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Environmental heterogeneity and spatiotemporal variability in plant defense traits

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At the scale of the local plant community, we know very little about how spatial and temporal environmental heterogeneity affects the diversity in types and levels of plant defenses. If environmental heterogeneity is an important mechanism influencing plant defense traits, then defense expression should co-vary spatially with environmental conditions and change as succession progresses. In this study, we examined how spatial heterogeneity and succession influence putative resistance and tolerance trait levels in late goldenrod *Solidago altissima*. We quantified the spatial distributions of herbivore damage and traits associated with resistance (leaf toughness, phenolics), tolerance (specific leaf area, relative growth rate, leaf addition rate and leaf senescence rate), and fitness (height, diameter, inflorescence biomass) of goldenrods within replicate early- and late-successional fields. Also, we characterized the local neighborhood (stem density, canopy cover, ground vegetative cover) and edaphic conditions (soil moisture, pH, N) surrounding each target ramet, and determined relationships between these environmental variables and goldenrod trait levels. The distribution of traits within fields was strongly non-random, and defense-trait levels were more strongly spatially structured (i.e. autocorrelated) in late- than in early-successional fields. Also, defense traits were most strongly correlated with aspects of the local plant neighborhood, and these relationships differed in important ways between successional stages. In late-successional fields, tolerance trait specific leaf area was positively correlated with canopy cover and negatively correlated with stem density. In early-successional fields, the relationship between ground vegetative cover and resistance (i.e. 1 – damage) was significantly stronger than in late-successional fields. A novel insight from this study is the possibility that changes in the biotic environment during succession may shift the expression of defense from a resistance to a tolerance strategy in our system. This study highlights the context dependence of plant defense trait levels, which may promote their spatial and temporal variability in heterogeneous landscapes.

In response to herbivore pressures, plants can express resistance traits to reduce herbivore damage or tolerance traits to reduce the negative fitness effects of herbivore damage. An active area of interest in plant defense theory focuses on understanding how variable defense traits co-occur and are maintained within natural populations (Mauricio et al. 1997, Fornoni et al. 2004, Núñez-Farfan et al. 2007). Recent studies have shown that geographic variation in interactions among organisms may lead to complex patterns of trait selection (Thompson and Cunningham 2002, Berenbaum and Zangerl 2006). At smaller scales, such as at the local community level, environmental heterogeneity also may influence selection for defense traits and promote their spatial and temporal variability (Núñez-Farfan et al. 2007). However, few empirical studies have examined plant defense at the local community level (but see Covelo and Gallardo 2004, Brenes-Arguedas and Coley 2005). Spatially-explicit studies that examine the spatio-temporal variability in plant resistance and tolerance to herbivory, as well as their interactions with environmental variables, are necessary to understand the mechanisms influencing the observed diversity in types and levels of plant defense traits in nature.

Environmental heterogeneity is thought to be a strong force selecting for and maintaining variation in the type and level of plant defense within natural plant populations (Fornoni et al. 2004, Agrawal et al. 2006). For example, plants may invest less in resistance traits when edaphic resources are limited (Bergelson 1994). Alternatively, resistance trait levels may increase when resources are low if plants invest more in defense when growth is costly (Coley et al. 1985). The relationship between edaphic conditions and plant tolerance is likewise equivocal (Maschinski and Whitham 1989, Hawkes and Sullivan 2001) and may depend on the type of limiting resource and part of the plant that is damaged (Wise and Abrahamson 2005). Environmental heterogeneity also encompasses biotic variables, such as the neighboring plant community (Agrawal et al. 2006). Neighboring plants may alter the defense levels of a focal plant, directly via competition or indirectly via associational resistance/susceptibility. Competition may decrease defense expression if there is a resource allocation tradeoff between defense traits and competitive ability (Cipollini and Bergelson 2002). Alternatively, competition may increase defense levels if traits serve a dual purpose, mitigating herbivory and competitive stress (Siemens et al. 2003, Jones et al. 2006). In the absence of competition, spatial associations among plants may influence defense levels. Previous studies have shown that the density, identity, and palatability of neighboring plants can reduce or enhance a plant's probability of being discovered and damaged by herbivores (Root 1973, Hay 1986, Agrawal et al. 2006). Despite the wealth of literature highlighting the importance of the abiotic and biotic environment in influencing plant defenses, no clear generalizations have emerged and very few empirical studies have examined defense traits in the context of natural environmental complexity (but see Covelo and Gallardo 2004, Brenes-Arguedas and Coley 2005).

Another area of plant defense research that has received very little attention is the expression of plant defense in response to temporal changes in the environment. Soil conditions, species composition, and competitive interactions among plants can change dramatically as a community undergoes succession (Hartnett and Bazzaz 1985, Huston and Smith 1987, Tilman 1987, 1990). In response to the changing plant community, the composition of the herbivore community may also vary temporally (Tilman 1990, Tscharntke and Greiler 1995, Siemann et al. 1999). Plant species with functional traits adapted to characteristics of early-successional environments are assumed to be replaced by species with traits better suited for characteristics of late-successional habitats (Tilman 1987, 1990). Similarly, plant defense traits may be most adaptive with respect to a particular successional stage of a community. Given what we know about how the biotic and abiotic environment can influence plant defense levels, and how the environment changes predictably during succession, it is likely that defense traits, herbivore damage, and environmental variables will be temporally dynamic.

Quantifying the distribution of plant defense traits within natural populations may reveal important insights into the relative contributions of stochastic and deterministic processes structuring their spatial patterns. For example, if the establishment of individuals occurs by lottery (Sale 1977, Chesson and Warner 1981), then resistant and tolerant plants may be randomly distributed within populations, regardless of environmental heterogeneity or successional stage of the community. However, if local selection pressures influence plant phenotypes (Via and Lande 1985, Thompson and Cunningham 2002), then resistance and tolerance trait levels may be non-randomly distributed (i.e. autocorrelated) within populations and correlated with aspects of the environment. Another possibility is that the initial assembly of resistant and tolerant plants within populations is random, but over time, non-random processes (e.g. local selection) may become increasingly important at structuring defense levels within a population. In this scenario, we may expect defense-trait levels of a long-lived plant to exhibit greater autocorrelation and stronger correlations with environmental variables within late-successional communities than within recently-colonized early-successional communities.

In this study, we examined how spatial and temporal environmental heterogeneity influenced the levels of plant defense traits by quantifying the spatial distributions of herbivore damage, putative-resistance, putative-tolerance, and fitness-related traits of *Solidago altissima,* late goldenrod, within replicate early- and late-successional, old-field communities. We also characterized the relationships between defense traits and neighbor variables (neighbor stem density, ground vegetative cover, canopy cover) and edaphic conditions (soil moisture, pH, N) to identify potential mechanisms driving spatial defense patterns. Lastly, we examined correlations among defense traits as well as between defense and fitness traits which would indicate tradeoffs and fitness costs associated with defense traits, respectively (Tilman 1990, Siemens et al. 2003). Using these data, we specifically tested the following predictions: 1) plant traits and environmental variables will vary within fields and between successional stages, 2) defense traits will be non-randomly distributed within fields and be strongly correlated with environmental variables (i.e. edaphic conditions, local neighborhood), 4) late-successional fields will be more strongly spatially structured (i.e. exhibit stronger spatial correlations among defense traits and environmental variables) than early-successional fields, and 5) negative correlations will exist between resistance and tolerance traits and between defense and fitness traits. To our knowledge, this is the first study to examine the potential causes of the spatial patterns of both resistance and tolerance traits within heterogeneous environments and examine how successional changes in the environment influence spatial patterns of defense.

Methods

The study system

Late goldenrod *Solidago altissima* subsp. *altissima*) is common throughout eastern North America (Semple and Cook 2006) and a dominant plant of mid-successional, old-field habitats. Goldenrods are insect pollinated and can reproduce sexually and vegetatively via rhizomes (Abrahamson and Weis 1997).

Goldenrods are model organisms for studying plant-insect interactions (Abrahamson and Weis 1997). More than 100 species of generalist and specialist herbivores feed on goldenrods (Maddox and Root 1990). Dominant herbivores include spittlebugs *Philaenus spumarius*, gall-making flies *Eurosta solidaginis*, and various grasshopper and beetle species. Previous studies have shown that these herbivores may variously affect goldenrod biomass, photosynthetic rates, leaf senescence, and reproduction (McCrea and Abrahamson 1987, Cain et al. 1991, Root 1996, Abrahamson and Weis 1997, Cronin and Abrahamson 1999).

Goldenrod resistance and tolerance to herbivory

A number of studies have revealed considerable genetic variability in goldenrod resistance to insect-herbivore attack (McCrea and Abrahamson 1987, Maddox and Root 1990, Cronin and Abrahamson 1999). Also, resistance of goldenrod genotypes to at least one herbivore, *E. solidaginis*, has been shown to be temporally dynamic (Cronin et al. 2001). We examined traits leaf toughness (LT) and total phenolics (TP) in the context of *S. altissima* resistance. These traits are assumed to be related to goldenrod resistance, although evidence for this is equivocal (Abrahamson et al. 1991, Abrahamson and Weis 1997, Siska et al. 2002). Tolerance traits include physiological traits that aid in compensatory growth and photosynthesis. Leaf addition rate, increased relative growth rate, specific leaf area, and delayed senescence have been experimentally shown to be associated with tolerance to herbivory in *S. altissima* (Meyer 1998) and other plant species (Moriondo et al. 2003). In addition to tolerating herbivory, these traits may also be associated with plant vigor, as well as serve in tolerating other types of environmental stresses (Chapin 1991, Siemens et al. 2003, Jones et al. 2006).

Field survey

Field surveys of *S. altissima* were conducted from March to November, 2006, in three early- and three late-successional fields located in east Baton Rouge and east Felicia Parishes, LA. Early fields had been mown within the past two years and were dominated by goldenrods, other forbs, and grasses (e.g. *S. altissima*, *Ambrosia* spp., *Liatris* spp., *Dichanthelium* spp.). Late fields were approximately 15 years post mowing and were dominated by trees and shrubs (e.g. *Triadica sebiferum*, *Cornus foemina*, *Acer negundo*, *Rubus* spp,). Distances between our six fields ranged from 1 to 50 km and there was no obvious clustering of successional stages among them. Therefore, our experimental fields were considered independent of each other. Fields varied in size from 1 – 3 ha and we focused our surveys on a 1 ha area within each field (this area was selected at random for fields > 1 ha in size). Colonization by goldenrod genets occurs through wind-dispersed achenes soon after field creation, and genets can persist for up to 75 years (Hartnett and Bazzaz 1985). Continued colonization and rapid clonal expansion occurs through the 5th year, at which time goldenrod density and genet diversity are maximal (Hartnett and Bazzaz 1985, Maddox et al. 1989). As succession progresses, the number of genets declines and within about 20 years, woody plants begin to dominate the landscape (Maddox et al. 1989). Thus, the early-successional fields represent a genet recruitment and expansion phase for *S. altissima*, and the late-successional fields represent a genet decline phase. If allowed to proceed throughout succession, we expect our field sites to eventually become either bottomland or upland hardwood forests (based on our observation of nearby undisturbed forests).

In each field, we mapped a grid with 80–121 nodes at 10 m intervals using a GPS with sub-m precision. The closest *S. altissima* ramet to each node was selected and marked with a plastic tag. The 10 m distance between ramets likely surpassed the dimension of most, but not all, genets. Every six weeks from March to November 2006 we measured the fitness-related traits ramet height and diameter at 10 cm. Studies have shown that goldenrods and other perennials that are larger in size (i.e. high values of stem height, diameter, and/or biomass) have higher survival and life-time fitness in terms of sexual and clonal reproduction (Goldberg 1988, Cain et al. 1991, Gardner and Mangel 1999). After the fall census, newly-opened inflorescences were collected, dried in an oven at 65°C for four days, and the biomass determined as an estimate of short-term sexual fitness.

During each census, herbivores were surveyed by visual counts and identified to family, and proportion of leaves damaged and leaf area damaged were calculated. Leaf area lost to herbivores was assessed through digital photographs of three haphazardly chosen damaged leaves using the program UTHSCSA ImageTool (Univ. of Texas Health Science Center at San Antonio, TX). At the end of each census, a copper wire was tied under each apical bud. In the subsequent census, it was then possible to identify and record chewing damage for leaves that were produced since the last census. This procedure allowed for a cumulative measure of damage without repeatedly measuring the same leaves. Recording damage exclusively on new leaves was appropriate since leaves from previous censuses tended to accumulate little additional damage (Hakes unpubl.). The percent of total plant tissue damaged by leaf-chewing herbivores was estimated from this procedure.

Relative resistance is often measured as 1 – the proportion of damage lost to leaf-chewing herbivores (Fineblum and Rausher 1995, Fornoni et al. 2004) and as herbivore density for mining, sucking, or galling herbivores (Maddox and Root 1990). This operational measure of resistance assumes that plants are equally accessible to uniformly distributed herbivore populations, which is almost certainly not the case in natural environments. For this reason, we avoid using our direct measure of herbivore damage to infer ramet resistance. Instead, we quantified leaf toughness (LT) and concentration of total phenolics (TP), which are traits that are putatively associated with resistance. Tolerance is ideally measured as a fitness norm of reaction among clonal replicates subjected to a gradient of herbivore damage or density (Mauricio et al. 1997, Fornoni et al. 2004). Because our study focused on naturally occurring ramets of unknown genetic background, we could not measure tolerance directly. Instead, we measured traits shown to be associated with compensatory growth and photosynthesis in response to herbivory (i.e. tolerance) in *S. altissima* (leaf addition rate (LAR), leaf senescence rate (LSR), relative growth rate (RGR) and specific leaf area (SLA); Meyer 1998). LAR and LSR were measured as the number of leaves added or senesced per day and RGR was calculated as the difference in ln-transformed height divided by the number of days between measurements (Meyer 1998).

In the summer census, we collected leaf tissue samples for assessment of LT, TP and SLA. Three leaves were collected haphazardly from the upper two-thirds of the stem. LT, measured as the average force needed to push a metal rod through leaf tissue, was assessed using a penetrometer (Siska et al. 2002). The collected leaves were transported to the laboratory on dry ice, lyophilized (72 h) and weighed. Leaf area was calculated from digital photographs of each leaf using ImageTool. SLA, or leaf area per unit dry leaf mass, was calculated. SLA is positively correlated with mass-based photosynthetic rate and higher SLA in re-growth leaves allows damaged plants to gain more leaf area for a given biomass investment (Meyer 1998). Leaves were ground with a mortar and pestle and we determined the concentration of TP (micromoles of ferulic acid equivalent per gram dry weight) in leaf samples using Folin-Ciocalteau spectrophotometry (Haynes et al. 2007).

Measurements of edaphic conditions were obtained for each ramet during mid-summer. A 25-cm deep soil core was extracted from two random locations 0.5 m from the target ramet and the top 5 cm of the cores were discarded. We combined the core samples, obtained their wet and dry weights, and computed the percent soil moisture. Soil pH was determined with a bench-top pH meter after mixing 10 g of dried soil sample with 100 ml deionized water for an hour, and then allowing the mixture to sit an additional hour. Percent total nitrogen content in soil was determined using a dry combustion procedure. Due to logistic constraints, soil pH and N analyses were conducted on every soil sample from only one early- and one late-successional field and on 20 randomly chosen soil samples from the remaining fields.

We assessed the neighboring plant community by randomly placing two 0.25 × 0.25 m sampling frames within a 0.5 m radius of each ramet during mid-summer. This distance largely encompasses the rhizosphere of a goldenrod ramet (Meyer and Schmid 1999), as well as its closest neighbors. The stem density of all neighboring goldenrods, other forbs, grasses and woody plants inside the frames were totaled and percent ground vegetative cover (i.e. goldenrods, other forbs and grasses) was estimated. Digital photographs of the canopy were taken with a camera and 0.42× fisheye lens and percent canopy cover (an indicator of light availability), was measured using light analyzer.

Data analysis

We first tested whether goldenrod ramet defense levels and local environmental conditions varied significantly within individual fields and between early- and late-successional fields using separate ANOVAs for each variable. Because both types of successional stages were not replicated within each field, our design was not fully factorial. Thus, a nested ANOVA was used in which independent fields were nested within a common successional stage. Tests were performed using Systat 11. All variables (Table 1) required transformations to normalize distributions with the exception of ramet height, LT and TP. Percent ground vegetative cover, canopy cover, and soil moisture were arcsine square-root transformed and percent leaf damage was logit transformed. All remaining variables were ln-transformed. We also performed sequential Bonferroni corrections to α to control for an inflated type I error rate associated with multiple tests. Because with so many tests ($n = 17$) this approach is quite conservative (Garcia 2004), we also emphasize effect sizes (i.e. the proportional difference between treatment means).

To test the predictions that plant traits and environmental variables in late-successional fields are more strongly spatially structured than in early-successional fields, we calculated Moran's I coefficients of autocorrelation separately for each variable at 10 distance classes using the spatial analysis program Passage ver. 2. (Rosenberg 2008). Moran's I is similar to Pearson's r in that $0 > I \geq -1$ indicates a negative autocorrelation (nearest neighbors are most dissimilar), $0 < I \leq 1$ indicates a positive autocorrelation (nearest neighbors are most similar), and the strength of autocorrelation increases with the absolute value of I. Our objective was to examine patterns of autocorrelation for suites of similar traits in early- and late-successional fields. Therefore, variables were grouped into like categories of putative defense traits (SLA, RGR, LAR, LSR, LT, TP), fitness-related traits

Table 1. Effect of field successional-stage (early vs late) on goldenrod fitness traits, herbivore damage, putative defense traits, neighbor variables and edaphic variables (mean ± SE). F-statistic and p-value determined from separate nested ANOVAs (field (n = 3) nested within successional stage (n = 2); Methods). Proportion of ramets flowering was calculated using t-test with DF = 4.

Trait	Early	Late	$F_{1,4}$ φ	p
Fitness				
Ramet height (cm)	152.59 ± 7.33	100.21 ± 6.36	29.27	0.006*
Ramet diameter (mm)	9.33 ± 2.97	5.00 ± 0.39	5.81	0.074
Proportion of ramets flowering	0.75 ± 0.06	0.33 ± 0.10	3.38 γ	0.028
Inflorescence biomass (g)	12.84 ± 1.19	9.77 ± 0.27	2.74	0.173
Damage				
% leaf tissue damaged	8.01 ± 3.75	10.51 ± 2.03	0.33	0.595
Defense traits				
LT (g)	102.20 ± 5.66	61.67 ± 11.14	10.85	0.030
TP (mmoles g^{-1})	369.46 ± 23.37	258.94 ± 66.04	2.76	0.172
LAR (no. day^{-1})	1.99 ± 0.47	0.72 ± 0.14	11.90	0.026
LSR (no. day^{-1})	1.29 ± 0.18	0.83 ± 0.05	16.06	0.015
RGR (cm^1 cm^{-1} day^{-1})	$7.2e^{-3} \pm 1.3e^{-3}$	$5.4e^{-3} \pm 3.3e^{-3}$	12.22	0.025
SLA (cm^2 mg^{-1})	0.15 ± 0.00	0.18 ± 0.02	4.59	0.099
Neighbor variables				
Total stem density (0.0625 m^2)	19.17 ± 5.23	9.28 ± 1.30	4.87	0.092
% ground vegetative cover	69.37 ± 5.22	41.06 ± 11.73	5.25	0.084
% canopy cover	8.80 ± 0.80	30.76 ± 12.62	2.70	0.176
Edaphic variables				
Soil % moisture	14.75 ± 2.42	14.10 ± 1.45	0.03	0.881
Soil pH	6.38 ± 0.18	6.77 ± 0.44	0.47	0.530
Soil total % nitrogen	0.13 ± 0.02	0.11 ± 0.01	0.74	0.439

φ = analyses were performed using transformed data (Methods).
γ = t-statistic.
*p-values < the critical level of α of 0.05 following sequential Bonferroni corrections.
SLA = specific leaf area, RGR = relative growth rate, LAR = leaf addition rate, LSR = leaf senescence rate, LT = leaf toughness, TP = total phenolics.

(ramet height, diameter, inflorescence weight), edaphic variables (soil moisture, pH, N), neighbor variables (canopy cover, ground vegetative cover, stem density), and herbivore damage. For each site and trait category, we computed the mean Moran's I at each distance class from the individual variables that make up that category. Differences in autocorrelation between early ($n = 3$) and late ($n = 3$) successional fields for a particular category were assessed by comparing the mean Moran's I ± 95% CI (mean of the site means) across distances. We conducted t-tests using Systat 11 to assess whether the strength of autocorrelation differed from zero, and differed between early- and late-successional fields at each distance class. Sequential Bonferroni corrections were made to α to account for multiple, non-independent tests.

We tested the predictions that defense traits were correlated with environmental variables, tolerance traits were negatively correlated with resistance traits, and defense traits were positively correlated with fitness traits. An important caveat associated with examining correlations among variables in nature is that the presence of significant autocorrelation implies that data points are not independent (Legendre 1993). To account for potential non-independence, we used partial Mantel's tests to assess the partial correlation between the distance values of two variables (e.g. damage and canopy cover) while controlling for the effect of spatial distance. The partial Mantel coefficient, r_M ranges from –1 to 1, but is generally lower and not directly comparable to Pearson's r coefficient (Fortin and Dale 2005). Instead, the magnitude of r_M is to be used in a comparative way with other r_M values (Fortin and Dale 2005). For each field, we performed partial Mantel's tests between each defense trait (or damage) and each fitness-related trait and environmental variable. We also performed partial Mantel's tests among defense traits for each field. Whenever r_M was found to be significant, we performed a follow-up test to determine the nature of the association between the distance values of two variables. We performed a Pearson's correlation analysis on the raw data that would give an indication of whether the association was due to a positive or negative correlation between the two variables. Partial Mantel tests were performed in Passage ver. 2 (Rosenberg 2008) and correlation analyses were conducted using Systat 11. Meta-analyses were used to summarize stage-specific relationships between all possible pairs of defense traits and environmental variables, defense traits and fitness traits, and among defense traits. Partial Mantel's (r_M) coefficients from each field were grouped by stage (early $n = 3$ and late $n = 3$) to yield a mean effect size r_M ± 95% CI. Using this approach, we tested the prediction that the magnitude of relationships (i.e. r_M) between defense traits and fitness-related traits, defense traits and environmental variables, and among defense traits differed from zero and differed between stages. Meta-analyses were performed using Comprehensive Meta Analysis ver .2 (Borenstein et al. 2005). Sequential Bonferroni corrections to α were made to account for multiple tests.

Results

Among the 17 variables examined in this study, early- and late-successional fields differed by an average of 70 ± 16% in trait values (Table 1). Goldenrod ramets in late-successional fields grew 34% shorter and had a stem diameter 46% smaller than ramets in early successional fields ($p < 0.05$, Table 1). Relative to ramets in early-successional fields, 56% less ramets flowered in late-successional fields and those that flowered had 24% lower inflorescence biomass ($p = 0.028$). We also note here that for four of our six defense traits (LT, RGR, LAR, LSR), the uncorrected p-values for the test for differences between the two successional stages was less than 0.05. All putative defense traits had greater mean values (i.e. RGR = 10%, LAR = 141%, LSR = 44%, LT = 63%, and TP = 40% greater) in early- than in late-successional fields with the exception of SLA which was 25% greater in the latter field type. With regard to neighbor variables, late-successional fields had a 52% lower density of neighboring stems, 41% lower ground vegetative cover, and 260% greater canopy cover than early-successional fields. On the contrary, edaphic conditions (soil moisture, pH and nitrogen levels) were quite similar between early and late successional fields (mean difference: 9 ± 4%). Finally, percentage of leaf area damaged by chewing herbivores (various grasshoppers) averaged 8.0 ± 3.7% (range: 0 – 51%) and 10.5 ± 2% (range: 0 – 62%) in early and late fields, respectively, but the difference in damage was not significant. Other types of herbivores and plant damage were scarce. Therefore, we focus solely on damage from leaf-chewing herbivores.

In addition to large effect size differences between early- and late-successional fields for the 17 variables in Table 1, there were also strong within-field spatial patterns in trait levels and the relationships among variables differed in important ways between successional stages. The distributions of trait levels, for all of the variables considered in Table 1 (with the exception of proportion of ramets flowering which was measured per field and not per ramet), were strongly spatially structured (statistically significant spatial autocorrelation at one or more distance classes in 69 of 96 cases). Goldenrods that were close neighbors expressed more similar trait values, and nearby locations tended to be more similar in environmental conditions, than goldenrods and locations that were far apart. For illustration, Fig. 1 shows the spatial variation in one variable, herbivore damage, for each of the six fields. On average, defense trait levels in late-successional fields exhibited strong, positive autocorrelations ($I > 0$) at 10 – 30 m, and strong, negative autocorrelations ($I < 0$) at 60 – 100 m (uncorrected p-values < 0.05 for eight of 10 distance classes; Fig. 2a). Defense traits in early-successional fields followed a similar pattern of positive autocorrelation at distances < 40 m and negative autocorrelation at distances > 40 m, but only exhibited significant negative autocorrelation at 90 m (Fig. 2a). As predicted when local adaptation and/or other non-random processes occur over successional time (Introduction), defense traits were an average of 7.2 ± 2.9 times more strongly autocorrelated (based on absolute values of Moran's I) in late-successional fields than in early-successional fields (uncorrected p-values < 0.05 for five of 10 distance classes), and this difference was significant at 20 m and 70 m (Fig. 2a). Neighbor and edaphic variables generally followed a similar trend of positive autocorrelation up to 30 m and negative autocorrelation beyond 60 m. However, the differences in strength of autocorrelation

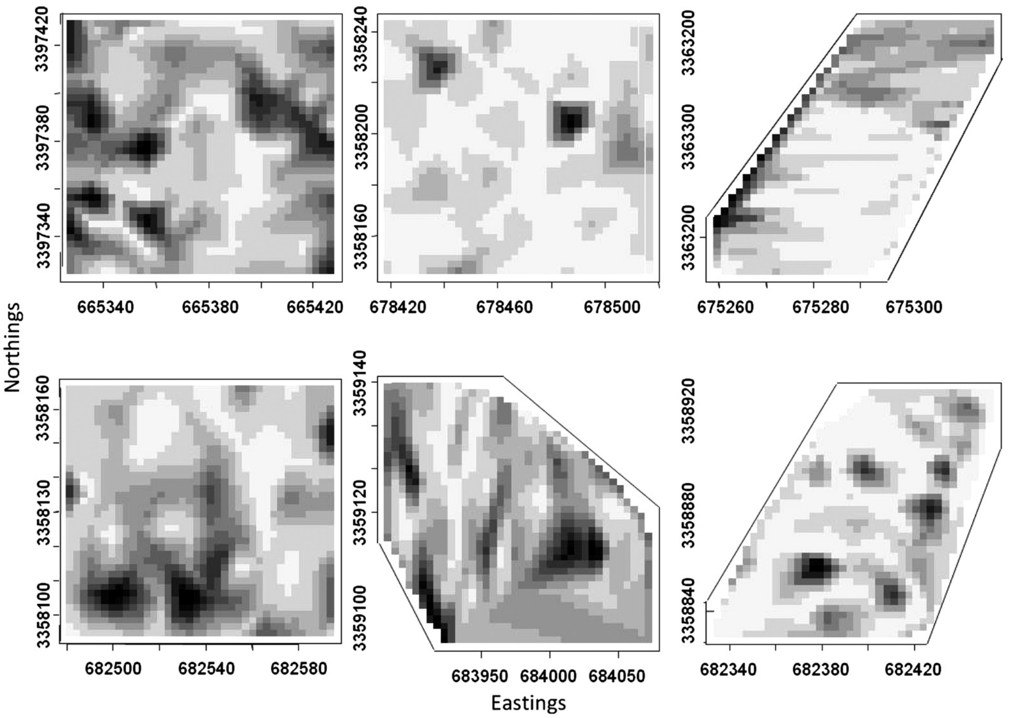

Figure 1. Distribution of damage intensity by leaf-chewing herbivores in three early-successional fields (top row) and three late-successional fields (bottom row). Each field is approximately 1 ha in size. Damage ranged from 0% of leaf tissue lost to herbivory (white) to 60% of leaf tissue lost to herbivory (black). Coordinates are given in meters in UTM zone 15N.

between early and late fields were not significant (Fig. 2b–c), and the only distance class where mean Moran's I differed significantly from zero was for edaphic variables at 10 m (Fig. 2c). Fitness-related traits and percent herbivore damage were not significantly autocorrelated and did not differ in strength between successional stages (Fig. 2d–e).

After correcting for spatial autocorrelation (using a partial Mantel's test), we found several important significant correlations among traits and environmental variables, and the strength of these relationships (indicated by r_M values) varied with successional stage. When r_M values were significant, the nature of these associations was revealed through Pearson's r correlation analyses using the raw data. Of the various putative resistance (LT, TP) and tolerance traits (SLA, RGR, LAR, LSR), only the tolerance traits were strongly associated with goldenrod ramet fitness traits (based on the mean ± 95% CI partial Mantel's r_M for sites within a successional stage). RGR and LAR were significantly correlated with ramet height in late-successional stages, but only LAR was correlated with height in early-successional stages (Fig. 3a). Inflorescence biomass was significantly correlated with LAR in early-successional fields and with LAR and LSR in late-successional fields (Fig. 3c). Correlations between tolerance and fitness traits in early- and late-successional fields did not differ statistically between successional stages, however, correlations between inflorescence biomass and LAR and LSR trended stronger (based on r_M values) in early- than in late- successional fields (Fig. 3c). For the partial Mantel r_M relationships that were significant, correlation analyses of the raw data indicated that tolerance traits were positively correlated with fitness-related traits (mean $r = 0.54 \pm 0.02$, $n = 17$).

The neighboring plant community was significantly associated with tolerance traits and damage levels only for a particular successional stage. The tolerance trait SLA was significantly associated with canopy cover and neighbor stem density in late-successional stages and these relationships were also stronger in late- than in early-successional fields (Fig. 3d–f). The relationship between damage and ground vegetative cover was significantly stronger in early- than in late-successional fields (Fig. 3e). In each late-successional field, SLA was positively correlated with canopy cover (mean $r = 0.50 \pm 0.09$) and negatively correlated with neighbor stem density (mean $r = -0.43 \pm 0.07$). Damage was positively correlated with neighbor stem density in 2/3 of early-successional fields ($r = 0.22$, $r = 0.07$) and negatively correlated to neighbor stem density in the remaining field ($r = -0.25$).

Regarding edaphic conditions, we found no significant relationships between soil moisture and defense-traits or damage level for either successional stage (Fig. 3g). Because soil pH and percent total nitrogen were measured completely for only one early- and one late-successional field (Methods), we could not assess whether correlations involving these variables were characteristic of the successional stage, or were unique to the particular field. In the late-successional field, the only significant relationship was between soil N and TP (Fig. 3h) and the direction of this relationship was positive ($r = 0.216$; based on correlation analyses using raw data). In the early-successional field, SLA had a significant negative association with soil N ($r = 0.079$; Fig. 3h) and a significant positive association with soil pH ($r = 0.04$; Fig. 3i).

Finally, contrary to predictions about tradeoffs between defense traits, relationships between putative resistance and

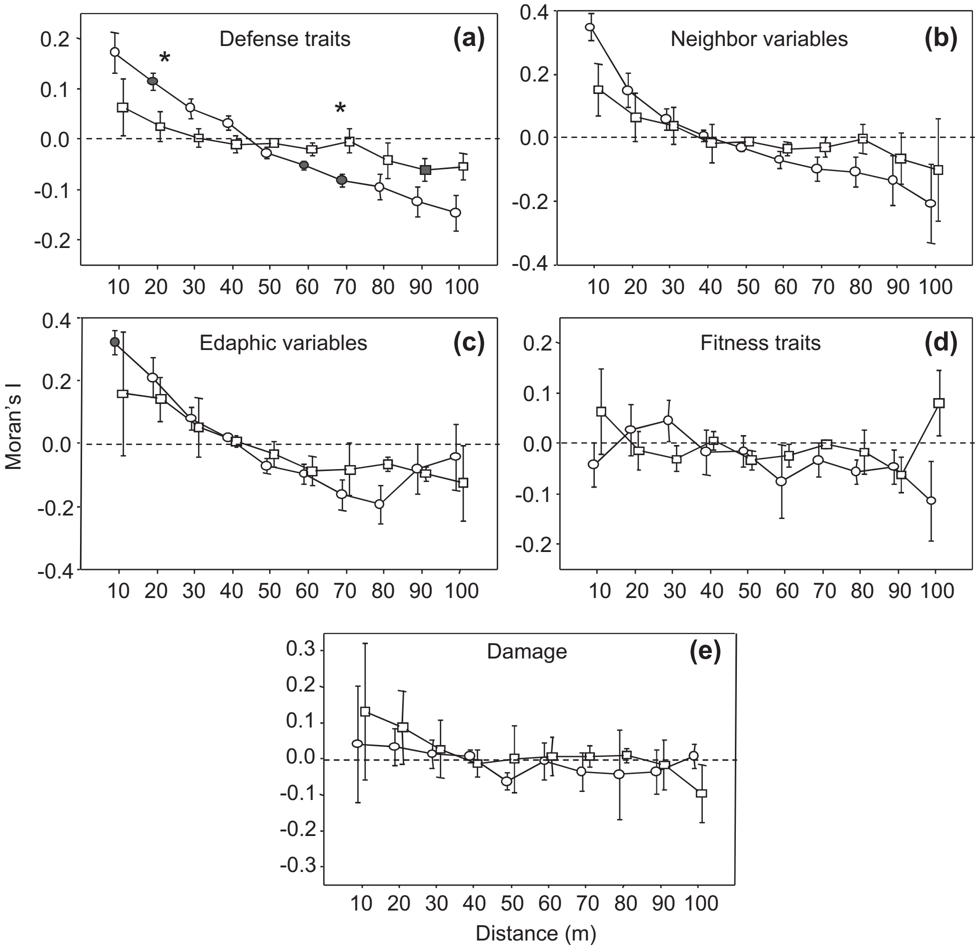

Figure 2. Correlograms of spatial autocorrelation for (a) defense traits (n = 6); (b) neighbor variables (n = 3); (c) edaphic variables, n = 3; (d) fitness-related traits (n = 3); and (e) herbivore damage across 10 m distance classes. Moran's I coefficient of spatial autocorrelation (mean ± 95% CI) for three early (squares) and three late (circles) successional fields. Filled shapes represent coefficients that are significantly different from zero, and * denotes coefficients that are significantly different between early- and late-successional fields. Sequential Bonferroni corrections to α were made to account for multiple, non-independent comparisons.

tolerance traits were weak after removing spatial autocorrelation ($r_M < 0.10$, Table 2). The only exception was the significant positive correlation between LAR and LSR, in early ($r_M = 0.455$), and late ($r_M = 0.612$) stages (Table 2). Lastly, damage levels were not significantly correlated with defense traits.

Discussion

To our knowledge, our study is the first to find evidence that environmental heterogeneity and its changes over the course of old-field succession may influence the expression of diverse types and levels of plant defense traits within natural plant populations. As predicted when non-random processes such as local adaptation influence the spatial structure of resistant and tolerant plants over time, plants exhibited a greater similarity in defense trait levels as the distance between plants decreased. Furthermore, this pattern was found to be stronger in late- than in early-successional fields. The biotic environment (i.e. neighboring plant variables) was found to be more important in influencing the spatial distribution of plant defenses than the abiotic environment (i.e. edaphic variables), and the relationships between neighboring plants and defense traits differed with respect to field successional-stage. Specifically, SLA was more strongly correlated with canopy cover and neighbor stem density in late-successional fields, and damage was more strongly correlated with ground vegetative cover in early-successional fields. Our data also suggests the possibility of a successional shift in defense expression, with increased levels of traits conferring tolerance later in succession.

Many plant species, particularly clonal species, exhibit morphologies, defense levels, etc, that are more similar among nearest neighbors (i.e. positive spatial autocorrelation). Our finding that plants within 20 m of each other had similar defense trait values was similar to the findings by Andrew et al. (2007) and Covelo and Gallardo (2004) that neighboring *Eucalyptus* trees within 20 m and *Quercus* trees within 6 – 10 m, respectively, had similar levels of defense chemicals (i.e. positive spatial autocorrelation). The greater similarity of defense trait levels among goldenrods at short distances in late- than in early-successional fields may be due to the underlying spatial genetic structure of

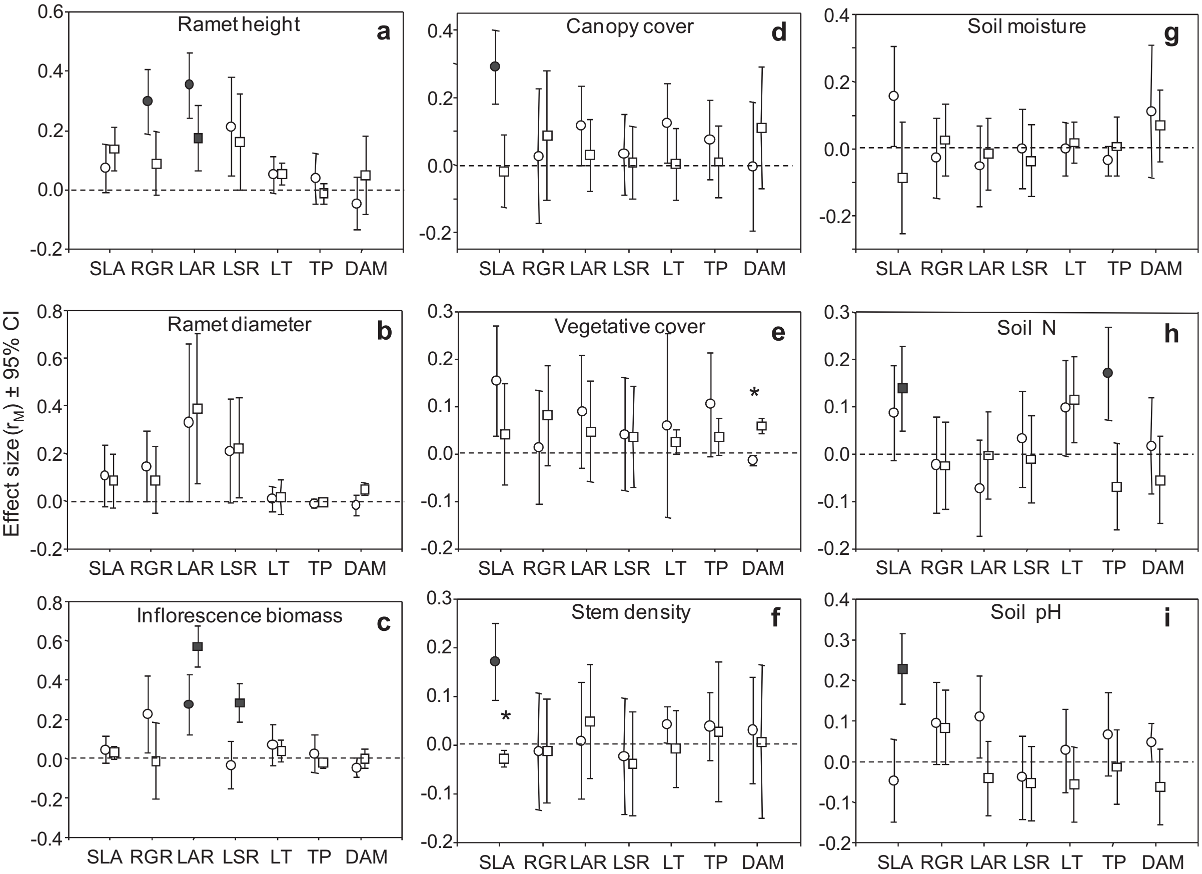

Figure 3. Relative strengths of relationships between each defense trait (or damage) and fitness-related traits (a) ramet height, (b) ramet diameter, and (c) inflorescence biomass, neighbor variables (d) canopy cover, (e) ground vegetative cover, and (f) neighbor stem density, and edaphic variables (g) soil moisture, (h) soil nitrogen, and (i) soil pH after controlling for spatial distance between individuals. Effect sizes are represented as mean partial Mantel's r_M ± 95% CI for three early (squares) and three late (circles) successional fields for variables (a–g). Partial Mantel's r_M ± 95% CI for soil N (h) and soil pH (i) were determined from only one early- and one late-successional field. Filled shapes represent correlations that were significantly different from zero based on meta-analysis (a–g) or permutation test (h–i). Sequential Bonferroni corrections to α were made to account for multiple, non-independent comparisons.

Solidago altissima. Studies examining spatial distributions of clonal plant and animal species have attributed their high positive autocorrelation to the expansion of genets over time (Hammerli and Reusch 2003). Goldenrod achenes are wind dispersed and not likely to be limited to the 1 ha scale of our study, thus, it is unlikely that dispersal limitation is influencing spatial patterns of *S. altissima* defense traits. However, vegetative growth can increase the clonal range of goldenrod genets over time (Hartnett and Bazzaz 1985, Maddox et al. 1989, Meyer and Schmid 1999, Wise et al. 2006). Thus, it is possible that the pattern of stronger autocorrelation of defense traits found in late-successional fields reflect a greater range of goldenrod clones.

Another explanation for the greater similarity in trait levels among nearest neighbors in late- versus early-successional fields is local adaptation to environmental variables which are themselves spatially autocorrelated (Legendre 1993). Of the three studies that have considered the spatial distributions of resistance traits (Covelo and Gallardo 2004, Brenes-Arguedas and Coley 2005, Andrew et al. 2007), two have suggested that these patterns may have been influenced by the spatial structure of environmental variables such as light availability (Covelo and Gallardo 2004, Brenes-Arguedas and Coley 2005). However, no explicit tests were performed in these studies to evaluate the relationships between environmental variables and defense levels.

Our study not only supports the growing body of evidence that neighboring plants can influence damage and defense expression, but also provides evidence that these relationships can vary in intensity over the course of succession. For example, the strong correlation between the tolerance trait SLA and canopy cover was only evident in late-successional fields where canopy cover was 2.6 times greater. There are several mechanisms that could explain this pattern. Canopy cover could indirectly affect tolerance trait levels if, for example, herbivore foraging increases in shaded habitats (Henriksson et al. 2003). However, the relationship between herbivore damage and canopy cover was extremely weak in late-successional stages (r_M = –0.005), providing little support to this explanation. More likely, the strong, positive correlation between SLA and canopy cover in late-successional fields suggests that SLA functions in tolerating low light conditions (Janse-ten Klooster et al. 2007) in addition to tolerating defoliation (Meyer 1998). It is known that physiological mechanisms that allow plants to tolerate herbivory may also allow plants to deal with a broader range

Table 2. Relative strengths of relationships (r_M) between all possible pairs of putative defense traits and damage after controlling for spatial distance between individuals. Partial Mantel's r_M are averaged for early (n = 3) and late (n = 3) successional fields.

		Defense traits					
		SLA	RGR	LAR	LSR	LT	TP
DAM	early	0.050	0.026	–0.042	–0.006	0.063	–0.041
	Late	0.061	–0.005	–0.047	–0.066	0.006	–0.040
SLA	early	.	0.075	0.007	–0.006	0.146	0.053
	late	.	0.003	0.045	0.071	0.063	0.044
RGR	early		.	0.046	0.031	–0.023	0.050
	late		.	0.122	0.010	0.044	–0.032
LAR	early			.	0.455*	0.005	0.003
	late			.	0.612*	0.006	0.074
LSR	early				.	–0.002	–0.031
	late				.	0.016	0.024
LT	early					.	0.082
	late					.	0.002
TP	early						.
	late						.

SLA = specific leaf area, RGR = relative growth rate, LAR = leaf addition rate, LSR = leaf senescence rate, LT = leaf toughness, TP = total phenolics, DAM = herbivore damage.
p-values (not shown) were calculated using Comprehensive Meta Analysis ver. 2.
*notes significance after sequential Bonferroni corrections to α.

of environmental stress (Chapin 1991, Siemens et al. 2003, Jones et al. 2006). Therefore, plant traits that promote tolerance to both herbivory and environmental stress may be adaptive and expressed at greater levels when both types of stress are present (Siemens et al. 2003, Jones et al. 2006).

The correlation between tolerance trait SLA and neighboring stem density was also statistically significant only for a particular successional stage. Interestingly, the relationship between SLA and neighboring stem density was significantly stronger in late- than in early-successional fields, even though stem density averaged 106% greater in early-successional fields. The negative correlations (from Pearson's r) between SLA and neighboring stem density suggest a possible tradeoff between SLA and competitive ability (Herms and Mattson 1992) that is only manifested in late-successional fields.

Another important neighbor effect involved the relationship between ground vegetative cover and damage that was significantly stronger (based on r_M values) in early- than in late-successional fields. We found that herbivore damage was positively correlated with ground vegetative cover in 2/3 of the early fields. This suggests that the greater percentage of neighboring goldenrods, other forbs, and grasses covering the understory in early-successional fields may attract and retain generalist herbivores, possibly by providing an increased concentration of resources for optimal foraging (Root 1973). Another possibility is that the early-successional plant community is more palatable than the late-successional plant community (Cates and Orians 1975, Reader and Southwood 1981) and that frequent contacts between goldenrod stems and palatable neighboring plants in high density areas promote associational susceptibility in early-successional fields. Experimental tests are needed to uncover the specific mechanisms responsible for the relationships between defense traits, damage, and neighbor variables in our system.

A novel insight from this study is the possibility that changes in the biotic environment over the course of succession may shift the adaptive value of defense expression from a resistance strategy to a tolerance strategy in our system. This suggestion is based on our findings that 1) the positive correlation between damage (commonly used to infer resistance; Methods) and ground vegetative cover was significantly stronger in early-successional fields (Fig. 3e), and 2) the significant positive correlations between the tolerance trait SLA and canopy cover and neighbor stem density were evident only in late-successional fields (Fig. 3d). In old-field and grassland habitats, succession results in a high turnover in community composition, including a decrease in density of forbs and grasses and an increase in woody plants and canopy cover (Hartnett and Bazzaz 1985). When suites of environmental stresses change predictably during succession (i.e. canopy cover increases and neighbor stem density and ground vegetative cover decreases) and plants are long-lived, then the optimal defense strategy may involve ontogenetic or plastic/induced changes to become increasingly more tolerant over time. Induced and ontogenetic shifts between resistance and tolerance expressions have been documented in many plants (Böege et al. 2007), but have not been examined in the context of successional changes in the environment.

The intriguing hypothesis that a successional shift in resistance and tolerance expression may be taking place warrants additional research. In a subsequent field experiment in which replicate goldenrod genets were transplanted into early- and late-successional fields, genets exhibited higher resistance and tolerance to herbivory in early- and late-successional fields, respectively (Hakes and Cronin unpubl.). Together these results suggest strong phenotypic plasticity in the expression of defense trait levels and that trait expression is subject to stage-specific environmental pressures. A succession-induced shift from a resistance to a tolerance strategy contradicts expectations from traditional plant-defense theory (Coley et al. 1985, Maschinski and Whitham 1989, Herms and Mattson 1992). This theory predicts that resistance should be higher in environments with greater environmental stress (i.e. late-successional fields), and growth and/or tolerance should be higher in environments with greater resource availability (i.e. early-successional fields). However, our findings do support recent defense theory that predicts tolerance may be more adaptive in stressful environments when traits serve dual purposes in tolerating herbivory damage and environmental stress, (Siemens et al. 2003). In our study, an increase in tolerance expression in more light-stressed, late-successional stages (Hakes and Cronin unpubl.) and significant positive associations between tolerance trait SLA and canopy cover (this study) suggests a dual role for goldenrod tolerance to herbivory. Clearly there is a need for more studies that evaluate defense theory in a successional context. Until now, successional changes in the environment have been neglected as an important mechanism influencing temporal changes in defense expression for long-lived plants.

An alternative explanation for the absence of significant relationships between SLA and canopy cover in early fields and between damage and ground vegetative cover in late fields could involve a statistical artifact. A priori, one might expect little variation in canopy and ground vegetative cover in early- and late-successional fields, respectively. This lack of variation in one of the variables could make it difficult to detect a significant relationship. However, coefficients of variation for canopy cover were similar in both successional stages (mean CV ± SE early = 0.86 ± 0.05, late = 0.73 ± 0.31), and contrary to the above prediction, coefficients of variation for ground vegetative cover were higher in late rather than early fields (early = 0.25 ± 0.03, late = 0.58 ± 0.12). These findings suggest that the weak correlations between SLA and canopy cover in early fields and between damage and ground vegetative cover in late fields were not an artifact of low statistical power.

This study adds support to the recent hypothesis that mixed patterns of plant resistance and tolerance may be maintained in natural populations when spatial and temporal environmental heterogeneity alters the expression of tolerance and resistance traits (Agrawal et al. 2006, Núñez-Farfan et al. 2007). This finding is contrary to conventional defense theory which has predicted through simple models that plant populations should eventually become fixed with the most adaptive defense trait or strategy (Mauricio et al. 1997). Instead, spatial patterns of defense traits are likely to be dependent on a plant's environmental context and may change in quantitative and qualitative ways during succession. For long-lived plants in successional habitats, the most adaptive defense strategy in response to this spatiotemporal variability in the environment may be to exhibit ontogenetic changes or phenotypic plasticity in defense strategies. We suggest that future plant defense research should consider incorporating a spatial and temporal approach to better understand the evolution of these traits in complex environments.

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