Genotypic diversity mediates the distribution of an ecosystem engineer

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Abstract

Ecosystem engineers physically modify environments, but much remains to be learned about both their effects on community structure and the factors that predict their occurrence. In this study, we used experiments and observations to examine the effects of the bunch galling midge, *Rhopalomyia solidaginis,* on arthropod species associated with *Solidago altissima.* We also examined four factors that influence its occurrence: host-plant genotype, plot-level genotypic diversity, nutrient availability, and patch size and isolation. The presence of bunch galls increased diversity and abundance and altered the structure of associated arthropod communities. The best predictors of the abundance of galls were host-plant genotype and plot-level genotypic diversity. Neither nutrient availability nor the landscape-level parameters patch size and isolation affected galling by *R. solidaginis*. Our results indicate that incorporating a genetic component to studies of ecosystem engineers can help predict the distribution and abundance of ecosystem engineers and ultimately their effects on biodiversity.

Keywords: Community genetics, *Solidago altissima, Rhopalomyia solidaginis,* ecosystem engineer, galling midge, host plant, herbivory, genotypic diversity

Introduction

Ecosystem engineers influence the distribution and abundance of other members of a community by providing shelter from the physical environment, protection from enemies, or changes in the availability of food resources (Jones et al. 1994, 1997). For example, dam-building beavers can dramatically alter the structure of stream and pond communities, influencing species diversity at multiple spatial scales (Wright et al. 2002, 2003). However, less conspicuous species can also engineer new habitats that are subsequently exploited by community members (Cappuccino 1993, Martinsen et al. 2000, Lill and Marquis 2003, Kagata and Ohgushi 2004, Moore 2006). For example, shelter-building caterpillars modify the structure of leaves on host plants. These structures are sometimes secondarily used by other arthropods, thereby increasing the diversity of arthropods on plants and altering community composition (Martinsen et al. 2000, Fukui 2001, Lill and Marquis 2003). Engineers can also have negative effects on biodiversity, if, for example, the newly constructed habitats attract predatory species (Martinson et al. 2000, Fournier et al. 2003). Even though ecosystem engineers maybe ubiquitous across most ecosystems, much remains to be learned about both the ultimate consequences of ecosystem engineers in communities – how they affect biodiversity – and the proximate causes of ecosystem engineering – what factors predict the occurrence of engineers in communities (Jones 1994, Jones 1997, Wright and Jones 2006).

In this study, we focus on a potential ecosystem engineer, the goldenrod bunch gall midge, *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae) to examine the consequences of *R. solidaginis* galls for the structure of communities associated with *S. altissima.* We also examine several factors that could influence the occurrence of *R. solidaginis* galls on *Solidago altissima*:

genotype of *S. altissima*, the number of genotypes in a patch of *S. altissima*, soil nutrient availability, and patch size and isolation.

Solidago altissima genotype and genotypic diversity. Within old-field fragments, local populations of *S. altissima* can contain clones that exhibit considerable trait variation, particularly in resistance to herbivore and galling species (Maddox and Root 1987). The number of *Solidago* genotypes in natural patches can vary from 1-12 (Maddox et al. 1989). When particular genotypes of *Solidago* are more susceptible to attack by gall midges than others (Cronin and Abrahamson 1999), a mosaic of patches which vary in the number of genotypes could influence galling. As genotypic diversity increases within a population, so should the abundance of galling insects. However, this has been little tested.

Soil nutrient availability. Soil nutrient availability can also influence the distribution of herbivores in general and gall-forming species in particular. For example, several fertilization experiments have shown that the abundance of different galling species is higher in fertilized than unfertilized plots (Blanche and Ludwig 2001, Moon and Stiling 2002, Stiling and Moon 2005). Thus, *Solidago* growing in nitrogen-rich environments may be more susceptible to galling than *Solidago* growing in nitrogen-poor sites.

Patch size and isolation. Finally, the spatial distribution of host plants may influence the distribution of galling species (McGeoch and Price 2004). Plants growing near other galled plants might have a higher probability of being galled than host plants that are far from one another because galling midges may be dispersal limited (Cronin et al. 2001, McGeoch and Price

2004). Other galling species are dispersal limited. For example, the stem galler, *Eurosta solidaginis*, has an average maximum lifetime dispersal range of 51 m (Cronin et al. 2001).

In this paper, we use a series of observations and manipulative experiments to address four specific hypotheses relating to the consequences and causes – or factors influencing the distribution- of galling by *R. solidaginis* on *S. altissima*: (1) Galling by *R. solidaginis* alters the structure of the insect community associated with *S. altissima*. (2) Galling rates depend on host-plant genotype and the number of genotypes (genotypic diversity) per patch. (3) Increased nutrient availability increases the galling rate. (4) *Solidago* patch size and isolation alters galling rates at landscape scales due to limited dispersal of the midge, with large patches close to other galled patches being galled most frequently.

The study system

Rhopalomyia solidaginis is a common herbivore that alters the architecture of *Solidago alissima* (tall goldenrod), a rhizomatous perennial that dominates old-field plant communities throughout the eastern United States and Canada. The gall is formed when the midge oviposits in the apical meristem of *S. altissima*, preventing further elongation of the stem and creating a rosette or bunch of leaves typically at the tip of the plant, but also on lateral buds (Plate 1). *Rhopalomyia solidaginis* has two generations per year. The first generation oviposits in May, producing inconspicuous galls that usually contain 1-4 larva, and adults emerge within a few weeks (N. Dorchin *pers. comm.*) These adults are short-lived and lay their eggs within 1-2 days, inducing the summer/fall generation galls, which are large and very conspicuous. Protected by the rosette are 1 to 12 chambers in the meristem, each containing a single midge larva (Raman and

Abrahamson 1995). The size of the engineered habitat varies according to the number of larvae per gall and the quality of the host plant (Raman and Abrahamson 1995). The larvae go through three instars and then pupate in the galls. Adult midges of the summer generation emerge from mid-August to September. These adults lay their eggs into the soil next to *S. altissima* plants where the larvae burrow into rhizomes to over-winter until the next spring (N. Dorchin *pers. comm.*).

The arthropod fauna associated with *Solidago* is both diverse (~ 138 species are known to complete their life cycle on various parts of the plant [Root and Cappuccino 1992]) and well-studied. Particularly well studied are interactions between *Solidago* and gall-forming midges (Hartnett and Abrahamson 1979, Abrahamson and McCrea 1986, Weis and Abrahamson 1986, Abrahamson et al. 1989, Raman and Abrahamson 1995, McEvoy 1998, Cronin et al. 2001), though no studies to our knowledge have examined the consequences of engineering by midges on the arthropod communities associated with *Solidago*.

Methods

Study site

All fieldwork was conducted at Freels Bend at the Oak Ridge National Laboratory (ORNL) National Environmental Research Park (NERP) near Oak Ridge, Tennessee (35°58′ N, 84°17′W). The site was abandoned from agricultural use in 1943. About 50% of the plants are galled at our study site (Crutsinger *unpublished data*), and we have observed up to 9 galls on an individual stem in the field.

The Consequences of Galling on the Structure of Arthropod Communities. In July of 2005, we identified 20 distinct *Solidago* patches. In each patch, we randomly selected two pairs of *Solidago* ramets. Each pair contained a galled ramet and its closest ungalled neighbor of similar size. We visually surveyed arthropods on both ramets and measured the maximum height and width of the gall to estimate gall area. We then collected the gall in a plastic bag and an equal length of stem from the ungalled neighboring ramet. These were taken back to the lab on ice and dissected under a dissecting microscope to count and identify all of the secondary users occurring inside the bunch gall and arthropods on the portion of ungalled stem down to morphospecies. We assigned each species to a trophic group (herbivore, detritovore, omnivore, or predator) based on their feeding morphology, observations in the field, and previous studies. Thus, for each galled and ungalled stem, we tallied the total number of individuals and species occurring on the ramet (visual scan and dissections of galls). We used two separate ANOVA models to determine whether patch (as a block) and host-plant status (galled or ungalled) affected arthropod richness and abundance. We also used two separate ANOVA models to determine whether patch (as a block) and gall status (galled or ungalled) affected richness and abundance of herbivores and predators. To determine whether community composition varied between the galled and ungalled plants, we used Primer statistical software (K. R. Clarke and R. N. Gorly. 2001. Primer version 5, Primer-E Ltd., Plymouth Marine Laboratory, Plymouth, UK) to perform non-metric multidimensional scaling (NMDS) ordination using Bray-Curtis similarity (Clarke 1993).

To test whether the effects of galling on arthropod community structure were due to the presence of the gall rather than some inherent characteristic of the particular plant or its location, we

conducted a gall exclusion experiment. In June 2005, we bagged 12 ungalled ramets with bridal veil to decrease the probability that the ramet would be galled by the second generation of *R. solidaginis*. The bags were left on the ramets until most gall initiation terminated in late July. We grouped each of these bagged ramets with its closest galled neighbor and an ungalled control ramet. Bags were removed and arthropods were allowed to recolonize the ramets for one week. After this period, we repeated the census techniques described above. In this experiment, meadow spittlebugs (*Philaenus spumarius*) were present in high abundance on many of the ramets. We used an ANCOVA to test for differences in arthropod richness and abundance among the treatment plants (bagged, galled, and ungalled) with the abundance of spittlebugs as a covariate. We followed these analyses with subsequent Tukey's multiple comparisons post-hoc tests to separate means.

We examined two possibilities for why arthropods might secondarily occur in bunch galls: as a food resource or as habitat. To test whether herbivores might preferentially forage on galled versus ungalled leaf tissue, we performed a cafeteria experiment. We offered 2nd instar *Spodoptera exigua* (beet army worm) larvae three similarly sized leaves: a leaf from the gall of a plant, a leaf from a galled plant but not part of the gall, and a leaf from an ungalled plant. Leaves were collected at the field site from 36 plants (18 galled and 18 ungalled) and were kept on ice until the experiment began the same day. In 18 Petri dishes, we arranged these three leaf types so that they were equidistant from an *S. exigua* larva placed in the middle of the Petri dish. After two days, we measured the percent of the leaf area damaged by the larva. We used ANOVA to examine whether Petri dish (as a block effect) and caterpillar herbivory rates differed among leaves from the galls, the stem of a galled plant, or the stem of an ungalled plant.

To examine whether more arthropods were associated with bigger galls as an indirect test of the hypothesis that galls simply provide habitat for arthropods, we tested whether richness and abundance were a function of gall area using two separate linear regressions.

Solidago altissima genotype and genotypic diversity. To test how gall density is influenced by genotype identity and plot-level genotypic diversity of *Solidago*, we constructed a common garden experiment. In February 2005, we collected rhizomes from 21 ramets from local patches, spatially separated by 50-100 m. We used Amplified Fragment Length Polymorphism (AFLP) techniques to ensure each ramet was a distinct genotype (for more detailed AFLP methods and of the common garden design see Crutsinger et al. *In review*). Ramets were grown from rhizome cuttings under the same light, nutrient, and watering regimes in the greenhouse until April and then transplanted into 1-m^2 plots spaced 1 m apart in 25 × 15 m grid. Each 1-m^2 plot contained 12 ramets. The experimental treatments consisted of all 21 genotypes in monoculture (2 reps of each) and diversity treatments containing 3, 6, or 12 different genotypes (7 reps of each). Diversity treatments were created by randomly drawing from the pool of 21 genotypes with the stipulation that no two replicates within each treatment could overlap identically in composition. Ramets were set out in a circular arrangement to ensure equal colonization of galling midges in a plot (Johnson and Agrawal 2006). In September 2005, we counted the total number of galls in each plot. We examined gall abundances instead of percent *Solidago* galled because we started the experiment with equal abundance of ramets in the same plot area. Because we found a significant positive relationship between gall abundance and genotypic diversity (see results below), we tested whether the effect of genotypic diversity on bunch gall abundance was simply due to additive effects (i.e. the sum effect of each genotype susceptibility in a mixture).

To test whether total gall abundance varied among the 21 genotypes, we used a one-way ANOVA, treating individual monoculture plots as replicates. We examined the effect of genotypic diversity on gall abundance using linear regression with the monoculture plots as the 1-genotype treatment and including 3, 6, and 12 genotypes in the model. To test for non-additive effects of genotypic diversity on gall abundance, we used Monte Carlo simulations using data from genotype monoculture plots to construct null genotype mixtures and their associated gall abundances. We compared the observed gall abundances to these null communities. Each null community consisted of 3, 6, or 12 genotypes sampled to match the exact identities corresponding to a particular plot combination (e.g., for a 3-genotype plot containing G3, G13, and G19, we sampled only from monoculture plots containing these three genotypes) (Johnson et al. 2006). For each sampled genotype, the appropriate number of individual ramets (4, 2, or 1) was randomly sampled without replacement from a randomly selected replicate monoculture plot. This process was repeated 5000 times for every mixed genotype plot. To calculate statistical differences between gall abundance in observed and null communities, we used a bootstrap approach. For each of 10,000 iterations, we sampled seven null communities and calculated mean number of galls at the plot-level. We measured *P*-values as the fraction of iterations in which the null mean was equal to or exceeded the observed mean. We calculated 95% confidence intervals using the percentile method (2.5^{th} and 97.5^{th} percentiles). If the effects of genetic diversity on gall abundance were additive, we would expect no difference between observed and predicted means ($P > 0.05$). All Monte Carlo simulations were coded in Microsoft Visual C++ 6.0 (Microsoft, Redmond, WA, USA).

Soil nutrient availability. To examine how soil nutrient availability affects rates of galling, we took advantage of an ongoing experiment at the study site that manipulates nitrogen availability at three levels. In the spring of 2004, 36 3m × 3m plots were placed in existing old-field vegetation, spaced 2m apart in a grid using existing vegetation. Plant available nitrogen was manipulated at three levels during 2004 and 2005: (1) addition of nitrogen (applied each May as urea fertilizer, at a rate of 10 g m^2), (2) addition of carbon (applied as sucrose at a rate of 167 g m^2 in May and again in August), and (3) an ambient control. Applications of sucrose, which is ~46% C with a molecular form readily available to microbes, results in immobilization of plant-available N in the soil solution (Zink and Allen 1998). When we censused galls for this study (July 2005), the site had been maintained for two seasons and nitrogen resin bags indicated significant differences in soil nitrogen availability (Sanders *unpublished data*). In each of the 36 plots (n=12 per treatment), we randomly placed a $1m^2$ quadrat and counted the total number of *Solidago* ramets and the proportion of these ramets that were galled by *R. solidaginis*. We used a one-way ANOVA to examine if the percent of ramets galled depended on soil nitrogen treatments (N-added, N-reduced, and Control). We arc-sin transformed the percent of ramets galled prior to analysis to achieve normality.

Patch size and isolation. To examine how patch size and isolation might influence rates of galling, we identified 20 distinct patches of *Solidago* in July 2005 in a neighboring old field. We did not conduct any experiments in this field. We estimated the area of each patch as 0.5 Length of the patch x 0.5 Width of the patch x π. Isolation was estimated as the average distance from the edge of the focal patch to the closest *Solidago* patches in all four cardinal directions. In each patch, we counted the total number of *Solidago* ramets and the proportion of those ramets that

were galled. We used linear regression to examine the relationship between the percent of ramets galled and each of the following variables: patch area, minimum isolation distance (or distance to the nearest neighboring patch), and mean isolation distance (mean distance of the four nearest patches in the cardinal directions). We arc-sin transformed the percent of ramets galled prior to analysis to achieve normality.

Results

The Effects of Galling on Arthropod Diversity and Community Structure. When comparing paired ramets, species richness was 110% greater (ANOVA; df = 1,F=34.86, P<0.001) and abundance was a 150% greater (ANOVA; df = 1, F = 17.87, P < 0.001) on galled than ungalled ramets (Fig. 1). There was no patch effect for either richness or abundance (P > 0.08 in both cases). Arthropod community composition differed significantly on galled versus ungalled plants (Global R = 0.326, P = 0.01). The richness of herbivores was 70% greater (ANOVA; df = 1, F = 17.33, P < 0.001), and abundance 110% greater (ANOVA; df = 1, F = 18.53, P < 0.001) on galled than on ungalled ramets. Predator richness was 210% greater (ANOVA; df =1, F = 23.70, P < 0.001) and abundance 250% greater (ANOVA; df = 1, F =16.85, P < 0.001) on galled than on ungalled ramets (Fig. 2). We found no effect of patch identity on herbivore richness and abundance or predator richness and abundance (P > 0.12 in all cases).

When we experimentally reduced galling rates, we found that galled ramets had significantly more arthropod species and greater abundance than did either bagged or control ramets (P < 0.05, Tukey's hsd). Bagged and control ramets were did not differ in either richness or abundance (P > 0.05, Tukey's hsd) (Fig. 3).

We found no effect of leaf type (galled, ungalled, control) on herbivore damage by *S. exigua* caterpillars (ANOVA; df = 2, $F = 0.61$, $P = 0.54$, df = 17, F=0.95, P=0.52). Both arthropod species richness ($R^2 = 0.21$, $P < 0.01$) and abundance ($R^2 = 0.15$, $P = 0.013$) were positively and significantly related to gall area (Fig. 4).

Soil nutrient availability. Soil N treatments did not differ in galling rates (ANOVA; df = 2, F = 0.29, $P = 0.75$).

Solidago altissima genotype and genotypic diversity. Gall abundance differed significantly among the 21 *S. altissima* genotypes (ANOVA; df = 20, $F = 3.51$, $P < 0.01$) with a 28-fold difference in gall abundance between the most susceptible (mean = 29.5 gall m^{-2}) and resistant genotypes (mean = 1 gall m^{-2}) (Fig. 5). Gall abundance increased with genotypic diversity (R^2 = 0.14, $P < 0.01$). There were 80% more galls in 12-genotype diversity plots compared to 1-genotype plots. There were significantly more galls in the 12-genotype mixtures ($P_{3\ genotypes}$ = 0.41, $P_{6\ genotypes} < 0.078$, $P_{12\ genotypes} < 0.001$) than what is predicted from additive effects alone (Fig. 6).

Patch size and isolation. Patch size ($R^2 = 0.01$, $P = 0.62$), minimum patch isolation ($R^2 = 0.11$, P = 0.13), and average patch isolation ($R^2 = 0.12$, $P = 0.12$) did not affect galling rates.

Discussion

Our results demonstrate that galling midges function as ecosystem engineers by providing habitat that is secondarily-used by a diverse and unique community of arthropod species, thereby

increasing arthropod diversity and altering the structure of arthropod communities associated with *Solidago altissima*. Experimental exclusion of galls confirmed that the presence of the gall and not some other aspect of host plant quality drove community-level responses.

Arthropods may use engineered habitats for three reasons: (1) refuges from predators, (2) as sites for preferential foraging and (3) protection from the environment. Leaf shelters can effectively reduce predation, providing a refuge for herbivorous arthropods (Damman 1987, Hunter 1987, Cappuccino 1993). It is unlikely that the gall is being used as a refuge from predators because we found more predators on galled ramets than ungalled ramets. Galls may provide preferential foraging for herbivores if the galling midge induces a qualitative change in leaf structure or chemical as has been shown for leaf rollers (Sagers 1992). From our cafeteria experiment, we conclude that the gall probably does not provide preferential foraging for herbivorous arthropods. It seems most probable that the gall is used as a favorable microhabitat, sheltering its inhabitants from unfavorable climates, such as extreme heat that can cause desiccation (Willmer 1982). This hypothesis is supported by our results showing arthropod abundance and richness was positively correlated with gall size.

While other studies have shown that arthropod species function as ecosystem engineers by increasing arthropod diversity through the creation of new habitats (Cappuccino 1993, Martinsen et al. 2000, Lill and Marquis 2003, Kagata and Ohgushi 2004), few studies have specifically linked the consequences of engineering with the factors that influence engineering (Jones 1994, 1997). Our results indicate that of the biotic, abiotic, and spatial influences that we examined,

galling by *R. solidaginis* was significantly influenced only by host-plant genotype and patch-level genetic diversity.

Recent research in community genetics has emphasized the potential for genetic variation within individual species, particularly dominant species such as *Solidago,* to have extended consequences for communities and ecosystems (Fritz and Price 1988, Treseder and Vitousek 2001, Whitham et al. 2003, Wimp et al. 2005, Schweitzer et al 2004, Johnson and Agrawal 2005, Bailey et al. 2006, Johnson et al. 2006). Several other studies examining the distribution of galling insects have also found that host plant genotype is an important factor influencing gall-maker preference (Fritz 1999, Rossi and Stiling 1998, Cronin and Abrahamson 1999, Ollerstam and Larsson 2003). However, few studies have shown that host-plant genotype can influence ecosystem engineers. Martinsen et al. (2000) found that the abundance of leaf rollers varies on backcross and F_1 hybrid cottonwoods, indirectly altering arthropod community structures on trees with different genotypes. Similarly, we found that host plant genotype influences the distribution of an engineer, which could, in turn, lead to landscape-level changes in arthropod community diversity and structure. We did not examine the particular phenotypic traits that are correlated with genotype susceptibility to galling, but small differences in host-plant phenology, physiology, development, and chemistry can be important to the success of these insects (Horner and Abrahamson, 1992; Craig et al., 1993, 1999, 2000; How et al., 1993, Abrahamson et al. 2003).

We found an 80% increase in the number of galls in 12-genotype plots compared to 1-genotype plots. No studies to our knowledge have shown that genotypic diversity can influence an

ecosystem engineer. These increases can be attributed to additive responses (sum of individual genotype susceptibility) in 3- and 6-genotype plots and the increased likelihood of including gall-susceptible genotypes the more genotypes added to a mixture. However, at the highest genotypic diversity treatment of 12 genotypes, we found significant non-additive increases in gall abundance. These results emphasize the importance of intraspecific genotypic diversity within local populations for members of communities, such as ecosystem engineers, who have significant roles in maintaining diversity within communities (Whitham et al. 2003).

Surprisingly, we found no response of galls to soil nitrogen manipulations even though several previous experiments have shown that increases in soil nitrogen increase the abundance of galls on host plants (Blanche and Ludwig 2001, Moon and Stiling 2002, Stiling and Moon 2005). Other results from the site also show no effect of nitrogen addition on other herbivore species (Sanders, unpublished). It also may be that the gallers control the amount of nitrogen in the leaf tissue, mediating the effect of nitrogen addition and reduction (Hartley and Lawton 1992). The simplest explanation, though, is that the gallers respond more to some other trait, perhaps one associated with the plant's genotype.

Patch size and isolation did not affect galling rates by *R. solidaginis*. Other studies have suggested that galling insects may be dispersal limited, creating patches of colonized and uncolonized host plants (Cronin et al. 2001, McGeoch and Price 2004). If the gallers are dispersal limited and in low enough abundances, we expect larger patches that are closer to other colonized patches to have the highest percentage of stems galled. Since we did not detect this pattern, it can either be inferred that the galling midges are not dispersal limited at least at the

scale of this study. It could also be that they are in such high abundances at the field site, dispersal limitation does not affect their distribution.

Ecosystem engineers may not simply alter the distribution of species that exploit the habitats they form, there may be evolutionary consequences between engineers and the physical changes they induce (Wright and Jones 2006). By attacking *Solidago*, *R. solidaginis* affects plant fitness by lowering seed reproductive allocation (Hartnett and Abrahamson 1979, Crutsinger *Unpublished data*). Since susceptibility to galling is a genotype mediated trait, differences in fitness between galled and ungalled genotypes could potentially feedback to selection against gall susceptible plants.

In sum, galling by *R. solidaginis* significantly increases the richness and abundance of other arthropod species on *S. altissima*. In agreement with a growing body of literature, we found strong extended consequences of host-plant genotype and genotypic diversity, suggesting that to understand more fully the consequences of ecosystem engineers, it may be necessary to understand the genetic factors underlying how ecosystem engineers mediate the effects of engineering species on communities and ecosystems.

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Figure Legends

Plate 1. Bunch gall on *Solidago* caused by the midge *Rhopalomyia solidaginis*. (Left) View looking down on the gall. (Right) Side view of the gall. Photo credit: G. Crutsinger.

Figure 1. Total average arthropod species richness and abundance on paired galled and ungalled *Solidago* ramets. Error bars are ± 1 SE.

Figure 2. Total average species richness and abundance of predators (black bars) and herbivores (grey bars) on paired galled and ungalled *Solidago* stems. Error bars are ± 1 SE.

Figure 3. Total average arthropod species richness and abundance for galled, ungalled control, and bagged (gall excluded) *Solidago* ramets. ? denotes significant differences. Error bars are ± 1 SE.

Figure 4. Correlation between bunch gall area (cm^2) and arthropod species richness and abundance found inside of the gall.

Figure 5. Average abundance of galls in m^2 plots of *Solidago* across 21 unique genotypes. Error bars are ± 1 SE.

Figure 6. The relationship between patch-level genotypic diversity and gall abundances. Open circles indicate plot-level observations, and the horizontal line indicates the treatment mean. The filled boxes show the number of galls predicted (± 95% confidence interval) by simple additive models.

Plate 1



Figure 1

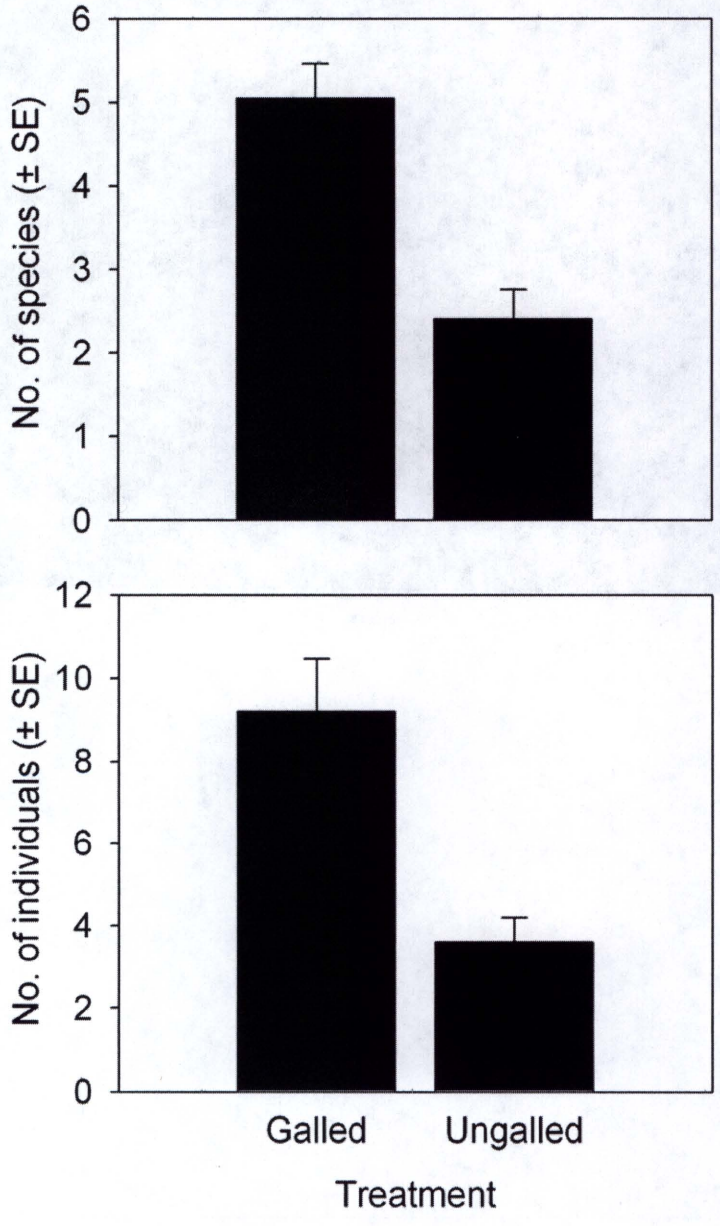

No. of species (± SE)
0
1
2
3
4
5
6
No. of individuals (± SE)
0
2
4
6
8
10
12
Galled
Ungalled
Treatment

Figure 2

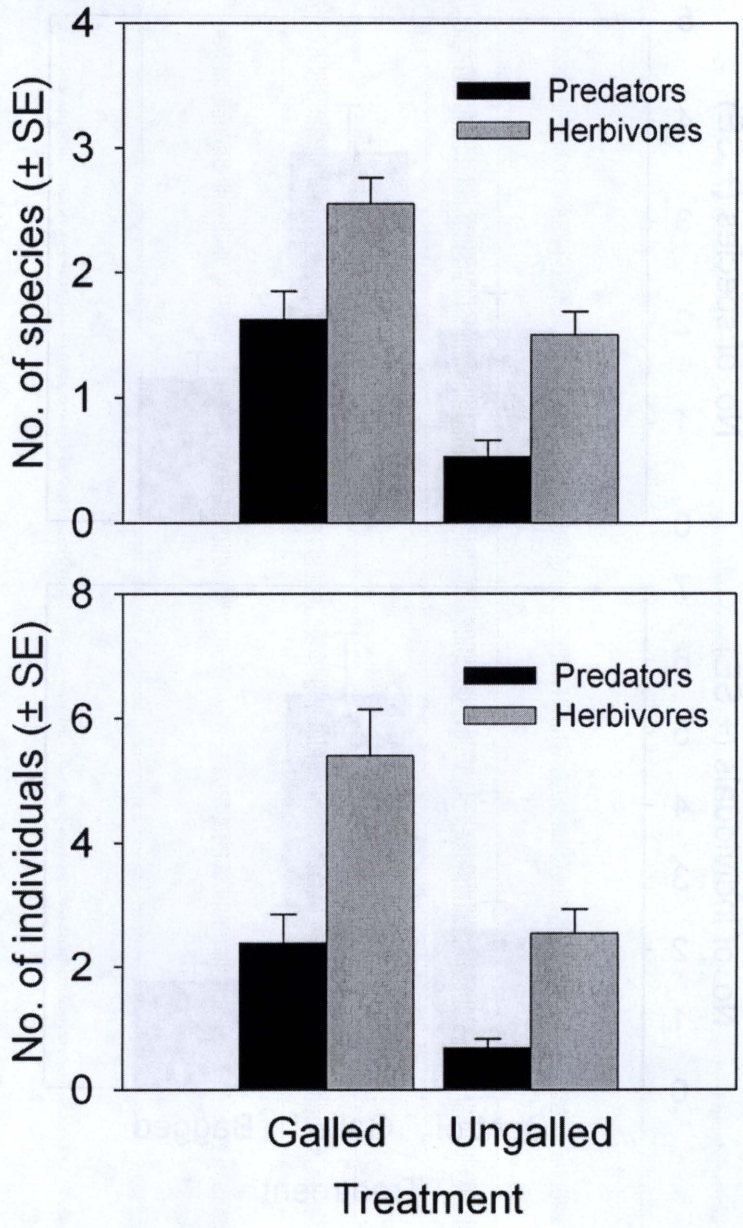

No. of species (± SE)
0
1
2
3
4
Predators
Herbivores
No. of individuals (± SE)
0
2
4
6
8
Predators
Herbivores
Galled
Ungalled
Treatment

Figure 3

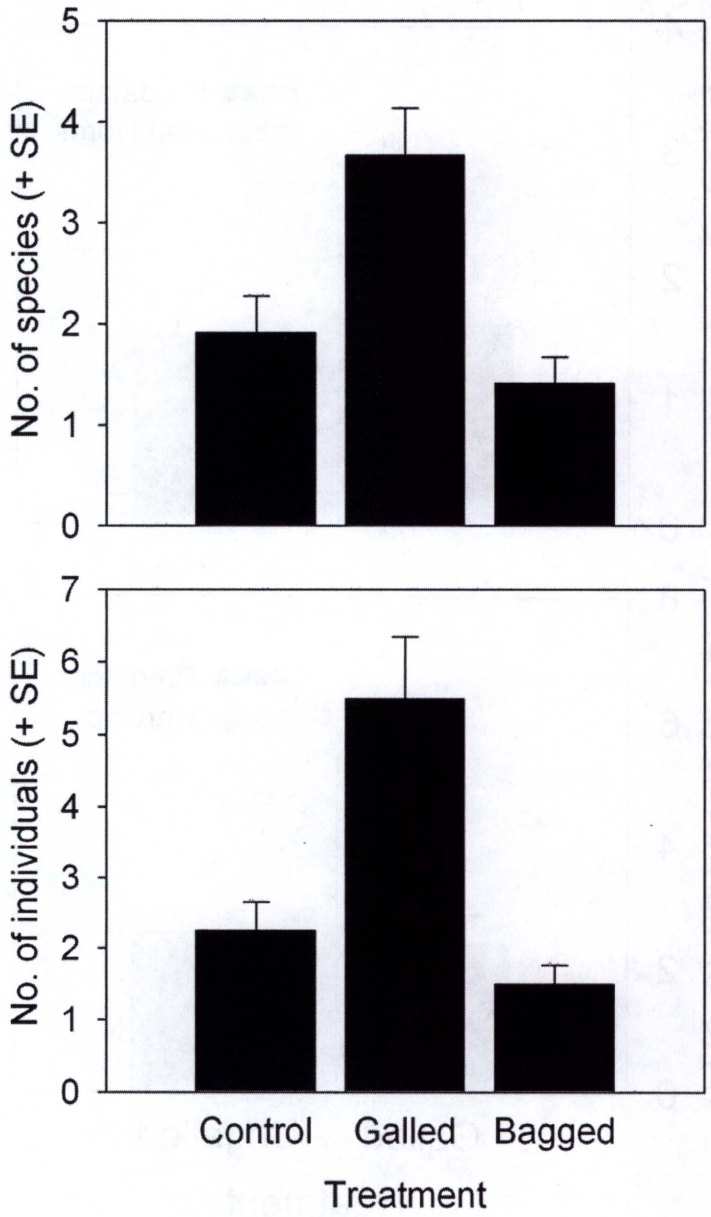

No. of species (+ SE)
0
1
2
3
4
5
No. of individuals (+ SE)
0
1
2
3
4
5
6
7
Control
Galled
Bagged
Treatment

Figure 4

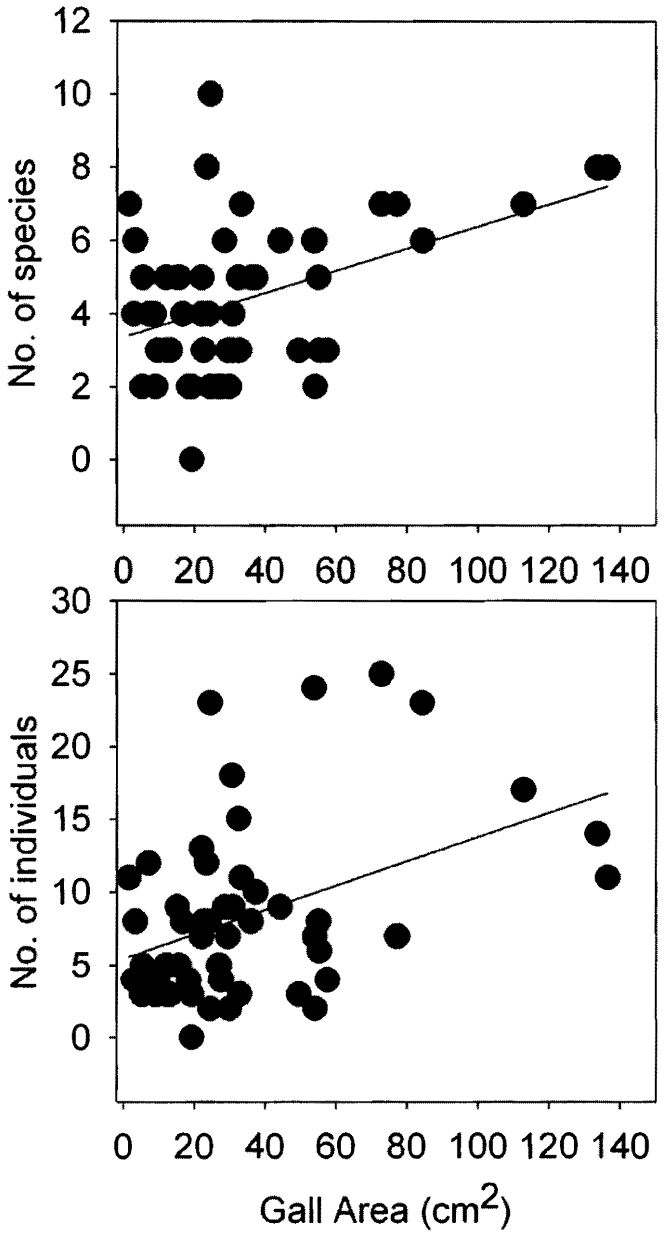

No. of species
12
10
8
6
4
2
0
0 20 40 60 80 100 120 140
No. of individuals
30
25
20
15
10
5
0
0 20 40 60 80 100 120 140
Gall Area (cm2)

Figure 5

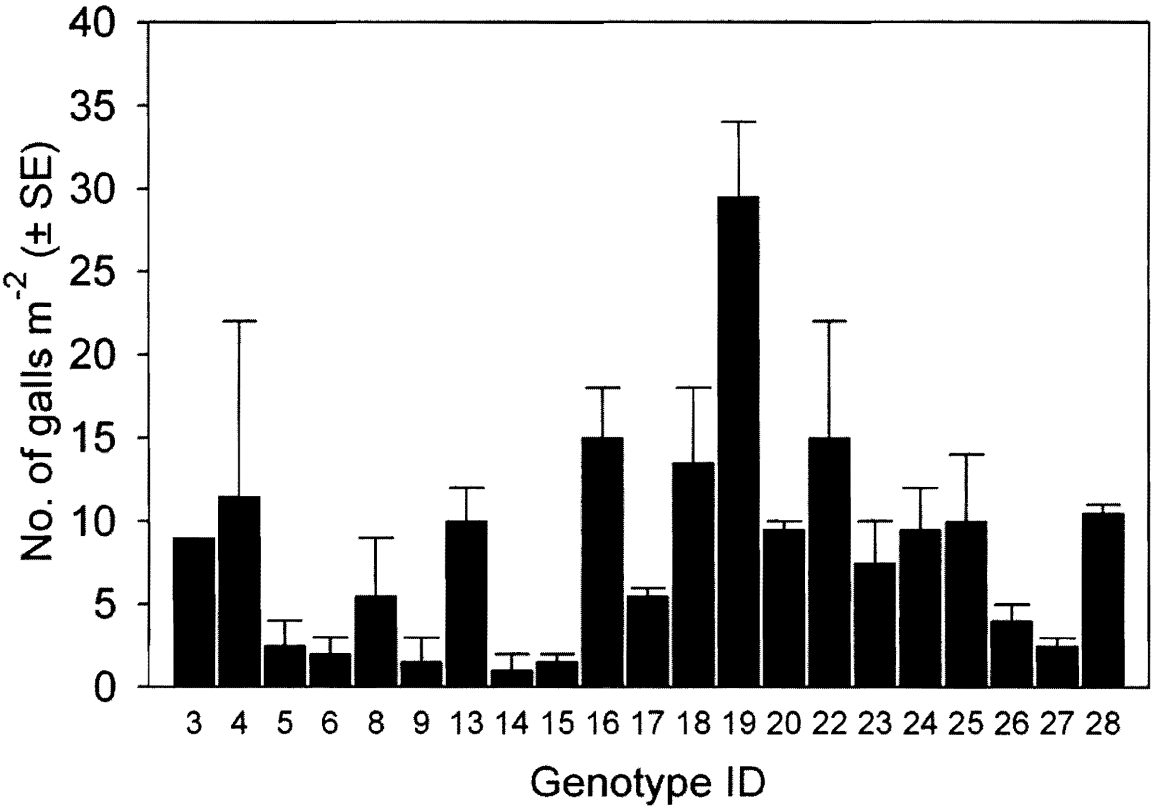

40
35
30
25
20
15
10
5
0
No. of galls m-2 (± SE)
3 4 5 6 8 9 13 14 15 16 17 18 19 20 22 23 24 25 26 27 28
Genotype ID

Figure 6

