flowering in our study, the effects of nutrient enrichment on the floral visitor community were still observable. For example, N + P treatments had the highest pollinator richness and evenness independent of genotype identity. Also, the variability within floral visitor communities (i.e., dispersion) was lower in phosphorus-enriched plots. As nutrient treatments did not consistently alter floral abundance, the effects on the floral visitor community were likely driven by changes in the quality and quantity of floral rewards like nectar and pollen (e.g., Lau and Stephenson 1993, 1994, Burkle and Irwin 2009*a*).

Overall, our work responds to recent appeals for comparisons of the importance of genetic variation and genotypic diversity relative to other ecological factors (Hughes et al. 2008, Hersch-Green et al. 2011). In the *S. altissima* system, the effects of genetic variation were greater than that of nutrient enrichment, but this is not always the case (Orians and Fritz 1996, Mutikainen et al. 2000, Stiling and Bowdish 2000). Additional work is needed in other systems to better understand potentially widespread effects of G × E interactions, particularly on floral traits and floral visitor attraction. Clear next steps include examining these patterns in other focal plant species or communities, tracking floral visitors over the entire season, and linking patterns of visitation to seed production and plant fitness.

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Supplemental Material

Appendix

Table A1. Morphological (height, leaf width, leaf length, leaf area, internode length, leaf area, stem diameter) traits collected from the ten selected *Solidago altissima* genotypes in 2009. Means and SE (in parentheses) are provided. For each trait, we performed a one-way ANOVA testing for the effects of genotype identity influencing each trait measured; different letters represent statistically different means for each trait at $\alpha = 0.05$ using Tukey's HSD.

Genotype	Height (cm)	Leaf width (cm)	Leaf length (cm)	Internode length (cm)	Leaf area (cm^2)	Diameter (mm)
1	82.1 (8.1)c	2.78 (0.0)abc	13.66 (0.9)abc	0.68 (0.1)c	38.05 (2.7)abcd	11.17 (1.8)abc
2	135.44 (17.9)ab	1.9 (0.3)c	7.52 (1.2)d	1.90 (0.3)a	14.34 (3.4)d	3.57 (2.2)c
4	139.13 (3.5)a	3.07 (0.1)ab	14.36 (0.6)a	1.10 (0.1)bc	44.50 (3.1)b	13.5 (1.2)a
6	106.9 (10.1)abc	2.67 (0.3)bc	8.72 (0.6)d	1.23 (0.2)abc	24.29 (3.6)ab	8.59 (1.4)abc
11	132.85 (0.2)abc	3.77 (0.2)ab	15.62 (0.6)ab	0.97 (0.2)abc	59.14 (6.5)ab	16.10 (0.8)abc
12	106.09 (5.4)bc	2.37 (0.1)bc	10.51 (0.5)cd	1.18 (0.1)abc	25.42 (2.6)cd	8.47 (1.9)ab
13	97.34 (6.2)c	3.77 (0.2)a	16.02 (0.6)a	0.97 (0.1)c	61.03 (4.5)a	11.39 (1.0)ab
16	102.51 (4.9)bc	2.98 (0.1)ab	13.29 (0.6)ab	1.04 (0.1)bc	40.12 (2.9)bc	11.91 (0.7)ab
20	124.62 (3.6)abc	1.93 (0.3)c	10.03 (0.9)cd	1.73 (0.2)ab	21.58 (4.7)d	6.19 (2.0)bc
26	108.78 (1.7)abc	2.49 (0.1)bc	12.60 (0.6)abc	0.9 (0.1)c	31.67 (2.7)bcd	12.47 (0.9)ab

Table A2. Resistance (percent leaf damage and aphid abundance in numbers of individuals) traits collected from the ten selected *Solidago altissima* genotypes in 2009. Means and SE (in parentheses) are provided. For each trait, we performed a one-way ANOVA testing for the effects of genotype identity influencing each trait measured; different letters represent statistically different means for each trait at $\alpha = 0.05$ using Tukey's HSD.

Genotype	Leaf damage (%)	Aphid abundance
1	26.66 (8.0)a	14.50 (12.7)a
2	5.92 (1.2)b	20.92 (8.1)ab
4	2.38 (1.3)b	33.81 (10.7)ab
6	7.21 4.3)b	181.53 (109.6)a
11	9.00 (0.0)b	0.00 (0.0)ab
12	3.66 (1.1)b	6.26 (2.5)b
13	5.55 (0.9)b	0.67 (0.6)b
16	6.55 (0.9)b	2.53 (1.4)b
20	2.33 (0.8)b	44.49 (14.9)ab
26	4.25 (1.1)b	0 (0.0)ab

Table A3. Reproductive (first/last day of the year of flowering, flowering duration in days and inflorescence mass) traits collected from the ten selected *Solidago altissima* genotypes in 2009. Means and SE (in parentheses) are provided. For each trait, we performed a one-way ANOVA testing for the effects of genotype identity influencing each trait measured; different letters represent statistically different means for each trait at $\alpha = 0.05$ using Tukey's HSD.

Genotype	First day flowering	Last day flowering	Flowering duration (d)	Inflorescence mass (g)
1	258.67 (0.7)a	281.00 (0.0)ab	22.33 (0.7)ab	29.20 (0)a
2	254.71 (2.4)a	285.43 (2.5)a	30.71 (2.3)a	22.51 (9.4)a
4	251.11 (1.5)a	265.00 (0.0)a	13.89 (1.5)b	48.01 (6.1)a
6	253.89 (2.9)a	272.22 (4.5)a	18.33 (2.1)ab	8.89 (3.7)a
11	258.00 (0.0)ab	281.00 (0.0)ab	23.00 (0.0)ab	27.85 (1.1)a
12	241.11 (2.1)a	270.44 (1.0)a	29.33 (2.7)ab	18.28 (4.5)a
13	259.14 (0.4)a	278.14 (2.2)a	19.00 (2.1)ab	35.67 (10.8)a
16	254.22 (2.3)a	273.44 (5.2)a	19.22 (3.9)ab	26.02 (11.3)a
20	245.00 (2.7)a	266.60 (3.0)a	21.60 (2.3)ab	22.49 (7.7)a
26	158.33 (39.6)b	179.78 (44.9)b	21.44 (5.6)ab	34.69 (11.4)a

Table A4. SIMPER results reporting the pairwise differences between *Solidago altissima* genotypes on the average species-specific abundance (transformed) of floral visitors along with the cumulative contributions (Cum%) towards overall compositional dissimilarities.

Genotype ID comparison	Floral visitor species	Genotype A	Genotype B	Cum. %
16 and 4	*Junonia coenia*	1.12	0.09	7.1
16 and 4	*Cisseps fulvicollis*	0.99	0	13.39
16 and 4	*Bombus impatiens*	1.4	0.53	19.45
16 and 4	*Apis mellifera*	3.88	2.96	25.49
16 and 4	*Poanes sp*	0.99	0.17	31.2
6 and 2	*Apis mellifera*	3.77	2.7	9.74
6 and 2	*Diabrotica undecimpunctata*	0.53	1.03	15.83
6 and 2	*Scolia dubia*	0.43	0.73	21.76
6 and 2	*Junonia coenia*	0.67	0	27.61
6 and 2	*Polistes metricus*	0.79	0.4	32.61
13 and 2	*Apis mellifera*	3.76	2.7	10.13
13 and 2	*Diabrotica undecimpunctata*	1.25	1.03	16.46
13 and 2	*Scolia dubia*	0.67	0.73	22.44
13 and 2	*Chauliognathus pennsylvanicus*	0.59	0.17	28.03
13 and 2	*Polistes metricus*	0.71	0.4	33.44
4 and 20	*Apis mellifera*	2.96	1.96	12.17
4 and 20	*Atteva aurea*	0.89	0	22.2
4 and 20	*Diabrotica undecimpunctata*	1.34	1.17	29.69
4 and 20	*Polistes metricus*	0.48	0.74	36.76
4 and 20	*Sarcophagid fly small*	0.53	0.31	42.55
11 and 2	*Chauliognathus pennsylvanicus*	1.21	0.17	10.82
11 and 2	*Apis mellifera*	3.6	2.7	19.78
11 and 2	*Atteva aurea*	1.05	0.53	27.03
11 and 2	*Scolia dubia*	0.48	0.73	34.18
11 and 2	*Diabrotica undecimpunctata*	1.5	1.03	40.65
2 and 20	*Apis mellifera*	2.7	1.96	9.41
2 and 20	*Diabrotica undecimpunctata*	1.03	1.17	17.61
2 and 20	*Scolia dubia*	0.73	0.45	25.44
2 and 20	*Bombus impatiens*	0.74	0.17	33.13
2 and 20	Sweat bee	0.57	0.36	39.99
16 and 20	*Apis mellifera*	3.88	1.96	12.8
16 and 20	*Bombus impatiens*	1.4	0.17	21.15
16 and 20	*Cisseps fulvicollis*	0.99	0	27.39
16 and 20	*Junonia coenia*	1.12	0.26	33.57
16 and 20	*Chauliognathus pennsylvanicus*	0.92	0.09	39.03
16 and 26	*Apis mellifera*	3.88	2.39	9.58
16 and 26	*Bombus impatiens*	1.4	0.26	16.78
16 and 26	*Junonia coenia*	1.12	0	23.88
16 and 26	*Cisseps fulvicollis*	0.99	0	29.77
16 and 26	*Poanes* sp.	0.99	0.09	35.48
6 and 20	*Apis mellifera*	3.77	1.96	16.87
6 and 20	*Diabrotica undecimpunctata*	0.53	1.17	24.49
6 and 20	*Junonia coenia*	0.67	0.26	29.95
6 and 20	*Bombus impatiens*	0.62	0.17	35.11
6 and 20	*Toxomerus* sp.	0.57	0.09	40.04
6 and 26	*Apis mellifera*	3.77	2.39	13.49
6 and 26	*Atteva aurea*	0.43	0.63	19.83
6 and 26	*Junonia coenia*	0.67	0	25.86
6 and 26	*Diabrotica undecimpunctata*	0.53	0.85	31.87
6 and 26	*Polistes metricus*	0.79	0.46	37.64
13 and 20	*Apis mellifera*	3.76	1.96	17.71
13 and 20	*Diabrotica undecimpunctata*	1.25	1.17	24.89
13 and 20	*Chauliognathus pennsylvanicus*	0.59	0.09	30.54
13 and 20	*Scolia dubia*	0.67	0.45	35.75
13 and 20	*Polistes metricus*	0.71	0.74	40.95
13 and 26	*Apis mellifera*	3.76	2.39	13.84
13 and 26	*Diabrotica undecimpunctata*	1.25	0.85	21.65
13 and 26	*Atteva aurea*	0.48	0.63	28.29
13 and 26	*Polistes metricus*	0.71	0.46	34.38
13 and 26	*Scolia dubia*	0.67	0.09	40.31
11 and 20	*Apis mellifera*	3.6	1.96	15.64
11 and 20	*Chauliognathus pennsylvanicus*	1.21	0.09	26.15
11 and 20	*Atteva aurea*	1.05	0	36.25
11 and 20	*Diabrotica undecimpunctata*	1.5	1.17	42.75
11 and 20	*Bombus impatiens*	0.74	0.17	48.53

Table A4. Continued.

Genotype ID comparison	Floral visitor species	Genotype A	Genotype B	Cum. %
11 and 26	*Apis mellifera*	3.6	2.39	12.46
11 and 26	*Chauliognathus pennsylvanicus*	1.21	0.09	23.57
11 and 26	*Atteva aurea*	1.05	0.63	32.47
11 and 26	*Diabrotica undecimpunctata*	1.5	0.85	40.69
11 and 26	Sweat bee	0.45	0.43	46.19
16 and 11	*Chauliognathus pennsylvanicus*	0.92	1.21	6.77
16 and 11	*Poanes* sp.	0.99	0.26	13.49
16 and 11	*Junonia coenia*	1.12	0.31	20.1
16 and 11	*Atteva aurea*	0.26	1.05	26.62
16 and 11	*Scolia dubia*	0.91	0.48	31.84
16 and 2	*Apis mellifera*	3.88	2.7	7.99
16 and 2	*Junonia coenia*	1.12	0	15.62
16 and 2	*Cisseps fulvicollis*	0.99	0.09	21.96
16 and 2	*Poanes* sp.	0.99	0.09	28.13
16 and 2	*Bombus impatiens*	1.4	0.74	34.24
13 and 26	*Apis mellifera*	3.76	2.39	15.18
13 and 26	*Scolia dubia*	0.67	0.09	21.94
13 and 26	*Chauliognathus pennsylvanicus*	0.59	0.09	28.18
13 and 26	*Junonia coenia*	0.57	0	34.18
13 and 26	*Diabrotica undecimpunctata*	1.25	0.85	40.05
6 and 4	*Diabrotica undecimpunctata*	0.53	1.34	7.88
6 and 4	*Apis mellifera*	3.77	2.96	14.99
6 and 4	*Junonia coenia*	0.67	0.09	21.55
6 and 4	*Polistes fucatus*	0.17	0.48	27.44
6 and 4	*Chauliognathus pennsylvanicus*	0.57	0.43	33.05
16 and 13	*Bombus impatiens*	1.4	0.43	7.34
16 and 13	*Cisseps fulvicollis*	0.99	0.26	13.94
16 and 13	*Poanes* sp.	0.99	0.09	20.19
16 and 13	*Diabrotica undecimpunctata*	0.88	1.25	26.32
16 and 13	*Chauliognathus pennsylvanicus*	0.92	0.59	32.36
13 and 4	*Apis mellifera*	3.76	2.96	8.01
13 and 4	*Chauliognathus pennsylvanicus*	0.59	0.43	15.32
13 and 4	*Sarcophagid fly small*	0.43	0.53	22.23
13 and 4	*Scolia dubia*	0.67	0.09	28.95
13 and 4	*Eristalis dimidiata*	0.45	0.17	35.05
6 and 11	*Chauliognathus pennsylvanicus*	0.57	1.21	9.74
6 and 11	*Diabrotica undecimpunctata*	0.53	1.5	19.18
6 and 11	*Atteva aurea*	0.43	1.05	26.32
6 and 11	Sweat bee	0.43	0.45	32.46
6 and 11	*Archytas* sp.	0.45	0.26	37.84
16 and 6	*Cisseps fulvicollis*	0.99	0.26	6.02
16 and 6	*Bombus impatiens*	1.4	0.62	11.94
16 and 6	*Junonia coenia*	1.12	0.67	17.79
16 and 6	*Diabrotica undecimpunctata*	0.88	0.53	23.23
16 and 6	*Chauliognathus pennsylvanicus*	0.92	0.57	28.43

Table A5. SIMPER results reporting the pairwise differences between nutrient treatments on the average species-specific abundance (transformed) of floral visitors along with the cumulative contributions (Cum%) towards overall compositional dissimilarities.

Nutrient comparison	Floral visitor species	Nutrient group A	Nutrient group B	Cum. %
NP-N	*Apis mellifera*	3.05	3.02	8.31
NP-N	*Diabrotica undecimpunctata*	1.2	0.97	15.12
NP-N	*Bombus impatiens*	0.73	0.36	21.12
NP-N	Sweat bee	0.33	0.58	27.07
NP-N	*Sarcophagid fly small*	0.63	0.26	32.79
NP-P	*Apis mellifera*	3.05	3.17	7.22
NP-P	*Atteva aurea*	0.49	0.8	14.33
NP-P	*Chauliognathus pennsylvanicus*	0.46	0.46	20.19
NP-P	*Sarcophagid fly small*	0.63	0.3	25.71
NP-P	Sweat bee	0.33	0.55	31.14
N-C	*Apis mellifera*	3.11	3.15	9.42
N-C	*Diabrotica undecimpunctata*	0.94	1.09	17.88
N-C	*Scolia dubia*	0.55	0.58	24.15
N-C	*Chauliognathus pennsylvanicus*	0.34	0.61	29.83
N-C	*Bombus impatiens*	0.39	0.66	35.42
P-C	*Apis mellifera*	3.2	3.15	8.55
P-C	*Atteva aurea*	0.92	0.35	15.88
P-C	*Diabrotica undecimpunctata*	1.05	1.09	23
P-C	*Chauliognathus pennsylvanicus*	0.5	0.61	29.17
P-C	*Scolia dubia*	0.45	0.58	34.59
NP-C	*Apis mellifera*	3.05	3.15	8.92
NP-C	*Diabrotica undecimpunctata*	1.2	1.09	16.18
NP-C	*Chauliognathus pennsylvanicus*	0.59	0.61	22.82
NP-C	*Atteva aurea*	0.5	0.35	27.96
NP-C	*Bombus impatiens*	0.75	0.66	33.07
P-N	*Apis mellifera*	3.2	3.11	8.58
P-N	*Atteva aurea*	0.92	0.37	16.78
P-N	*Diabrotica undecimpunctata*	1.05	0.94	23.65
P-N	*Scolia dubia*	0.45	0.55	29.51
P-N	*Polistes metricus*	0.71	0.63	35.03

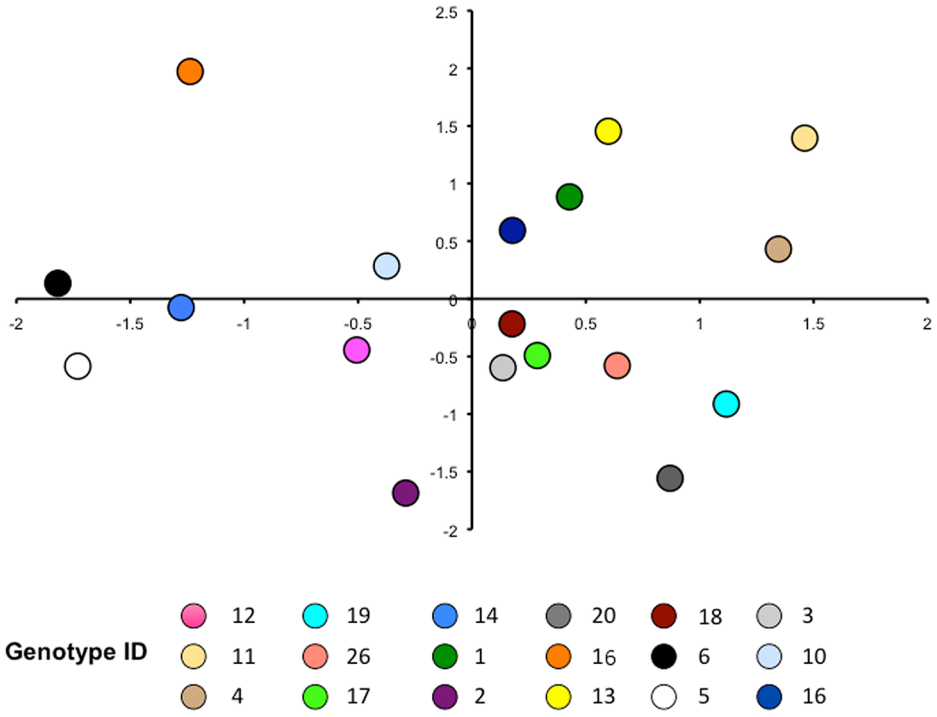

Fig. A1. First two PC axes generated from a principal component analysis that included multivariate plant morphological (height, leaf width, leaf length, leaf area, internode length, leaf area, stem diameter), reproductive (first/last day of the year of flowering, flowering duration in days and inflorescence mass), physiological (specific leaf area), and herbivory (percent leaf damage, aphid abundance) from 2009. In order to maximize trait variance, we selected eight *Solidago* genotypes with aim to maximize their separation across the x-axis (PC 1) and y-axis (PC 2). The selected genotypes included: 2, 4, 6, 11, 13, 16, 20, and 26.

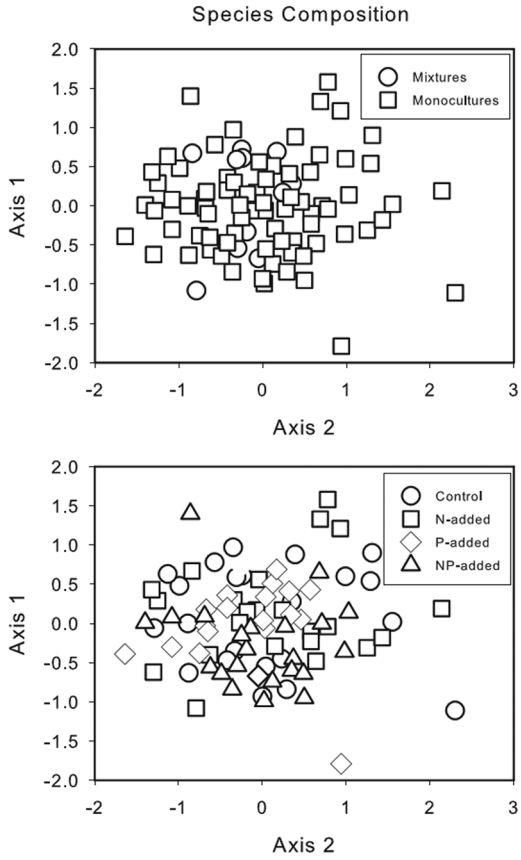

Fig. A2. PERMDISP results for floral visitor species composition. Intraspecific diversity is displayed in the top panel and nutrient enrichment in the bottom panel.

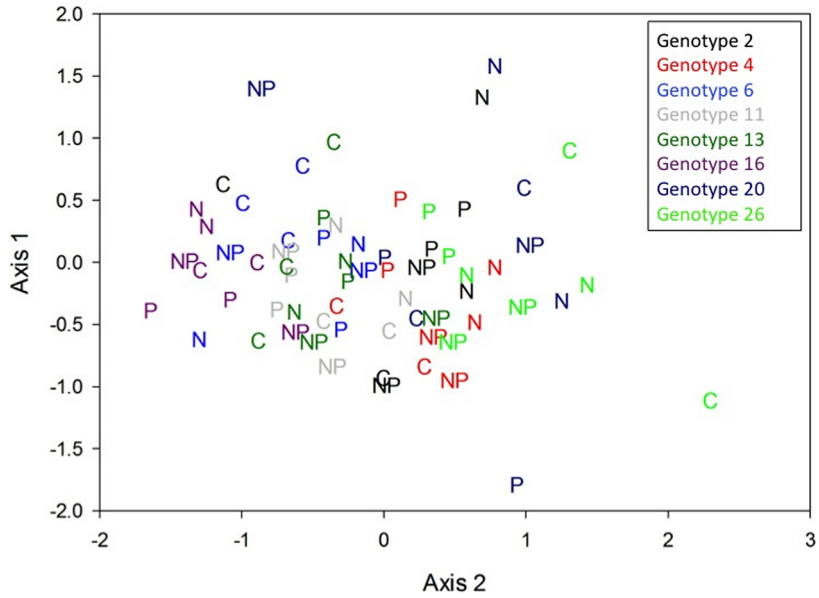

Fig. A3. Non-metric multidimensional scale (NMDS) plot of the interaction between genotype ID and nutrient enrichment treatment on floral visitor composition.