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Genetic diversity within a dominant plant outweighs plant species diversity in structuring an arthropod community

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Abstract. Plant biodiversity is being lost at a rapid rate. This has spurred much interest in elucidating the consequences of this loss for higher trophic levels. Experimental tests have shown that both plant species diversity and genetic diversity within a plant species can influence arthropod community structure. However, the majority of these studies have been conducted in separate systems, so their relative importance is currently unresolved. Furthermore, potential interactions between the two levels of diversity, which likely occur in natural systems, have not been investigated. To clarify these issues, we conducted three experiments in a freshwater sand dune ecosystem. We (1) independently manipulated plant species diversity, (2) independently manipulated genetic diversity within the dominant plant species, *Ammophila breviligulata*, and (3) jointly manipulated genetic diversity within the dominant plant and species diversity. We found that genetic diversity within the dominant plant species, *Ammophila breviligulata*, more strongly influenced arthropod communities than plant species diversity, but this effect was dependent on the presence of other species. In species mixtures, *A. breviligulata* genetic diversity altered overall arthropod community composition, and arthropod richness and abundance peaked at the highest level of genetic diversity. Positive nonadditive effects of diversity were detected, suggesting that arthropods respond to emergent properties of diverse plant communities. However, in the independent manipulations where *A. breviligulata* was alone, effects of genetic diversity were weaker, with only arthropod richness responding. In contrast, plant species diversity only influenced arthropods when *A. breviligulata* was absent, and then only influenced herbivore abundance. In addition to showing that genetic diversity within a dominant plant species can have large effects on arthropod community composition, these results suggest that understanding how species diversity and genetic diversity interact to influence community structure may be critically important for predicting the consequences of biodiversity loss.

Key words: Ammophila breviligulata; *arthropod diversity; biodiversity–ecosystem function; genetic diversity; Great Lakes; nonadditive effects; sand dunes; species richness.*

Introduction

Understanding how declines in plant biodiversity influence the diversity of higher trophic levels is an important challenge for predicting the consequences of global biodiversity loss. Most experimental work to date has examined how reductions in plant species richness influence arthropod assemblages in terrestrial ecosystems and generally shows arthropod diversity declines with reduced plant species richness (Siemann et al. 1998, Knops et al. 1999, Haddad et al. 2009). However, even before a plant species is lost from the community, it likely undergoes losses in genetic diversity due to shrinking population sizes (Ellstrand and Elam 1993). Recent work has documented that arthropod diversity is also sensitive to declines in genetic diversity within a species (Crutsinger et al. 2006, 2008, Johnson et al. 2006, Cook-Patton et al. 2011), and the effects of reduced genetic diversity in dominant or foundation species are expected to be especially severe (Whitham et al. 2006, Hughes et al. 2008).

Despite the fact that both plant species diversity and genetic diversity have documented effects on arthropod community structure, little is known about their relative importance. Because phenotypic variation among genotypes is expected to be lower than variation among species, one might predict a weaker effect of genetic diversity relative to species diversity. Only one study to date has directly compared the two levels of diversity in a single experiment. Cook-Patton and colleagues (2011) found that plant species diversity had a stronger effect on arthropods than genetic diversity within a single, nondominant plant species. However, results from independent experiments that manipulated genetic diversity suggest that when these results are compared to those from other experiments that manipulated species diversity, genetic diversity can rival or exceed

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the effects of species diversity (Crutsinger et al. 2006, Johnson et al. 2006). Thus, further comparative experiments are needed.

Furthermore, it is unknown if genetic diversity within a species and plant species diversity interact to influence arthropod communities. Dominant and foundation species play key roles in structuring communities (Angelini et al. 2011); therefore, arthropod responses to genetic diversity within a dominant plant species may be especially strong. However, the presence of other plant species may modify the effect of the dominant species on community structure. For example, the presence of other species could dilute a positive effect of genetic diversity on arthropod diversity (e.g., by making it more difficult for some arthropods, such as specialist herbivores or decomposers, to respond to the dominant species) or may interact with genetic diversity to strengthen the effect (e.g., by increasing the range of available resources). Whether these effects occur and whether they depend on levels of genetic diversity or species diversity is unknown, as experiments simultaneously manipulating plant species diversity and genetic diversity are lacking.

Here, we investigated how genetic diversity within a dominant plant species, *Ammophila breviligulata*, and species diversity independently and interactively influenced arthropod community structure in freshwater sand dunes. In addition to documenting patterns of arthropod response, we also determined whether additive or nonadditive effects of diversity influenced these responses. Specifically, we addressed the following questions: (1) How do plant species diversity and genetic diversity within a dominant plant species independently influence arthropod community structure? (2) Do plant species diversity and genetic diversity within a dominant species interact to affect arthropod community structure?

Methods

To test how plant species diversity and genetic diversity within a dominant species affect arthropod community structure, we established three field experiments. We tested for effects of each level of plant diversity on arthropod community structure using *independent plots* that manipulated either genetic diversity within the dominant plant species or plant species diversity. Then, to test for interactions between the two levels of diversity, we established *crossed plots* where genetic diversity within the dominant species and plant species diversity were simultaneously manipulated. When significant effects of plant diversity on arthropod communities were detected, we determined whether the effects were additive (predictable from responses to plant monocultures) or nonadditive (affected by emergent properties of diverse plant communities). These distinctions provide a first approximation of the mechanisms underlying biodiversity effects. For example, if arthropod diversity increases because of the inclusion of certain plant species in the community (Hutchinson 1959, Strong et al. 1984), the response can be predicted from arthropod responses to component plants in monoculture (an additive diversity effect). However, if the effect cannot be predicted from arthropod responses to component plants in monoculture (a nonadditive diversity effect), arthropods are responding to other complex traits of the diverse community, such as over-yielding in primary productivity or increases in the structural diversity of the community (Dennis et al. 1998, Halaj et al. 2000) caused by increased plant diversity.

Independent plots provided baseline expectations for the effect of plant species diversity and genetic diversity on arthropod community structure. Deviations from this baseline in crossed plots may be a result of two nonmutually exclusive effects: (1) interactions between diversity levels, evidenced by statistically significant genetic diversity × species diversity interactions in the crossed plots or (2) context-dependent effects of diversity, such that the effect of either species diversity or genetic diversity is different in crossed plots and independent plots, absent an interactive diversity effect. The latter effect indicates that the response to diversity depends on the *presence of other plant species*, but not necessarily on the *amount of diversity*.

Study system.—The three experiments were established in 2008 in the Lake Michigan dunes at Sleeping Bear Dunes National Lakeshore (44°43.689′ N, 86°07.369′ W; see Plate 1). Plant communities and arthropods were surveyed monthly from May to August 2010. Great Lakes sand dunes support plant communities of relatively low species richness (1–5 species/m^2 [K. M. Crawford, *unpublished data*; Cowles 1899, Lichter 1998]), and natural populations of the dominant plant, *Ammophila breviligulata*, typically include 1–3 genotypes/m^2 (Fant et al. 2008). The importance of genetic diversity within *A. breviligulata* is of particular interest, as commercially available material for restoration is generally monotypic (Fant et al. 2008). During primary succession, *A. breviligulata* acts as an ecosystem engineer by colonizing the dunes and stabilizing sand, which allows other species that are less tolerant of sand burial to colonize (Olson 1958). Such low diversity makes this an ideal ecosystem for realistic, yet feasible manipulations of plant diversity.

Plant material.—We collected plant material for the common garden experiments from Sleeping Bear Dunes National Lakeshore during July 2007. For the genetic diversity manipulations, ramets of *Ammophila breviligulata* were collected in a roughly 2-m^2 area from 14 source populations and propagated at VansPines Nursery, Holland, Michigan, USA. Despite collecting *A. breviligulata* plant material from such a small area within the 14 populations, our collections from each population were composed of more than one genotype (Crawford and Rudgers 2012). Increasing the number of source populations of *A. breviligulata* significantly increased

plot-level genetic diversity (as measured by inter-simple sequence repeat (ISSR) markers following Fant et al. [2008], details in Crawford and Rudgers [2012]). Therefore, instead of manipulating genetic diversity by changing the number of *A. breviligulata* clones in a plot, we manipulated genetic diversity by changing the number of *A. breviligulata* source populations included in a plot. The 14 populations stretched across 40 linear kilometers of Lake Michigan coastline and were separated from each other by at least 1 km. In some systems, collecting plant material across such a large spatial scale may raise genetic diversity in the experimental treatments to a level not expected to occur locally (see Tack et al. 2012). However, *A. breviligulata* disperses through water following wave action along the coast (Maun 1984). Therefore, our collection of genetic material likely represents high levels of genetic diversity that are possible after a colonization episode. For the species diversity manipulations, nine additional native species were collected, including four grasses (*Calamovilfa longifolia*, *Elymus canadensis*, *Koeleria pyramidata*, and *Schizachyrium scoparium*), four woody species (*Arctostaphylos uva-ursi*, *Prunus pumila*, *Vitis riparia*, and *Salix cordata*) and a forb (*Asclepias syriaca*). These species all co-occur with each other and with *A. breviligulata* in plant communities past the first stage of primary succession. The woody species were propagated from cuttings collected from three to five mature individuals. The other species were propagated from seeds collected from a single population, with the exception of *C. longifolia* and *K. pyramidata*, which were collected near the common garden and directly transplanted into the plots. Cuttings and seeds were propagated by Richey Nursery Company, Spring Lake, Michigan, USA.

Common garden.—Plots were established where the National Park Service demolished homes to perform a restoration of the dune habitat. A total of 3012 individual plants were planted in 160 experimental plots. The plots were separated into three different areas (where three houses were demolished by the park service) that were spaced less than 50 m apart and surrounded by a matrix of native dune vegetation. These areas rested on the same dune, so were equidistant from the lake. Soils in the three areas were very similar: sand with no detectable C or N. Plots for all three experiments were completely randomized and spaced at least 2 m apart in a grid. All plots were surrounded by bare ground within the restored areas. To maintain diversity treatments, plots were weeded monthly during the growing seasons of 2008–2010. Further details on plot establishment are presented in Crawford and Rudgers (2012).

Independent plots.—For the species diversity experiment, plots contained one, three, or six species, excluding *A. breviligulata*, pulled from a pool of nine total species. For the genetic diversity experiment, plots contained one, three, or six source populations of *A. breviligulata* pulled from a pool of 14 total source populations. We minimized the potential for quasi-replication (the replication of more similar communities at higher diversity levels that confounds diversity effects with community composition [Huston and McBride 2002]) by maximizing compositional dissimilarity among replicate communities within each treatment (i.e., what types were present). For example, replicates with three species were allowed to have only two of the nine species in common. If a randomly generated treatment replicate deviated from this stipulation, the replicate was discarded and a new replicate was randomly generated. Diversity plots of three or six species/source populations were established at a density of 24 plants per 1.5×1.5 m plot using equal numbers of individuals for each species or source population. Each treatment was replicated seven times. Due to space and labor limitations, monocultures were half the size of diversity plots (1.06×1.06 m), but planted at the same density as individuals in the diversity plots (12 individuals per plot). These plot sizes are as large or larger than the plot size in several comparable experiments that have tested how plant diversity influences arthropod communities (circles 40 cm in diameter [Johnson et al. 2006], 1-m^2 plots [Crutsinger et al. 2006], circles 50 cm in diameter [Cook-Patton et al. 2011]). Every source population monoculture (14 total) and species monoculture (nine total) was replicated three times to allow the partitioning of additive vs. nonadditive effects.

Crossed plots.—We crossed three levels of species diversity (one, three, or six species excluding *A. breviligulata*) with three levels of genetic diversity within *A. breviligulata* (one, three, or six source populations). Each combination was replicated seven times for a total of 63 crossed plots. Replicates had 24 plants per 1.5×1.5 m plot, consisting of 12 individuals of *A. breviligulata* and 12 individuals of the other species. This mimics the natural density and composition of dune plant communities after the earliest stage of primary succession (K. M. Crawford, *unpublished data*). Each species or *A. breviligulata* source population was represented by equal numbers of individuals within each plot.

Arthropod sampling.—In 2010, we sampled arthropods using pitfall traps constructed from 50-mL centrifuge tubes left in place for five days. One tube was placed in the center of each plot during each survey. We collected all individuals per trap, identified them to morphospecies, and preserved them in 70% ethanol. All specimens were identified to order, except three individuals of subphylum Myripoda, and 80% were identified to family using Arnett (2000), Triplehorn and Johnson (2005), and Marshall (2006) (Appendix B). When possible, we also used these resources to assign morphospecies to functional groups (herbivore, predator, parasitoid, omnivore, detritivore, or non-feeding; Appendix B). Trapping was repeated monthly (May–August), but not more often to assure that arthropod populations were not depleted. Traps captured both

ground-dwelling and aerial arthropods (35% of individuals were adult Diptera), and community composition was similar to that of visually surveyed arthropods on plants (K. M. Crawford, *unpublished data*).

Statistical analyses

We have recorded data on every individual plant in the experiment multiple times a year since the experiment was established in 2008 (see also Crawford and Rudgers 2012). During the experiment, some plant mortality occurred. Statistical models incorporating mortality as realized diversity did not differ qualitatively from models using the initially planted diversity, so the latter models are presented for simplicity. Arthropod morphospecies recorded only once during the entire sampling (singletons, 25 total, 2% of all morphospecies, 0.1% of all individuals) were excluded from analyses. In addition to these analyses, we tested how herbivore and predator richness and abundance responded to diversity. However, since we were unable to assign 30% of morphospecies and individuals to feeding groups, these results should be interpreted with some caution. We report these methods and detailed results in Appendix A.

Community composition.—To test how community composition responded to our diversity treatments, we used permutational multivariate analysis of variance (PERMANOVA; PRIMER software; Anderson et al. [2008]). Data were transformed by adding one to each value so that similarities could be calculated for samples with no observed arthropods (four plots in July, one plot in August) (Clarke and Gorley 2006). PERMANOVA models incorporating square-root transformed data, which reduces the influence of highly abundant species (Clarke and Warwick 2001), provided qualitatively similar results. We used Bray-Curtis similarity to calculate pair-wise similarity between samples (following McCune and Grace 2002), and ran 9999 permutations. The full PERMANOVA models for the independent plots included either plant species diversity or genetic diversity within *A. breviligulata*, time, plot (nested in genetic diversity or species diversity), and all possible interactions. For the crossed plots, the model also included both diversity levels and the genetic diversity by species diversity interaction. Significant treatment effects were followed by pair-wise tests between treatment levels.

To visualize results, we performed ordination with nonmetric multidimensional scaling (NMDS) in PRIMER using Bray-Curtis similarity (Clarke and Gorley 2006). To ensure that stress values were equal across runs, NMS was performed at least three times with 999 restarts (Clarke and Warwick 2001). To determine which morphospecies were driving ordination patterns, we examined how much of the variation among groups was explained by each morphospecies using SIMPER (PRIMER; Clarke and Gorley 2006). For morphospecies that explained more than 10% of the variation among treatments, we tested how the abundance of the morphospecies was affected by the treatments using repeated-measures models, described next.

Arthropod abundance, richness, and evenness.—We tested for the effects of plant diversity and time on arthropod abundance, richness, and evenness using repeated-measures mixed models. Models treating species diversity and genetic diversity as categorical predictor variables rather than continuous predictor variables had a better fit based on AIC. For independent plots, models included fixed effects of either plant species diversity or genetic diversity within *A. breviligulata*, time, and all possible interactions (Proc MIXED, KR-corrected [SAS Institute 2009]). For crossed plots, models included both diversity levels and the genetic diversity $\times$ species diversity interaction, time, and interactions with time. Based on AIC, we used an unstructured variance–covariance matrix, and data met assumptions of normality of residuals and homogeneity of variances. In crossed plots, either no arthropods or only one individual was collected from 10 plots in July and one plot in August; these were excluded from the evenness analysis. To examine whether the arthropod diversity response was driven by arthropod abundance, we constructed rarefaction curves for each treatment (EcoSim 7.72, 10 000 iterations [Gotelli and Colwell 2001, Gotelli and Entsminger 2001]).

It is likely that arthropod abundance increases with plant biomass, independent of any effects of plant species diversity. In crossed plots, plant diversity significantly affected primary productivity (Crawford and Rudgers 2012). To test for an influence of plant biomass, we examined the correlation between arthropod abundance and plot-level biomass (Proc CORR [SAS Institute 2009]).

Additive vs. nonadditive effects.—When a statistically significant effect of plant diversity was detected, we tested whether the effect could be predicted by the response of the arthropod community in component monocultures (additive diversity effect) or if plants interact in diverse communities to cause an emergent response that cannot be predicted from monoculture values alone (nonadditive diversity effect). Monte Carlo simulations used to test for nonadditivity require data for individual plants in monoculture (e.g., Crutsinger et al. 2006, Johnson et al. 2006, Crawford and Whitney 2010), but we collected plot-level data using the pitfall traps. Therefore, we calculated the net biodiversity effect by utilizing Loreau and Hector's (2001) modified method (for an application, see Johnson et al. [2006]). For this analysis, we focused on the response of arthropods averaged over the 2010 growing season. First, the response in each monoculture plot was divided by the number of plants in monoculture (12), yielding a per-plant estimate. Then, the per-plant value was averaged over the three monoculture plots, yielding an average per-plant response for each species and source population. Monoculture plots were half of the size of diversity plots but consistently contained as many

TABLE 1. Results from repeated-measures mixed models testing the effects of plant diversity and time on arthropod abundance, richness, and evenness, and from PERMANOVA models testing how plant diversity influenced community composition.

Diversity manipulation and effects	Arthropod community responses											
	Composition			Abundance			Richness			Evenness		
	df	Pseudo F	P (perm)	df	F	P	df	F	P	df	F	P
SD only												
SD	2, 114	1.81	0.0686	2, 38	2.92	0.0663	2, 38	1.29	0.2874	2, 38	0.22	0.8041
Time	3, 114	24.802	0.0001	3, 36	31.41	<0.0001	3, 36	31.04	<0.0001	3, 35	7.76	0.0004
Time × SD	6, 114	1.14	0.2894	6, 47	1.55	0.1823	6, 47	0.44	0.8470	6, 45	2.04	0.0800
GD only												
GD	2, 159	0.96	0.4864	2, 53	0.66	0.5194	2, 53	3.43	0.0398	2, 52	0.89	0.4151
Time	3, 159	25.56	0.0001	3, 51	29.99	<0.0001	3, 51	71.86	<0.0001	3, 51	13.87	<0.0001
Time × GD	6, 159	0.76	0.7954	6, 67	0.55	0.7708	6, 67	1.01	0.4268	6, 67	0.87	0.5193
Crossed GD × SD												
GD	2, 162	3.29	0.0005	2, 54	3.17	0.0497	2, 54	3.11	0.0525	2, 47	2.70	0.0778
SD	2, 162	0.72	0.7500	2, 54	1.26	0.2921	2, 54	0.02	0.9771	2, 47	1.95	0.1530
GD × SD	4, 162	1.00	0.4746	4, 54	0.64	0.6389	4, 54	0.58	0.6808	4, 47	1.30	0.2823
Time	3, 162	64.83	0.0001	3, 52	57.82	<0.0001	3, 52	122.35	<0.0001	3, 48	16.55	<0.0001
Time × GD	6, 162	2.87	0.0001	6, 68	2.72	0.0199	6, 68	1.10	0.3729	6, 62	1.68	0.1406
Time × SD	6, 162	0.86	0.6959	6, 68	1.06	0.3932	6, 68	0.57	0.7549	6, 62	1.07	0.3876
Time × GD × SD	12, 162	0.82	0.8354	12, 86	0.90	0.5511	12, 86	0.68	0.7648	12, 79	0.94	0.5119

Notes: "Crossed GD × SD" included plots with both levels of diversity manipulated. Independent diversity manipulations are "GD only" and "SD only," and included plots where only genetic diversity (GD) within *Ammophila breviligulata* or species diversity (SD) was manipulated.

arthropod individuals. This suggests that arthropods do not respond to our differences in plot size: the same number of arthropods recruit to a patch regardless of the number of plants. This is consistent with our finding that arthropods do not respond to plant biomass (see *Results*), suggesting they are not attracted to the number of plants, but to the presence of a patch and the composition of the plant community. Since monoculture plots contained half the number of plants relative to diversity plots, and arthropods did not respond to the number of plants, monoculture per-plant averages for arthropod abundance and richness were halved before calculating the additive expectations to keep the number of arthropods per plant comparable between monocultures and diverse plots. We generated the additive expectation by matching the composition of individual plants in each of the experimental diversity plots with the expected per-plant response for each species or source population derived from monocultures data. To test for deviation from the additive expectation, we used distribution-free randomization tests (Edgington 1987, Manly 1991) with the factors plot, species diversity, genetic diversity, data set (observed vs. expected), and all possible interactions (Proc MIXED in the randomization wrapper with 9999 iterations [Cassell 2002]; SAS v. 9.1 [SAS Institute 2009]). A significant data set effect indicates a nonadditive effect of diversity is occurring. A significant data set × diversity effect indicates that the degree of nonadditivity differs among diversity levels.

RESULTS

We collected 13 608 individual arthropods representing 17 orders, >70 families, and >100 morphospecies. Families with the most individuals were ants (Formicidae >3300 individuals), biting midges (Ceratopogonidae >2700), ant-like flower beetles (Anthicidae >1700), and non-biting midges (Chironomidae >1100). Morphospecies identifications, functional group assignments, and abundances are provided in Appendix B, Table B1.

Independent plots

Community composition.—When manipulated independently, neither species diversity nor genetic diversity within *A. breviligulata* significantly affected arthropod community composition, although there was a marginally significant trend for species diversity (Table 1). The arthropod community shifted in composition though time (Table 1), and the shift was similar to that observed in crossed plots (discussed in *Crossed plots*).

Arthropod abundance, richness, and evenness.—Separately, neither species diversity nor genetic diversity significantly affected arthropod evenness (Table 1). There was a trend for species diversity to influence arthropod abundance (Table 1). Species monocultures contained 50% more individuals than three species treatments and 20% more than six species treatments. Genetic diversity did not influence arthropod abundance. However, arthropod morphospecies richness did respond to genetic diversity within *A. breviligulata* (Table 1, Fig. 1A). Unexpectedly, richness was lowest when there were three source populations of *A. breviligulata*: 19% lower than when six source populations were present (Tukey's HSD, $P = 0.05$) and 15% lower than when one source population was present (Tukey's HSD, $P = 0.05$). When the additive expectation was compared to the actual data, averaged over the field season, we detected a significant data set × genetic diversity effect ($P = 0.0057$). Specifically, when three

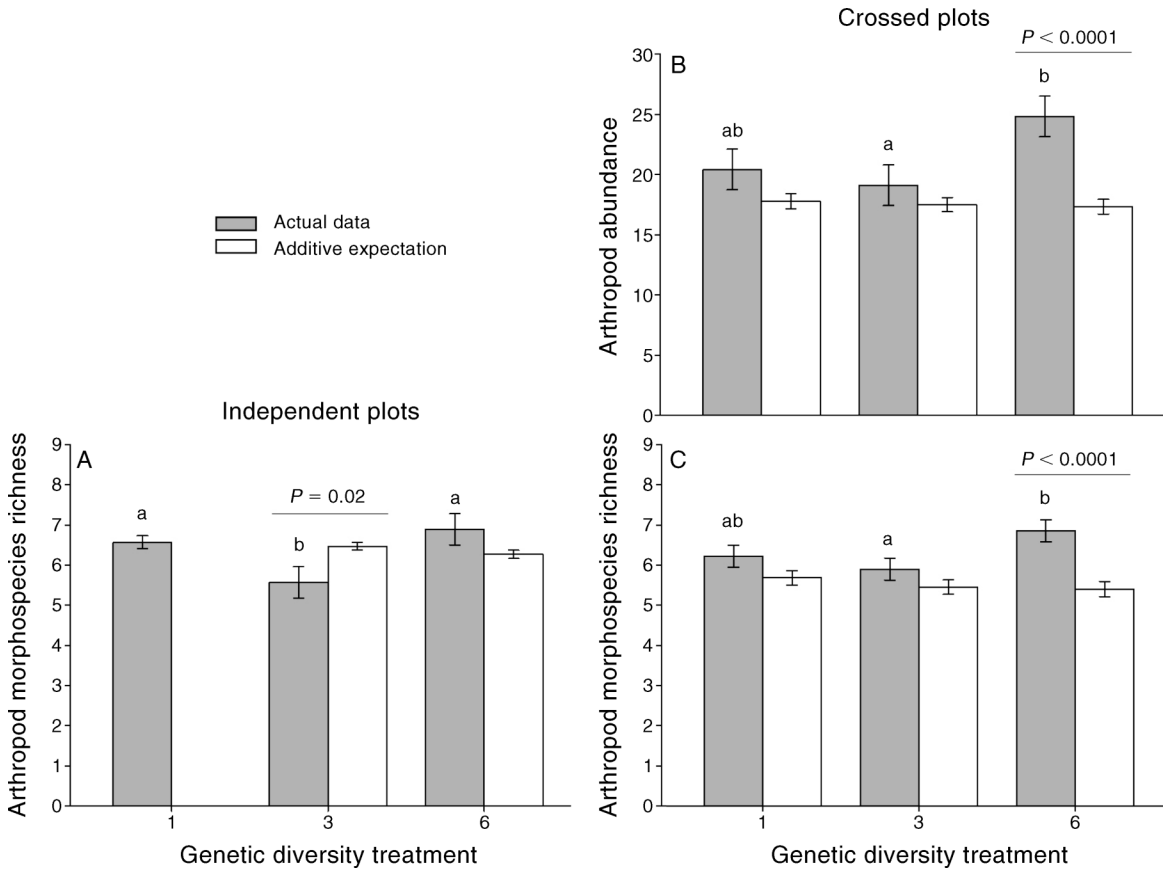

FIG. 1. Observed treatment means and the additive expectation for the effect of genetic diversity on arthropod morphospecies richness in both (A) independent and (C) crossed plots, and the observed and expected effect of genetic diversity on abundance in (B) crossed plots. Bars show mean ± SE. Observed treatment means that share a letter are not statistically significantly different from each other. Expected and observed pairs connected by an overhead bar labeled with a *P* value for the comparison (Tukey's HSD) are significantly different from each other, indicating a significant nonadditive effect of diversity. For the independent plot, there is no expected value for richness when one population of *A. breviligulata* is present, because values to conduct the additivity analysis were drawn from those monoculture plots.

source populations of *A. breviligulata* were present, the observed number of morphospecies was 14% lower than the additive expectation (Fig. 1A; Tukey's HSD, $P = 0.02$). Plant species diversity did not influence arthropod richness (Table 1). For a breakdown of the responses of each morphospecies to genetic diversity in the independent plots, see Appendix B, Table B2.

Response of herbivores and predators.—In contrast to the arthropod community as a whole, herbivore abundance was significantly affected by plant species diversity in independent plots ($F_{2,38} = 4.44$, $P = 0.0185$). Plots containing three species had the lowest number of herbivores. This, in turn, significantly lowered the herbivore to predator ratio in this treatment ($F_{2,35} = 3.55$, $P = 0.0395$). Herbivore richness and predator abundance and richness did not respond to diversity. Genetic diversity within *A. breviligulata* had no effect on either herbivore or predator abundance or richness. For more details, see Appendix A.

Crossed plots

Community composition.—Despite the lack of a significant effect in the independent manipulation, *A. breviligulata* genetic diversity significantly influenced the composition of arthropod communities in the presence of other species (Table 1, Fig. 2). Across all time points, arthropod communities in plant communities containing six source populations of *A. breviligulata* significantly differed in their composition relative to arthropod communities in plant communities containing either one ($t = 1.9677$, $P = 0.0021$) or three ($t = 2.1184$, $P = 0.0024$) source populations. These effects shifted through time, as indicated by a significant time × genetic diversity interaction (Table 1, Fig. 2). In May and June, arthropod communities in plant communities with six source populations of *A. breviligulata* were significantly different from arthropod communities associated with one source population (May, $t = 2.2748$, $P = 0.0011$; June, $t = 1.9872$, $P = 0.0021$) or

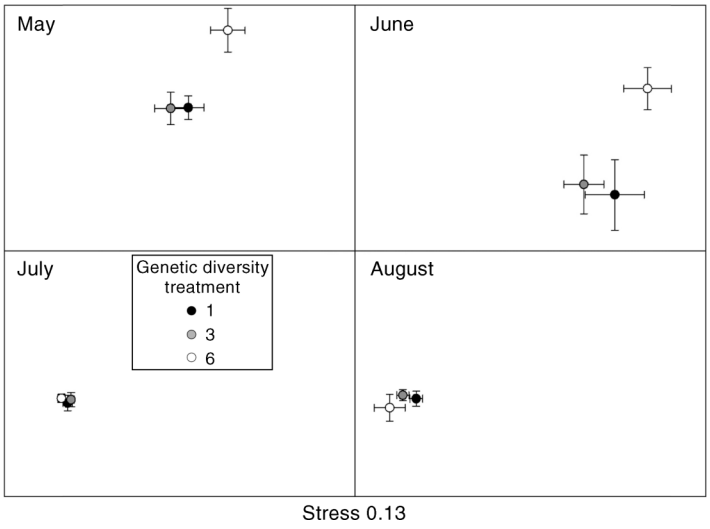

FIG. 2. Nonmetric multidimensional scaling ordination showing the interaction between *Ammophila breviligulata* genetic diversity and time on arthropod community composition in crossed plots. Centroids of the genetic diversity treatments are graphed for each month; error bars show ±SE. The distance between symbols reflects similarity in species composition. All subplots are graphed on the same scale for comparison among time points.

three source populations (May, $t = 2.4391$, $P = 0.0014$; June, $t = 2.1699$, $P = 0.0018$). In July, there was no significant effect of genetic diversity on arthropod community structure. In August, arthropod communities differed between plant communities with one vs. three source populations ($t = 1.4652$, $P = 0.0269$). In contrast to the significant effect of genetic diversity, species diversity did not affect overall arthropod composition in the crossed plots (Table 1).

The significant effect of genetic diversity in crossed plots was driven by five of the most abundant taxa, which together explained 68% of the dissimilarity in arthropod community composition between plant communities with three vs. six source populations and 66% of the dissimilarity in arthropod community composition between plant communities with one vs. six source populations. For both comparisons, a biting midge (Diptera: Ceratopogonidae) explained >20% of the dissimilarity, and an ant (Hymenoptera: Formicidae) explained an additional 17% of the dissimilarity. Three other arthropods—an ant-like flower beetle (Coleoptera: Anthicidae), an orbatid mite (Acari: Orbatidae), and a non-biting midge (Diptera: Chironomidae)—each explained ~10% of the dissimilarity. Throughout the growing season, declines in the numbers of the two midges and the ant-like flower beetle shifted community structure, with these three taxa collectively explaining 50% of the dissimilarity between May and August.

Three of the five morphospecies driving differences in arthropod community structure increased with genetic diversity. Specifically, orbatid mites were ~150% more abundant and non-biting midge were ~50% more abundant in plant communities with six source populations of *A. breviligulata* relative to plant communities with three source populations (mite $F_{2,54} = 3.52$, $P = 0.0364$; midge $F_{2,54} = 4.05$, $P = 0.0230$). Similarly, the biting midge was 100% more abundant with six source populations of *A. breviligulata* vs. one or three source populations ($F_{2,54} = 8.76$, $P = 0.0005$).

Arthropod abundance, richness, and evenness.—In the presence of other plant species, *A. breviligulata* genetic diversity affected arthropod abundance (Table 1, Fig. 1B). Plant communities with six source populations had nearly 30% more arthropods than plant communities with three source populations (Tukey's HSD, $P = 0.05$). When observed abundances were compared to the additive expectation, there was a significant data set (observed vs. expected) × genetic diversity interaction ($P < 0.0299$). Specifically, with six source populations of *A. breviligulata*, there were 43% more arthropod individuals than expected (Fig. 1B; Tukey's HSD, $P < 0.0001$). Arthropod abundance was not correlated with community-level plant biomass ($r = 0.11$, $F_{1,61} = 0.80$, $P = 0.38$), indicating that differences in arthropod abundance were not driven by diversity-mediated increases in primary production. Abundance peaked in June, averaging 40 individuals per plot, and was lowest in July, with 6.5 individuals per plot (Table 1). As with arthropod composition, the effect of genetic diversity on arthropod abundance varied through time, with the largest difference between diversity treatments in May (Table 1). There was neither a significant main effect of species diversity on abundance nor a significant interaction between species diversity and genetic diversity (Table 1). For a breakdown of the responses of each morphospecies to genetic diversity in the crossed plots, see Appendix B, Table B3.

Similar to the results from independent plots, there remained a strong trend for *A. breviligulata* genetic diversity to influence arthropod morphospecies richness in the presence of other plant species (Table 1, Fig. 1C). However, this trend took a slightly different form. Instead of mirroring the effect of genetic diversity in independent plots, the pattern for richness was more similar to the effect of genetic diversity on arthropod

PLATE 1. Native sand dunes adjacent to the experimental plots at Sleeping Bear Dunes National Lakeshore, Michigan, USA. Photo credit: K. M. Crawford.

abundance in crossed plots. Plant communities with six source populations of *A. breviligulata* contained 16% more species than plant communities with three source populations of *A. breviligulata* (Tukey's HSD, $P = 0.05$). As with abundance, when we compared the observed richness to the additive expectation, there was a significant data set × genetic diversity interaction ($P = 0.038$). There were 27% more morphospecies present than expected for communities containing six source populations (Fig. 1C, Tukey's HSD, $P < 0.0001$). Species accumulation curves show that species richness was beginning to level off with increased sampling effort, suggesting that the communities have almost been sampled to saturation (Appendix C; Fig. C1). The curves also showed that the observed differences in richness were primarily due to differences in abundances of individuals (correlation between abundance and richness, $r = 0.57$, $F_{1,61} = 28.51$, $P < 0.0001$).

Response of herbivores and predators.—In crossed plots, there was no effect of plant diversity on herbivore or predator abundance or richness or the herbivore to predator ratio. For more details, see Appendix A.

DISCUSSION

Genetic diversity within the dominant plant species, *Ammophila breviligulata*, played a larger role in structuring arthropod communities than plant species diversity. Genetic diversity influenced arthropod abundance, species richness, and community composition. Plant species diversity only marginally influenced arthropod composition and abundance, and affected herbivore abundance, all in the absence of *A. breviligulata*. Interestingly, although there was no interaction among levels of species diversity and genetic diversity, the influence of genetic diversity was strongly context dependent. In the presence of other species, genetic diversity in *A. breviligulata* significantly affected arthropod abundance and overall community structure. However, in the absence of other species, genetic diversity in *A. breviligulata* had no effect on arthropod abundance or community structure. It should also be noted that we observed strong intra-annual variation in arthropod community composition. Although it rarely interacted with plant diversity, temporal patterns were detected in every aspect of arthropod community composition that we examined. The large intra-annual turnover in arthropod community composition is likely due to ephemeral mass emergence patterns of abundant species in this system (e.g., lake midges). These large changes in community composition make it even more surprising to find consistently strong effects of genetic diversity on structure. Overall, these results demonstrate that the effects of plant diversity on other trophic levels can depend on other community properties, specifically, plant community composition. Our findings highlight the importance of incorporating both intra- and interspecific diversity into predictions of the effects of biodiversity loss.

Whether positive or negative nonadditive effects of genetic diversity were detected was also context depen-

dent. In the presence of other plant species (crossed plots), positive nonadditive effects of diversity caused arthropod abundance and richness to be greater than expected in plots with the highest level of genetic diversity, illustrating that the arthropod response was an emergent property of diverse plant communities. Arthropod abundance was not correlated with plant biomass, so it is possible that the nonadditive effects were driven by enhanced structural complexity or altered plant quality in more genetically diverse communities. In contrast, in the absence of other plant species (independent plots), we detected a negative nonadditive effect of diversity when three source populations of *A. breviligulata* were grown together. It is unclear what might underlie this effect, and it is unclear how common context dependency in nonadditive effects might be. More experiments would help shed light on these issues.

To our knowledge, this is the first study to show a stronger effect of plant genetic diversity than species diversity on arthropod communities in the same system. While this result is surprising, two prior studies have suggested that it may occur. Crutsinger et al. (2006) found that the effect size of genetic diversity on arthropod diversity (12 genotype populations compared to monocultures) for populations of *Solidago altissima* in old fields was nearly twice as large as the effect size of plant species diversity on arthropod diversity (16 plant species compared to monocultures) for prairies in the Cedar Creek biodiversity experiment (Siemann et al. 1998). Similarly, Johnson et al. (2006) found that genetic diversity within experimental patches of *Oenothera biennis* explained an amount of the variation in arthropod richness (16%) similar to manipulations of plant species diversity (15–23%; Siemann et al. 1998, Knops et al. 1999, Haddad et al. 2001). In contrast, the only other study to date that directly compared plant species diversity and genetic diversity in the same system reported a weaker effect of plant genetic diversity than species diversity on arthropod richness (Cook-Patton et al. 2011). In our experiment, we tried to ensure that the diversity levels in our experimental plots mimicked what is found naturally in the sand dune ecosystem. *Ammophila breviligulata* and the other species in our experiment co-occur on dunes that are just past the first stage in primary succession, when dunes are dominated by *A. breviligulata*. Here, species richness averages between 1 and 5 species/m^2 (K. M. Crawford, *unpublished data*), so our species diversity treatments reflect this natural variation. Ramets of *A. breviligulata* disperse through water following wave action along the coastline (Maun 1984), and we have also observed natural recruitment from seeds. Because of these recruitment mechanisms, populations can harbor high levels of genetic diversity at a small spatial scale despite *A. breviligulata*'s propensity to propagate clonally. One study of *A. breviligulata* population genetics in Illinois, where *A. breviligulata* was rare, found that populations naturally contained 1–3 genotypes/m^2 (Fant et al. 2008). This pattern does not appear to hold for Michigan populations, because we always observed more than three genotypes in 2-m^2 natural plots. In sum, there remains a possibility that our manipulation of genetic diversity may overestimate its effect by inflating genetic diversity within a small area, but more studies of *A. breviligulata* population genetics are needed to confirm this. Genetic diversity effects may also be particularly strong because *A. breviligulata* is a foundation species and an ecosystem engineer (e.g., Whitham et al. 2006). *Ammophila breviligulata* affects the physical environment by stabilizing sand (Olson 1958, Cheplick 2005). As found for other foundation species, it also likely increases soil moisture and reduces temperature (Breshears et al. 1997, 1998). In addition, *A. breviligulata* makes up a significant portion of total plant biomass on the dunes. By the end of the third growing season, *A. breviligulata* comprised 80% of the total aboveground biomass in crossed plots, providing most of the structure and resources available to arthropods.

The majority of studies investigating the effects of plant species diversity on arthropod community composition have reported increasing arthropod species richness with increasing plant species richness (e.g., Siemann et al. 1998, Knops et al. 1999, Wenninger and Inouye 2008). One reason we did not detect this positive relationship may be because there are very few specialist herbivores in our system. Theory predicts that arthropod species richness will be greater in diverse plant communities because the probability of including specialist herbivores (and their predators) increases (Hutchinson 1959, Strong et al. 1984). While highly specialist herbivores do exist in our system, they represent a very small fraction of the community (2 of 100 species and 0.1% of total individuals were specialists). Thus, it was unlikely that increases in plant species diversity would significantly increase arthropod richness through the response of specialists.

The significant effect of genetic diversity on arthropod community structure was driven by the responses of some of the most numerically dominant species in the system, specifically Chironomid and Ceratopogonid midges. These midges begin life as aquatic larvae and then emerge as adults *en masse* to mate. Midge adults typically do not feed. Based on their feeding ecology, it is highly unlikely that either midge responded to an increase in the types of food resources available at high levels of genetic diversity. Therefore, we hypothesize that the midges responded to plant structural complexity, which significantly increased with greater *A. breviligulata* genetic diversity (K. M. Crawford, *unpublished data*). A positive response to structural complexity is also supported by the nonadditive increase in arthropod abundance when six source populations of *A. breviligulata* were present. Structural complexity is a property of entire communities; therefore, the response of arthropods to structural complexity cannot be

predicted by their responses to plant monocultures. Many arthropods prefer structurally complex habitats (Halaj et al. 2000, Borges and Brown 2001, Topp et al. 2008, Pearson 2009). For example, Carabid beetle abundance was greater in areas with logging residue than on bare ground (Nitterus and Gunnarsson 2006), and spiders responded positively to plant structural complexity (Halaj et al. 2000).

In summary, our results demonstrate that genetic diversity within a dominant plant species can have a greater effect on arthropod community structure than plant species diversity. Given the identities of arthropod species that responded most strongly to our treatments (midges, mites), it may be that plant diversity primarily alters the distribution of arthropods across the landscape, with genetic diversity forcing different constellations of arthropod communities, rather than directly affecting the abundances of arthropods through plants' role in the food web. Although we suspect that mite abundances respond directly to the decomposition web, it remains unclear whether plant decomposition or dead midges drive them. In sum, our results suggest that to avoid the negative consequences of plant diversity loss for arthropod community structure and associated species interactions, it may be as important to preserve diversity in dominant plant species as it is to preserve plant species diversity. Unfortunately, current dune restoration practices are eroding natural levels of genetic diversity within populations of *A. breviligulata*, as commercially available propagules are generally monotypic (Fant et al. 2008). Notably, we found that the effect of *A. breviligulata* genetic diversity was strongest in the presence of other plant species, and mostly disappeared when *A. breviligulata* was grown alone. Therefore, to further improve our ability to predict the consequences of biodiversity loss, we must begin to account for both intra- and interspecific biodiversity.

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Supplemental Material

Appendix A

Response of functional groups to plant diversity (*Ecological Archives* E094-091-A1).

Appendix B

Response of each morphospecies to genetic diversity (*Ecological Archives* E094-091-A2).

Appendix C

Rarefaction curve for crossed plots (*Ecological Archives* E094-091-A3).