OIKOS 103: 505–518, 2003

Genetic diversity and invasibility: a test using a model system with a novel experimental design

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Weltzin, J. F., Muth, N. Z., Von Holle, B. and Cole, P. G. 2003. Genetic diversity and invasibility: a test using a model system with a novel experimental design. – Oikos 103: 505–518.

Biological invasion is one aspect of ecosystem function that may be controlled by the biological diversity of the invaded community, and there have been a number of recent studies that investigated relationships between diversity and invasibility. Most experimental studies report that higher species or functional group diversity increases resistance to invasion, but the role of genetic diversity is unknown. We used a model organism, *Arabidopsis thaliana* (Brassicaceae), to investigate relationships between genotypic richness and community invasibility by creating communities with 1, 2, 4, and 8 genotypes of *A. thaliana* at constant low (417 plants m^{-2}) and high (834 plants m^{-2}) densities, that once established, were invaded with a congener, *Arabidopsis suecica*. To reduce the potential effects of methodological confounding related to "sampling effects," "variance reduction effects," or confounding of abundance with diversity, we (1) created random communities from a relatively large pool of functionally and phenotypically similar genotypes, (2) evaluated individual and community traits across richness treatments, and (3) analyzed similarity of communities within treatments (for "quasi- replication") and between adjacent treatments (for "nestedness"). Genotypic richness had no effect on *A. suecica* demography (emergence, survivorship), size (biomass, rosette area), or reproductive potential (rates of bolting and fruiting or number and size of bolts). In contrast, the density of *A. thaliana* genotypes had strong effects on the size and reproductive potential of *A. suecica*, which suggests that characteristics of the recipient community other than genotypic richness (e.g. light) form the most important determinant of community invasibility. Individual- and community-level traits of community members (cover, biomass, survivorship) did not differ among richness treatments, and within- and between-treatment similarity was reduced (relative to other recent experiments) but not eliminated. We evaluate our results vis-a-vis recent analyses of diversity-invasibility experiments, and provide directions for future investigations of genetic diversity.

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Much interest in how diversity regulates ecosystem function has been generated in the last several years (Tilman et al. 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Tilman et al. 1997a, Hector et al. 1999, Kinzig et al. 2001, Loreau et al. 2002), primarily as a result of concern over increasingly depauperate biota due to intensive land use (Loreau et al. 2001) and the potential undesirable effects of this altered biota on ecosystem processes (McGrady-Steed et al. 1997). Biological invasion is one aspect of ecosystem function that may be controlled by the biological diversity of the invaded community (Elton 1958), and there have been a number of recent studies that investigated relationships between diversity and invasibility (see reviews by Hus-

Accepted 10 May 2003

ISSN 0030-1299

ton 1994, Levine and D'Antonio 1999, Hector et al. 2001, Wardle 2001, Levine et al. 2002).

Some of these diversity-invasibility studies have shown that as diversity of communities increases, invasibility of those communities decreases (Tilman et al. 1997a, Levine 2000, Naeem et al. 2000, Dukes 2002, Kennedy et al. 2002), although evidence to the contrary has also been found (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Palmer and Maurer 1997, Wiser et al. 1998, Smith and Knapp 1999, Stohlgren et al. 1999). Levine and D'Antonio (1999) noted that observational studies of natural systems tend to indicate a positive relationship between diversity and invasibility (Wiser et al. 1998, Stohlgren et al. 1999). In contrast, invader-addition studies that did not manipulate the resident communities, and experimental studies that directly manipulated the recipient plant communities, produced mixed support for this relationship (Robinson et al. 1995, Tilman et al. 1996, Palmer and Maurer 1997, Tilman et al. 1997a, Hector et al. 2001 and references therein). Some of these disparities may be resolved by considering the scale and location of the research: correlational studies (usually conducted across systems) may be unable to separate effects of diversity from covarying factors or environmental heterogeneity, whereas experiments can control confounding factors (as discussed by Naeem 2002).

One aspect of diversity seldom studied in correlational or experimental investigations of diversity–invasibility relationships is the role of genetic diversity. The majority of research to date has focused on the role of species (Naeem and Li 1997, Lavorel et al. 1999, Tilman 1999, Levine 2000, Dukes 2002, Kennedy et al. 2002) or functional groups (Naeem and Li 1997, Lavorel et al. 1999, Dukes 2001) in constraining invasions. However, underlying genetic differences between and within species represent a fundamental level of functional diversity that may unmask patterns of invasibility that exist at higher levels (Hooper et al. 2002). To our knowledge, few ecological studies have examined the role of genetic diversity, per se, on the structure and function of communities or ecosystems, let alone invasibility.

Arabidopsis thaliana (Brassicaceae) is a model organism well-suited to the assessment of relationships between genetic diversity and resistance to invasion. Its widespread use in molecular biology has provided the research community with numerous strains of well-known genetic and phenotypic variation (Pigliucci 2002). Moreover, the use of *A. thaliana* genotypes allows us to constrain differences (e.g. biomass, height, functional group, growth habit, reproductive habit) among individuals while maintaining variability in phenotypes within randomly assembled communities (Alonso-Blanco and Koornneef 2000, Pigliucci 2002). Although its use to date has been largely restricted to molecular, physiological, developmental, and cellular biology, the use of *A. thaliana* in ecological studies is promising and expanding (Bergelson 1994, Mauricio 1998, Andalo et al. 2001, Mitchell-Olds 2001, Pigliucci and Marlow 2001, Cipollini 2002).

Assessment of diversity–invasibility relationships in experiments

Huston (1994, 1997) and Wardle (1999, 2001) argue that our inability to draw generalizations about relationships between invasibility and diversity (based on experiments at any level of organization – genetic, species, or functional group) may stem from research methodology or experimental design. In brief, when communities of different richnesses are assembled from necessarily limited species pools, four confounding factors may emerge. First, the "selection probability effect" or "sampling effect" (Aarssen 1997, Huston 1997, Tilman et al. 1997b) may produce misleading effects because increasing richness in randomly assembled communities is associated with an increasing likelihood that a community will contain a species or group of species that produce certain properties, such as high biomass (Fig. 1a). Second, a limited species pool results in increasing community similarity among randomly assembled replicates within each increasing richness treatment, which leads to a "variance reduction effect" (Huston 1997) whereby replicates of high richness treatments are not independent replicates of the desired richness treatment, but are instead largely copies of one particular community identity (i.e. "quasi-replication", Huston and McBride 2002; Fig. 1b). Third, a limited species pool may also result in increasing community similarity between randomly assembled richness treatments as they approach the limits of the species pool, especially when lower richness treatments are intentional or artifactual subsets of the high richness treatments, a consequence of the "variance reduction effect" (Huston 1997; Fig. 1c). Finally, several recent experimental designs have intentionally or unintentionally allowed relative abundance (Tilman et al. 1996, Tilman 1997, Levine 2000, Naeem et al. 2000, Symstad 2000, Lyons and Schwartz 2001, Kennedy et al. 2002) to covary with experimental gradients of richness (Fig. 1d). Regardless of species composition, differences in plant abundance or density increases the likelihood of interactions (e.g. competition, mutualism) that may affect the invasibility of a community.

Alternately, some of these "simple sampling effects" have been considered "fundamental and ecologically important effects of diversity" that share characteristics with "niche models" that explicitly consider species interactions (Tilman et al. 2002). Further, Naeem (2002) viewed niche complementarity and sampling effects as co-occurring processes, in that "one or both mechanisms are likely to be responsible for observed

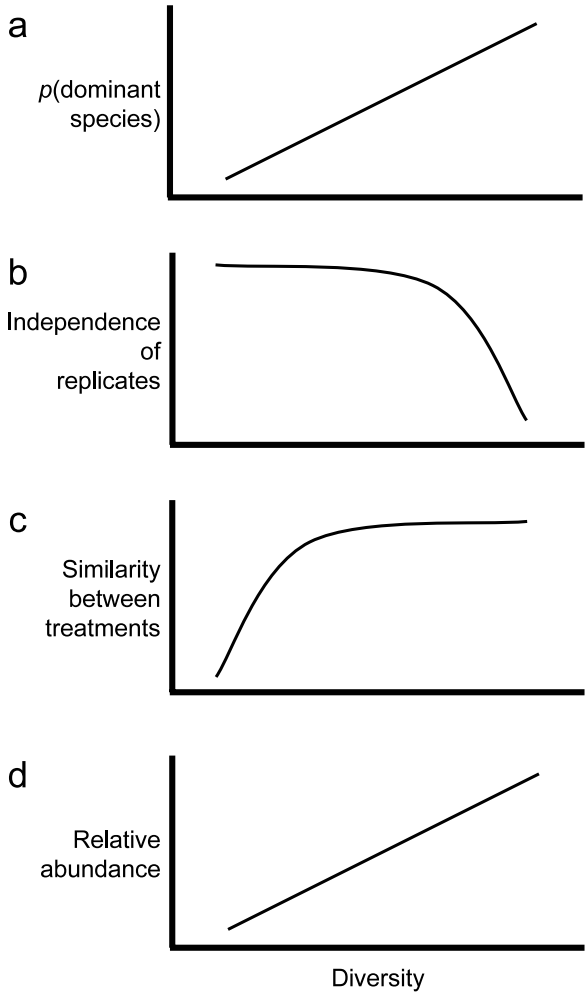

Fig. 1. (a) The ''sampling effect,'' wherein increasing richness in randomly assembled communities is associated with an increasing likelihood that a community will contain a dominant species (portrayed as a linear relationship for simplicity). This effect may yield a misleading trend in the mean response along the gradient of diversity, and can be minimized by keeping the probability that a functionally or morphologically dominant species is included in any given community low and constant across the gradient of diversity. (b) The ''variance reduction effect,'' caused when replicates within high richness treatments are not independent replicates of the desired richness treatment, but are instead largely copies of one particular community identity (i.e. ''quasi-replication''; Huston and McBride 2002). Independence of replicates thus decreases along the gradient of diversity; one way to minimize this effect is to keep the independence of replicates high and constant across the gradient of diversity. (c) A form of the ''variance reduction effect,'' wherein randomly assembled communities increase in similarity between adjacent treatments along the gradient of richness. This ''nestedness'' effect can be minimized by keeping the similarity of adjacent treatments low and constant across the gradient of diversity. (d) Systematic changes in mean relative abundance (e.g. cover, biomass, density) along the gradient of diversity (portrayed as a linear relationship for simplicity) may yield spurious ''richness effects'' or obscure genuine trends. One way to minimize this effect is to keep the relative abundance of each species constant across the gradient of diversity.

patterns of association between diversity and ecosystem function'', and he noted that ''direct experimental tests that specifically examine how these two factors contribute to ecosystem function remain to be done'' (ibid). In this spirit, a number of recent studies have investigated approaches to separating sampling and complementarity effects in biodiversity experiments (Loreau 1998, Leps et al. 2001, Loreau and Hector 2001, Schmid et al. 2002).

One additional approach to reduce the potential confounding of diversity treatments with other community attributes, or at least minimize ''sampling effects,'' ''variance reduction effects,'' or ''quasi-replication'' from diversity effects, per se, is to explicitly incorporate design elements that 1) minimize the ''sampling effect'' by developing a relatively large pool of potential community members that are functionally or phenotypically similar (Fig. 1a); 2) minimize within- and between-treatment similarity of communities that cause ''variance reduction effects'' and ''quasi-replication'' by assembling experimental communities from a relatively large pool of species (Fig. 1b, c); and 3) controlling relative abundance (e.g. density, cover, biomass) of experimental communities across treatments (Fig. 1d). Moreover, the relative success of these methodological approaches should be evaluated through statistical assessment of individual and community traits (e.g. morphology, function, similarity, abundance) across treatment gradients.

We followed these guidelines in an experiment designed to investigate the relationship between genetic diversity and community invasibility using created communities of *A. thaliana* genotypes with different genotypic richnesses at constant high and low densities. We evaluated the success of our methodological approaches by examining attributes of individuals within the communities (e.g. mass, cover), and attributes of the communities themselves (e.g. community biomass, total basal area cover, percent survivorship), to determine whether they differed among the different richness and density treatments. Once the communities of *A. thaliana* genotypes were established, we introduced another species of *Arabidopsis* (*A. suecica*) as the invader. The use of a species with a phenotype similar to the community members minimized differences in morphology or function that might have affected interactions between the two species. We tracked demography (emergence and survival), size (mass, rosette area), and reproductive potential (number and size of reproductive stems) of *A. suecica* as metrics of invasion success. We predicted that if resistance to invasion is an emergent property of community richness, then invasion success of *A. suecica* would be inversely correlated with our richness treatments.

Methods

Study organisms

We a priori selected 23 accessions of *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) from the Arabidopsis Information Management System (AIMS; http://www.aims.cps.msu.edu/aims) (Table 1). The term "accession" is used in germplasm collection to refer to a genotype of a plant species collected at a specific time and/or location, and in the case of *A. thaliana*, maintained thereafter as an inbred line (Alonso-Blanco and Koornneef 2000). We hereafter refer to accessions as genotypes. The 23 genotypes selected included only those considered to be early-flowering spring ephemerals (Pigliucci and Marlow 2001). Especially tall (>40 cm) or short (<30 cm) genotypes were excluded to minimize differences in size among potential community members. We obtained seeds for each genotype from LEHLE seeds (http://www.arabidopsis.com) and AIMS.

We selected one genotype of *Arabidopsis suecica* (Fr.) Norrlin, an allopolyploid hybrid derived from *A. thaliana* and *A. arenosa* (AIMS Stock Number CS3219), as our invader. *A. suecica* is found in Sweden, Finland, the Baltic States, and Norway (Hylander 1957, Love 1961) at elevations up to 200 m above sea level.

Experimental design

We constructed experimental communities comprised of *A. thaliana* genotypes at four levels of genotypic richness (1-, 2-, 4-, and 8-genotype communities) crossed with two levels of density (8 and 16 plants pot^{-1}, or 417 and 834 plants m^{-2}, respectively). Each treatment combination was replicated 5 times (for a total of 4 richness $\times$ 2 density $\times$ 5 replicates = 40 pots). Within each treatment combination, replicates were comprised of genotypes selected at random (without replacement) from the pool of 23 genotypes. For example, a pot with a richness of 8 genotypes and a density of 16 plants contained two individuals of each of 8 genotypes, and a replicate of this treatment combination contained two individuals of each of as many as 8 different genotypes.

In addition, we established a set of 5 bare pots with no community members to serve as zero-density controls for the introduction of *A. suecica*. Zero-density controls were not considered crossed with the density and richness treatments because density was zero and richness was not applicable. Zero-density controls were otherwise treated like all other pots. Finally, we grew one individual of each genotype in each of 3 replicate pots to determine genotype performance in the absence

Table 1. Mean ($\pm$ 1 SE) area of basal rosette, number of bolts, and length of longest bolt of individual *A. thaliana* (n = 3 except Nd-0, where n = 1 because of mortality) grown alone at the time of introduction by *A. suecica*, and area of basal rosette, number of bolts, length of longest bolt and individual mass at experiment termination. Mean ($\pm$ 1 SE) and range of values for each column are provided in the bottom two rows.

Ecotype	Origin	Altitude (m)	Introduction of *A. suecica*			Termination of experiment			
			Rosette area (mm^2)	Bolt number	Bolt length (mm)	Rosette area (mm^2)	Bolt number	Bolt length (mm)	Mass/ individual (g)
Aa-0	Germany	200–300	514 ± 160	0.33 ± 0.33	15 ± 15	1733 ± 274	5.67 ± 1.33	278 ± 19	0.17 ± 0.01
Be-0	Germany	100–200	1716 ± 970	0.33 ± 0.33	12 ± 12	2605 ± 662	6.33 ± 0.88	337 ± 20	0.41 ± 0.1
Bl-1	Italy	100–200	3125 ± 1345	0 ± 0	0 ± 0	5923 ± 2779	10.67 ± 1.86	360 ± 40	0.78 ± 0.33
C24		–	2600 ± 130	4.33 ± 1.2	142 ± 26	599 ± 108	6.33 ± 0.33	288 ± 9	0.23 ± 0.02
Chi-1	Russia	100–200	2361 ± 1226	1.67 ± 1.2	63 ± 33	1944 ± 687	18 ± 6.51	277 ± 26	0.27 ± 0.08
Col-0	USA	–	2379 ± 125	4 ± 0	207 ± 22	1610 ± 572	14.33 ± 4.67	295 ± 5	0.29 ± 0.05
Col-PRL		–	2389 ± 249	2.33 ± 0.67	140 ± 30	2867 ± 452	16 ± 1.53	298 ± 15	0.43 ± 0.09
Col-g11		–	2047 ± 275	4.33 ± 0.33	182 ± 16	1505 ± 292	15 ± 1.15	293 ± 9	0.32 ± 0.03
Cvi-0	Cape Verdi Islands	1200	2659 ± 1152	0 ± 0	0 ± 0	5524 ± 838	7.67 ± 0.88	320 ± 64	0.93 ± 0.19
Di-0	France	300–400	1947 ± 800	1.67 ± .88	147 ± 77	877 ± 551	4.33 ± 1.33	333 ± 18	0.13 ± 0.05
Est-0	Russia	100–200	2235 ± 70	3.33 ± 1.2	182 ± 28	245 ± 68	6.33 ± 1.86	327 ± 7	0.21 ± 0.05
Gre-0	USA	–	1448 ± 831	0.67 ± 0.67	43 ± 43	3741 ± 1571	5.67 ± 2.6	290 ± 50	0.36 ± 0.12
Kas-1	India	1580	1543 ± 329	0 ± 0	0 ± 0	2395 ± 833	8 ± 0.58	280 ± 13	0.4 ± 0.09
Kin-0	USA	–	2442 ± 1262	0.67 ± 0.33	45 ± 35	1545 ± 419	9.67 ± 0.67	360 ± 38	0.45 ± 0.19
Kn-0	Lithuania	1–100	1428 ± 544	2.33 ± 0.67	133 ± 57	982 ± 275	13.33 ± 4.37	312 ± 14	0.13 ± 0.07
La-0	Poland	1–100	1632 ± 136	3.33 ± 0.33	133 ± 13	367 ± 183	6.33 ± 0.88	253 ± 19	0.18 ± 0.01
Mh-0	Poland	100–200	1600 ± 172	1.67 ± 0.67	147 ± 53	873 ± 479	10 ± 2.65	350 ± 10	0.18 ± 0.02
Mt-0	Libya	100–200	2308 ± 1131	4 ± 1.53	157 ± 47	2287 ± 1031	13 ± 1	350 ± 30	0.34 ± 0
Nd-0	Germany	200–300	1257	1	10	2376	10	310	0.22
No-0	Germany	200–300	3001 ± 296	3.67 ± 1.45	148 ± 55	2880 ± 545	12.33 ± 1.2	342 ± 10	0.38 ± 0.05
RLD		–	2404 ± 724	3.33 ± 1.2	158 ± 53	1610 ± 353	6.67 ± 0.33	278 ± 39	0.18 ± 0.06
RLD1		–	1252 ± 358	2.67 ± 1.2	155 ± 37	190 ± 68	6.33 ± 1.45	267 ± 20	0.07 ± 0.01
S96	Netherlands	–	2680 ± 204	2.33 ± 0.33	102 ± 9	1088 ± 350	6.67 ± 2.33	317 ± 9	0.23 ± 0.06
Mean ± 1 SE	–	–	2042 ± 133	2.1 ± 0.3	101 ± 15	1990 ± 312	9.5 ± 0.8	309 ± 7	0.3 ± 0.01
Range	–	–	514–3125	0–4.3	0–207	190–5923	4.3–18.0	253–360	0.1–0.9

of potential competition. We did not introduce *A. suecica* into these single-individual genotype pots.

We established all pots (i.e. community, single-individual, and zero-density controls) on 13 February 2000. Seeds were vernalized on moist filter paper in a dark chamber at 4°C for 5 days prior to planting. We planted seeds into standard $16 \times 12 \times 6$ cm plastic pots filled with water-saturated, autoclaved Pro-Mix general-purpose soil (Premier Horticulture, Inc.). We used a wet-pipette method to plant seeds in triplicate (to maximize establishment) onto the soil surface in pre-determined grid locations. Pots with 8 and 16 plants had 2 and 4 columns of 4 grid locations centered longitudinally within each pot, respectively. This design was chosen to maximize distance between individual plants, and facilitate plant identification and monitoring based on maps printed on permanent data sheets. Seeds of single-individual genotypes were sown into the center of their respective pots.

All pots were placed in a greenhouse at the University of Tennessee; because light might have been limiting at this time of year, we provided supplemental lighting in the form of overhead 300-watt grow lights set for a 16:8 (day:night) hour photoperiod. All pots were watered frequently to maintain soil moisture contents near field capacity. We re-randomized pots across the bench on a daily basis for the first 30 days, and bi-weekly thereafter, to minimize effects of unknown environmental gradients in the greenhouse on plant growth.

Seedling emergence was monitored daily for the first 30 days of the experiment. As seedlings emerged, we waited for ~ 7 days to ensure establishment, then removed (i.e. thinned) seedlings as necessary to maintain one plant per grid location. If a seedling failed to emerge or establish at any grid location within the first two weeks of the experiment, we replanted it with seed or transplant stock of the same genotype.

Thirty days after experiment initiation, when the majority of plants had established basal rosettes, we measured diameter of the basal rosette in two orthogonal directions, number of bolted stems > 1 cm in length, and length of the longest bolt for each plant in the experimental communities, and each plant grown alone. We then planted three vernalized seeds of *Arabidopsis suecica* by wet pipetting to each of three locations within each experimental community: the geometric middle of the pot, and midway between the middle of the pot and the two short sides of the pot. *A. suecica* were monitored daily for emergence and survival. When multiple *A. suecica* became established at a location, we recorded the number emerged and thinned them to one individual after ~ 7 days.

On 11 April 2000, when more than half of the plants in each community were senescent, we terminated the experiment and recorded (1) survivorship and above-ground biomass for each *A. thaliana* community member, (2) diameter of the basal rosette, number of bolted stems, length of the longest bolt, and above-ground biomass for each *A. thaliana* grown alone, and (3) survivorship, rosette diameter, number of bolted stems given bolting, length of the longest bolt given bolting, plant reproductive status (i.e. with or without fruits) given bolting, and above-ground biomass for each *A. suecica*.

We calculated basal rosette areas based on measurements of rosette diameter; this necessarily overestimated actual foliar cover, because of the oblong nature of the leaves that comprised the rosette. Above-ground biomass was determined by clipping individual plants at the soil surface below the basal rosette of leaves, and drying individual samples at 50°C to constant mass. For *A. suecica*, we calculated mean time to emergence, and proportional rates of emergence (number of established plants/number of seeds planted), survivorship (number of plants alive/number of seedlings alive after post-emergence thinning), bolting (number of plants that bolted/number of plants alive at experiment termination), and fruiting (number of plants that produced fruit/number of plants, given bolting). Survivorship of *A. thaliana* community members was calculated in a similar manner. Proportional data are expressed as percentages.

We determined community-level biomass and percent cover (total area of plants/total area of soil surface $\times$ 100) of *A. thaliana* communities by summing biomass and basal area values of individuals within pots. As calculated, total cover of basal rosettes in a pot could exceed 100% because rosettes sometimes overlapped, particularly in the high-density treatment, and because of the aforementioned method of calculating foliar cover. Because of senescence, areas of individual basal rosettes were sometimes smaller at experiment termination than at the time of the invasion by *A. suecica*; this occurred for some *A. thaliana* grown alone, but especially for *A. thaliana* grown as members of the community. Therefore, we did not calculate basal rosette area for *A. thaliana* plants in experimental communities at experiment termination because the degree of senescence of the rosette in most of those plants rendered such measurements unreliable. Differences in rates of phenological development between the different genotypes contributed to variation in the effect of senescence on areas of basal rosettes (Table 1).

Statistical analysis

We used standard two-way analysis of variance (ANOVA; procedure GLM, SAS Institute 1989) models to evaluate main and interactive (fixed) effects of community richness (1-, 2-, 4-, and 8-genotypes) and density (8 plants pot^{-1}, 16 plants pot^{-1}) on all aforementioned response variables for *A. thaliana* commu-

nity members and *A. suecica* invaders. We considered bare pots (i.e. without *A. thaliana*) into which we introduced *A. suecica* as a special case: in terms of a community of *A. thaliana* genotypes, these pots had a richness of zero and a density of zero, and as such levels of richness and density could not be crossed. Therefore, we included this treatment in a separate analysis of density effects on *A. suecica*, wherein we used a one-way ANOVA to evaluate effects of density (0-, 8-, and 16 plants pot^{-1}) on the aforementioned *A. suecica* response variables.

Prior to statistical analysis, all data were tested for normality with the Shapiro-Wilk W-statistic (Shapiro and Wilk 1965). Data not normally distributed ($P < 0.05$) were transformed prior to analysis with arcsine-square root transformations for proportional data and log- transformations for all other data (Zar 1996); data presented in tables are non-transformed means. We used Fisher's protected LSD (Fisher 1960) a posteriori mean separation tests to compare levels within factors for significant ($P < 0.05$) main effects and first-order interactions.

We determined the similarity of replicate communities (as a measure of independence of replicates based on presence/absence of genotypes) within each richness treatment for low- and high-density pots by calculating Jaccard's coefficient of similarity (Sj; Krebs 1989) for all combinations of replicate pots within each treatment combination of richness and density ($n = 10$ pair-wise combinations). We used Kruskal-Wallis tests (Kruskal and Wallis 1952) to evaluate effects of richness on Sj for low- and high-density treatments (based on stipulated diversity, which differed little from actual diversity at the time of invasion or at the end of the experiment because of low mortality, see Results); when the test statistic (H) was significant ($P < 0.05$), we used separate Kruskal-Wallis tests to compare Sj for all pair-wise combinations of richness within each density treatment.

We determined the similarity between adjacent levels of richness (i.e. 1-genotype vs 2-genotype, 2- vs 4-genotype, and 4- vs 8-genotype) as a measure of independence of richness treatments, or nestedness, for low- and high-density pots by calculating Sj for all combinations of replicate pots within these adjacent richness treatments ($n = 25$ pair-wise combinations). As before, we used Kruskal-Wallis tests to evaluate differences in Sj for the adjacent richness treatments as a whole, and for pair-wise combinations of richness within each density treatment.

To determine whether variation in community characteristics declined with increasing richness (i.e. the variance reduction effect), we tested the homogeneity of coefficients of variation among levels of richness for low- and high-density communities separately (with chi-square tests as outlined in Zar 1996). Response variables tested for homogeneity of coefficients of variation included all response variables measured for the *A. thaliana* communities at the time of introduction of *A. suecica* and at experiment termination.

Results

Demography, size, and reproduction of *A. suecica* invaders

Time to emergence for individual *A. suecica* introduced into experimental communities of *A. thaliana* genotypes was about 0.5 to 1.5 days faster in pots with 8 genotypes than in pots with 1, 2, or 4 genotypes, which did not differ (Table 2 and 3). Otherwise, genotypic richness had no effect on *A. suecica* demography (i.e. emergence or survivorship), size (i.e. biomass, rosette area), or reproduction potential (i.e. rate of bolting and size of bolts, and number of plants that produced fruit) (Table 2). All *A. suecica* produced a single bolt, except one individual in the 4-genotype treatment that produced two bolts (data not shown).

In contrast, the density of *A. thaliana* genotypes had strong effects on the size and reproductive potential of *A. suecica* introduced into the experimental communities. *A. suecica* grown alone produced 4 or 50 times more biomass than when grown with *A. thaliana* at low and high densities, respectively (Table 4). Similarly, basal rosettes of *A. suecica* grown alone were 3 to 64 times larger than when *A. suecica* were grown in low- and high-density communities, respectively. Moreover, rates of bolting and lengths of bolted stems of *A. suecica* were 5 to 6 times greater when plants were grown alone then when they were grown in the high-density communities. Time to emergence in high-density communities was intermediate relative to low-density communities and bare pots (Table 4). Seedling survivorship tended to be greater in bare pots than in pots with *A. thaliana* at either low or high densities ($P = 0.11$; Table 4). Rates of emergence, the

Table 2. P-values for main and interactive effects of density (8 pot^{-1}, 16 pot^{-1}) and richness (1-, 2-, 4-, and 8-ecotypes) on emergence (%), time to emergence (days), survival (%), mass (mg), area of basal rosette (mm^2), percent of individuals that bolted, percent of plants that produced fruit, and length of longest bolt (mm) for individual *A. suecica* introduced into experimental communities of *A. thaliana* ecotypes.

Response variable	Richness	Density	Richness × Density
Emergence (%)	0.46	0.13	0.17
Time to emergence (d)	0.05	0.27	0.93
Survival (%)	0.75	0.37	0.78
Mass (mg)	0.96	0.25	0.55
Area (mm^2)	0.54	0.16	0.91
Bolted individuals (%)	0.93	0.45	0.56
Plants with fruits (%)	0.30	0.70	0.32
Bolt length (mm)	0.62	0.12	0.67

Table 3. Effect ($\pm$ 1 SE) of richness (1-, 2-, 4-, and 8-ecotypes) on emergence (%), time to emergence (days), survival (%), mass (mg), area of basal rosette (mm^2), percent of individuals that bolted, percent of plants that produced fruit, and length of longest bolt (mm) for individual *A. suecica* introduced into experimental communities of *A. thaliana* ecotypes. Within rows, means with the same letter were not different ($P > 0.05$).

Response variable	1	2	4	8
Emergence (%)	73.4 $\pm$ 7.1	70.2 $\pm$ 7.0	65.7 $\pm$ 6.3	80.1 $\pm$ 6.4
Time to emergence (d)	5.1 $\pm$ 0.4 a	4.0 $\pm$ 0.5 a	4.1 $\pm$ 0.3 a	3.5 $\pm$ 0.3 b
Survival (%)	59.8 $\pm$ 12.0	46.5 $\pm$ 14.2	46.4 $\pm$ 12.3	56.3 $\pm$ 10.0
Mass (mg)	1.1 $\pm$ 0.5	0.8 $\pm$ 0.3	2.1 $\pm$ 1.3	1.2 $\pm$ 0.6
Area (mm^2)	57.7 $\pm$ 30.4	16.0 $\pm$ 7.3	38.4 $\pm$ 14.5	46.2 $\pm$ 23.8
Bolted individuals (%)	22.1 $\pm$ 11.1	22.2 $\pm$ 16.5	14.3 $\pm$ 9.9	22.1 $\pm$ 7.9
Plants with fruits (%)	8.3 $\pm$ 8.3	33.0 $\pm$ 33.0	49.5 $\pm$ 16.5	33.0 $\pm$ 10.4
Bolt length (mm)	21.8 $\pm$ 9.6	31.5 $\pm$ 8.5	50.0 $\pm$ 35.0	40.4 $\pm$ 12.1

number of bolts, and the proportion of plants that produced fruit did not differ along the gradient of densities. There were no interactive effects of density and richness on morphological, phenological, or reproductive characteristics of the *A. suecica* invaders (Table 2).

Demography, size, and reproduction of A. thaliana community members

At introduction of A. suecica

At the time when *A. suecica* was introduced into the *A. thaliana* communities, the area of the basal rosette and the number and length of bolts of individual *A. thaliana* did not differ among levels of richness (Table 5 and 6). Similarly, the basal area cover for the community as a whole did not differ along the gradient of richness.

In contrast, characteristics of the experimental communities differed depending on the density of *A. thaliana*. Basal area cover was about 75% greater in high-density than low-density treatments (Table 5 and 7). The number of bolts per individual *A. thaliana* in the community was about 25% greater in the low-density than high-density communities. The areas of individual rosettes, and the length of bolts for individual plants, were not affected by the density treatments.

Table 4. P-value and effect ($\pm$ 1 SE) of density (0 pot^{-1} = none, 8 pot^{-1} = low, 16 pot^{-1} = high) on emergence (%), time to emergence (days), survival (%), mass (mg), area of basal rosette (mm^2), percent of individuals that bolted, number of bolts if bolted, percent of plants that produced fruit, and length of longest bolt (mm) for individual *A. suecica* introduced into experimental communities of *A. thaliana* ecotypes. Within rows, means with the same letter were not different ($P > 0.05$).

Response variable	P-value	Density		
		None	Low	High
Emergence (%)	0.38	69.0 $\pm$ 7.5	76.8 $\pm$ 4.5	67.9 $\pm$ 4.9
Time to emergence (d)	0.06	5.7 $\pm$ 0.9 a	4.0 $\pm$ 0.3 b	4.3 $\pm$ 0.2 ab
Survival (%)	0.11	86.4 $\pm$ 8.3	46.4 $\pm$ 8.2	58.1 $\pm$ 8.7
Mass (mg)	0.0003	24.5 $\pm$ 6.4 a	2.0 $\pm$ 0.6 b	0.5 $\pm$ 0.2 b
Area (mm^2)	$<$0.0001	1407 $\pm$ 327 a	64 $\pm$ 22 b	22 $\pm$ 6 b
Bolted individuals (%)	0.006	73.4 $\pm$ 19.4 a	26.6 $\pm$ 8.1 b	14.5 $\pm$ 6.8 b
Number of bolts	0.34	1.3 $\pm$ 0.2	1.1 $\pm$ 0.1	1.0 $\pm$ 0
Plants with fruits (%)	0.92	33.0 $\pm$ 13.5	28.9 $\pm$ 9.7	26.4 $\pm$ 12.3
Bolt length (mm)	0.0007	112 $\pm$ 10 a	46 $\pm$ 10 b	18 $\pm$ 4 c

Table 5. P-values for main and interactive effects of density (8 pot^{-1}, 16 pot^{-1}) and richness (1-, 2-, 4-, and 8-ecotypes) on area of basal rosette, number of bolts, and length of longest bolt of individual *A. thaliana*, and percent basal area cover for the community as a whole, at the time of introduction of *A. suecica*. Similarly, this table provides P-values for biomass of individual *A. thaliana*, biomass for the community as a whole, and percent survivorship of individuals within communities at the termination of the experiment.

Time	Response variable	Richness	Density	Richness $\times$ Density
Introduction of *A. suecica*	Rosette area/individual	0.18	0.18	0.40
	Bolt number/individual	0.62	0.06	0.50
	Bolt length/individual	0.46	0.35	0.83
	Basal area cover/community	0.39	$<$0.0001	0.71
Termination of experiment	Mass/individual	0.53	$<$0.0001	0.56
	Mass/community	0.32	0.09	0.24
	Survival	0.86	0.47	0.88

Table 6. Effect (± 1 SE) of richness (1, 2, 4, or 8-ecotypes/community) on area of basal rosette (mm^2), number of bolts, and length of longest bolt (mm) of individual *A. thaliana*, and percent basal area cover for the community as a whole, at the time of introduction of *A. suecica*. Similarly, this table provides means (± 1 SE) for biomass of individual *A. thaliana* (g), biomass for the community as a whole (g), and percent survivorship of individuals within communities at the termination of the experiment. Response variables did not differ among levels of community richness ($P > 0.05$).

Time	Response variable	1	2	4	8
Introduction of *A. suecica*	Rosette area/individual (mm^2)	1313 ± 142	1797 ± 174	1490 ± 152	1531 ± 145
	Bolt number/individual	1.5 ± 0.3	1.8 ± 0.2	1.9 ± 0.2	1.6 ± 0.2
	Bolt length/individual (mm)	103 ± 23	90 ± 12	118 ± 15	83 ± 12
	Basal area cover/community (%)	78 ± 13	101 ± 10	85 ± 14	87 ± 9
Termination of experiment	Mass/individual (g)	0.09 ± 0.01	0.09 ± 0.01	0.09 ± 0.01	0.08 ± 0.01
	Mass/community (g)	0.96 ± 0.11	1.02 ± 0.09	0.90 ± 0.09	0.79 ± 0.08
	Survival (%)	98 ± 1	96 ± 2	94 ± 4	99 ± 1

Table 7. Effect (± 1 SE) of density ($8\ pot^{-1}$ = low, $16\ pot^{-1}$ = high) on area of basal rosette (mm^2), number of bolts, and length of longest bolt (mm) of individual *A. thaliana*, and percent basal area cover for the community as a whole, at the time of introduction of *A. suecica*. Similarly, this table provides means (± 1 SE) for biomass of individual *A. thaliana* (g), biomass for the community as a whole (g), and percent survivorship of individuals within communities at the termination of the experiment. Within rows, means with the same letter were not different ($P > 0.05$).

Time	Response variable	Density	
		Low	High
Introduction	Rosette area/individual (mm^2)	1638 ± 134	1428 ± 80
	Bolt number/individual	1.9 ± 0.2 a	1.5 ± 0.1 b
	Bolt length/individual (mm)	106 ± 11	91 ± 12
	Basal area cover/community (%)	64 ± 6 a	112 ± 7 b
Termination	Mass/individual (g)	0.11 ± 0.01 a	0.06 ± 0.004 b
	Mass/community (g)	0.84 ± 0.05	1.00 ± 0.08
	Survival (%)	97 ± 2	96 ± 2

At experiment termination

At experiment termination, individual mass, total mass, and survivorship of *A. thaliana* within the communities did not differ along the gradient of community richness (Table 5 and 6). In contrast, community density had strong effects on individual *A. thaliana*, which had 2 times more mass when grown at low densities than high densities (Table 5 and 7). Because density was 2 times greater (by design) in high- than low-density treatments, total community biomass was only about 20% greater in high-density than low-density pots ($P = 0.09$; Table 7). Survivorship of *A. thaliana* community members at experiment termination was uniformly high (i.e. $\geq 96\%$), and did not differ between density treatments.

Versus A. thaliana grown alone at time of introduction and at experiment termination

A. thaliana grown alone exhibited substantial variation among genotypes at the time of introduction of *A. suecica*, and at experiment termination, for all measured variables of size and reproductive potential (Table 1, Fig. 2). For example, at the time when *A. suecica* were introduced into the communities, basal rosette areas of *A. thaliana* genotypes grown alone ranged from $514\ mm^{-2}$ to $3125\ mm^{-2}$, a 6-fold difference (Table 1). Genotypes grown in communities exhibited somewhat less variation in size at the time of *A. suecica* introduction; e.g. basal rosette areas ranged from $729\ mm^{-2}$ to $3149\ mm^{-2}$, a 4-fold difference (Fig. 2).

Otherwise, *A. thaliana* in communities at the time of introduction of *A. suecica* were similar to *A. thaliana* grown alone in terms of average rosette areas, numbers of bolts, and lengths of bolts, although this depended somewhat on the density of the community (Table 1 and 7). In contrast, *A. thaliana* in communities at experiment termination were on average about one-fifth to one-third the mass – depending on the density of the community – of *A. thaliana* that had been grown alone throughout the experiment (Table 1 and 7).

Similarity within and between richness treatments

Jaccard's coefficient of similarity (Sj) for replicate communities within richness treatments ranged from 0%, (i.e. no overlap in genotype identity) for low- and high-density communities of a single genotype, to 18% and 24% for low- and high-density communities of 8 genotypes, respectively (Table 8). For low-density communities, overlap in genotypes within replicate communities did not differ between adjacent levels of richness; that is, there was no more overlap in genotype identity

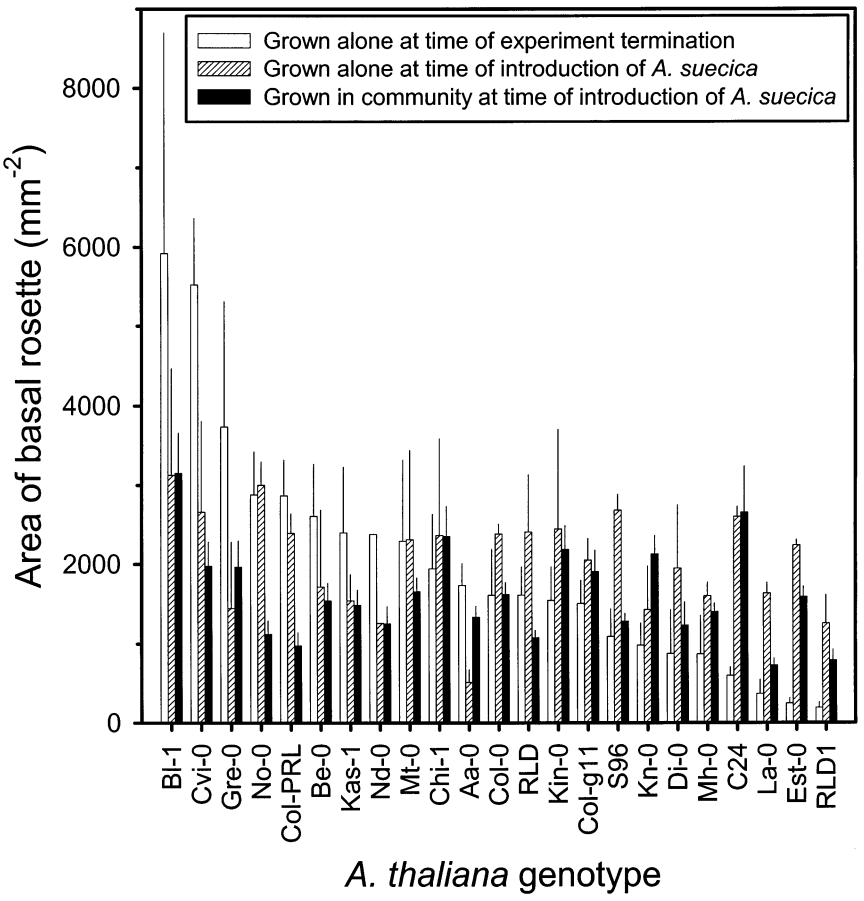

Fig. 2. Mean individual areas of basal rosettes (mm^{-2}; vertical lines represent 1 SE) for 23 genotypes of *A. thaliana* at the time of introduction of *A. suecica* when grown alone, at experiment termination when grown alone, and at the time of introduction of *A. suecica* when grown within randomly assembled communities at pooled low and high density. Genotypes are graphed by descending rosette area at experiment termination when grown alone.

Table 8. Kruskal-Wallis test statistic (H), P-value, and Jaccard's coefficient of similarity (± 1 SE) for replicate pots within each richness treatment (1-, 2-, 4-, or 8-ecotypes/community) in low- and high-density treatments. Within rows, means with the same lower-case letter did not differ ($P > 0.05$).

Density	H	P-value	1	2	4	8
Low	15	0.002	0 ± 0 a	0.07 ± 0.04 ab	0.11 ± 0.03 bc	0.18 ± 0.06 c
High	24	<0.0001	0 ± 0 a	0.03 ± 0.03 ab	0.08 ± 0.04 b	0.24 ± 0.03 c

for the replicate 8-genotype communities than for the replicate 4-genotype communities. However, there was more overlap in genotype identity for 8-genotype communities than for either 1- or 2-genotype communities. Similarly, overlap in genotypes for high-density communities did not differ between adjacent richness treatments except for 8-genotype communities, which had a 24% overlap in genotypes.

Sj for adjacent (i.e. between) richness treatments (e.g. 1-genotype vs 2-genotype) tended to increase as increasingly complex communities were compared in pair-wise fashion. For example, low-and high-density communities with 1 genotype and 2 genotypes shared only 2% and 6% of their genotypes, respectively, whereas communities with 4 genotypes and 8 genotypes shared 15–17% of their genotypes (Table 9).

Table 9. Kruskal-Wallis test statistic (H), P-value, and Jaccard's coefficient of similarity (± 1 SE) for adjacent levels of community richness (i.e. 1- vs 2-, 2- vs 4-, and 4-ecotype vs 8-ecotype) in low- and high-density treatments. Within rows, means with the same lower-case letter did not differ ($P > 0.05$).

Density	H	P-value	1 vs 2	2 vs 4	4 vs 8
Low	26	<0.0001	0.02 ± 0.02 a	0.09 ± 0.03 b	0.15 ± 0.02 c
High	22	<0.0001	0.06 ± 0.03 a	0.06 ± 0.02 a	0.17 ± 0.02 b

Homogeneity of coefficients of variation among richness treatments

Coefficients of variation (CV) were homogenous among levels of richness for both low- and high-density communities for all *A. thaliana* response variables measured at the time of *A. suecica* introduction (i.e. rosette area and number and length of bolts per individual, and % basal area cover for the community as a whole, $P > 0.40$; data not shown). At experiment termination, mass of individual *A. thaliana*, and mass of the *A. thaliana* community as a whole, also had CV that were homogenous among richness treatments ($P > 0.45$). In contrast, CV for survivorship of *A. thaliana* community members were not homogenous in either low-density communities ($P < 0.0001$) or high-density communities ($P = 0.02$): CV for survivorship in low- density communities were 5.7%, 5.7%, 18.1%, and 0% for 1-, 2-, 4-, and 8-genotype treatments, respectively. In a similar pattern, CV for survivorship in high-density communities were 3.5%, 8.6%, 11.8%, and 3.5% for 1-, 2-, 4-, and 8-genotype treatments, respectively.

Discussion

Invasion of *A. thaliana* communities by *A. suecica*: pattern and mechanism

Demography, size and reproductive potential of *A. suecica* introduced into experimental communities of *A. thaliana* genotypes were relatively unaffected by the genotypic richness of the recipient community. In contrast, the density of the recipient community had strong effects on the size and reproductive potential of *A. suecica*, and tended to be inversely correlated with survivorship of *A. suecica*. These facts suggest that characteristics of the recipient community other than genotypic richness are the most important determinant of community invasibility. In this study, structural characteristics associated with the density of the community, including individual- and community-level cover and biomass, appear to form the greatest constraint on invasion by *A. suecica*.

Similarly, biomass, cover, density or bare ground have been shown to control rates and patterns of invasion in other recipient communities (Peart and Foin 1985, Burke and Grime 1996, Crawley et al. 1999, Lavorel et al. 1999, Rejmánek 1999, Kennedy et al. 2002). It is likely that such variations in community structure control the spatial and temporal pattern of resources, which may ultimately provide niche opportunities for invasions (Huston 1994, Sher and Hyatt 1999, Davis et al. 2000, Fridley 2002, Shea and Chesson 2002). Because we did not quantify levels of resources that may have been affected by differences in density (e.g. light, soil moisture), we were unable to definitively attribute differences in *A. suecica* performance between the three density treatments to limitations by any particular resource. However, because the pots were well watered throughout the experiment, the availability of light or competition for other resources may well have been the most important factors affecting *A. suecica* performance.

Alternatively, spatial and temporal variations in natural enemies (Mack et al. 2000, Keane and Crawley 2002), disturbance regimes (Burke and Grime 1996, Smith and Knapp 1999), or soil biota (Klironomas 2002) may control rates and patterns of invasions (Shea and Chesson 2002). Because of the controlled nature of this experiment, these factors are unlikely explanations for the observed response of *A. suecica* to variations in community density. On the other hand, if uncontrolled, these factors could have generated different responses of *A. suecica* to variations in community density or diversity.

Moreover, as a starting point for what we hope are future investigations of genetic diversity, we chose to restrict our design by excluding especially tall or short genotypes, as well as late-flowering genotypes. Thus, our experiment was not designed to test effects of the extremes of genetic (or phenotypic) diversity, although we did observe substantial variation in phenotypes. Future investigations could explicitly vary genotypic diversity and phenotypic (i.e. trait) diversity (e.g. in a factorial design), to 1) determine the role of genetic diversity in invasibility, community structure and ecosystem function, and 2) disentangle potentially confounded effects of genotypic and phenotypic diversity.

Assessment of diversity–invasibility relationships in experiments

As described in the introduction, a number of experiments have recently attempted to elucidate relationships between diversity or richness and biological invasions, as well as the mechanisms underlying those relationships. To date, emergent properties have been somewhat elusive, but may become more apparent once issues of scale and confounding are resolved (Bengtsson et al. 2002, Levine et al. 2002). In addition, in response to issues of experimental design and alternative mechanisms (Huston 1997, Levine and D'Antonio 1999, Wardle 1999, 2001, Huston and McBride 2002), a number of recent studies have investigated approaches to separating sampling and complementarity effects in biodiversity experiments (Loreau 1998, Leps et al. 2001, Loreau and Hector 2001, Schmid et al. 2002).

In this study, we used an alternative approach designed to reduce the probability of sampling (or selection probability) effects (SE) and variance reduction effects (VRE) a priori by (1) homogenizing our pool of potential community members through the use of geno-

types of *A. thaliana*, and (2) increasing the size of the pool of potential community members relative to the size of our most-rich community. We coupled these a priori considerations of design with (3) post-hoc assessment of characteristics of the experimental communities and their individual members across the gradient of richness, including (a) means and coefficients of variation, and (b) community similarity within each level of richness, and between adjacent levels of richness.

Although we employed genotypes of a single species to homogenize our species pool (# 1 above), the genotypes chosen still exhibited considerable variation in size and phenological development (Table 1, Fig. 2). By increasing the size of our species pool (# 2 above), we substantially reduced the likelihood of a SE relative to several recent experimental studies of richness-invasibility relationships (Wardle 2001): our maximum ratio of community to pool size was 8/23, or 35%, which compares favorably to ratios of 60% (Naeem et al. 2000) to 100% (Crawley et al. 1999, Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Dukes 2001).

Post-hoc analysis of all characteristics of our communities (# 3a above), which should indicate the net results of an unintended SE with increasing richness, indicated that individual- and community-level characteristics of the recipient communities did not differ along the gradient of richness (Table 5, Fig. 1a). Further, with the exception of survivorship, which had the greatest CV at richness = 4, CVs were homogenous across our richness treatments. In sum, by increasing the size of our species pool and homogenizing their morphological and functional characteristics, we reduced the SE and VRE because size, demography, and reproductive potential remained constant across our gradient of richness.

Post-hoc analysis of community membership indicated that similarity between adjacent richness treatments (# 3b above) tended to increase along the gradient of increasing diversity (Table 9, Fig. 1c). The 15–17% overlap in identity between the two highest-diversity treatments compares favorably with potential ratios between 33% and 78% in recent experiments (Crawley et al. 1999, Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Dukes 2001). Regardless, this asymptotic trend in richness may have compromised our ability to detect the true response of *A. suecica* to community richness. Between-treatment overlap could be minimized by further decreasing the ratio of community size to species pool size.

Post-hoc analysis of similarity of replicates within richness treatments (# 3b above) indicated that replicates became more similar along the gradient of increasing richness, reaching a maximum of 24% (Table 8, Fig. 1b). Although we suspect within-treatment overlap in genotype identity was relatively modest in our experiment, most research reports do not contain enough information for a comparison. Regardless, whether intentional (Naeem et al. 1994), or an experimental artifact derived from a limited pool size, this "quasi-replication" also contributes to the VRE, which confounds separation of statistical from biological responses when evaluating diversity–invasibility relationships (Huston 1997, Fukami et al. 2001, Huston and McBride 2002). Similar to between-treatment overlap, within-treatment overlap could be minimized by increasing the total species pool relative to the maximum size of the community.

Finally, one explanation for conflicting experimental support for Elton's (1958) hypothesized relationship between richness and invasibility might be that plant density is not always explicitly controlled when richness is experimentally manipulated (Tilman et al. 1996, Naeem et al. 2000, Lyons and Schwartz 2001, Levine 2000; Kennedy et al. 2002; see also reviews by Huston 1997 and Levine and D'Antonio 1999, Fig. 1d). In studies that did control for density, diversity-invasibility relationships ranged from neutral (Peart and Foin 1985, Lavorel et al. 1999, Dukes 2001, this study) to positive (Palmer and Maurer 1997) or negative (Naeem et al. 2000). Regardless, experimental investigations of relationships between diversity and invasibility should consider issues of scale and other potentially confounding factors in their design (Levine and D'Antonio 1999, Bengtsson et al. 2002, Levine et al. 2002, Naeem 2002).

Conclusions and future directions

Ecological systems are by nature inherently variable; when this variability is combined with random assembly of communities from limited species pools, experimental investigations of relationships between community diversity and invasibility may experience confounding that may obscure genuine trends. SE and VRE have been considered emergent properties of ecosystems (Tilman 1997, Tilman et al. 1997a, van der Heijden et al. 1999, Naeem et al. 2000, Tilman et al. 2002), but as noted by Naeem (2002), these effects likely co-occur with diversity effects, and explicit investigations of their relative importance have yet to be tested. Alternate approaches to consideration of SE, and VRE by association, include the empirical use of monocultures (Wardle 1999, 2001) or low diversity plots (Leps et al. 2001), separation through statistical models (Loreau 1998, Loreau and Hector 2001, Schmid et al. 2002), explicit inclusion of SE or VRE as factors in the experimental design (e.g. by intentionally varying SE or VRE within a factorial design, and evaluating their relative importance; Naeem 2002), or by minimizing their potential effects through experimental design.

We used a model system to reduce some of the constraints inherent to random-assembly experiments.

We minimized SE by assembling random communities from a relatively large pool of taxa a priori selected to have modest phenotypic variation. This methodological approach also reduced the potential for confounding caused by VRE, which is derived from overlap in taxonomic identity both within and between treatments. Additional increases in the size of the potential pool relative to the maximum size of the assembled pool would further reduce this effect. Finally, our experimental design eliminated confounding of richness with abundance, while demonstrating that the density of individuals does indeed form an important constraint on invader success – perhaps mediated by resource availability (Jonsson and Malmqvist 2003).

In contrast, the results of our experiment indicated that genotypic richness was uncorrelated with invasion success. Because we did not determine resource use complementarity along our richness gradient, we cannot discount this as a potential mechanism that could ultimately constrain community invasibility (Dukes 2002). Moreover, future studies should focus on the role of extremes of genetic diversity on invasibility or other aspects of community structure and function. Further, effects of SE and VRE could be investigated by experimental designs that explicitly vary these factors along gradients of genetic or phenotypic diversity. Finally, research could be conducted in more natural settings (e.g. along environmental gradients), where other factors may also form important constraints on invasions. However, this study suggests that genetic variation, per se, is not necessarily a factor underlying mechanistic relationships between diversity and invasibility.

Acknowledgements – We conceived the research question, and designed and conducted the experiment as part of an experimental graduate student course in spring semester 2000. J. Moss helped design the experimental protocols, assisted with the acquisition and culture of the sample units, and contributed to data collection and compilation. A. Fuquay, J. Kerr and M. Moriarty helped collect and process data. T. Fukami provided helpful comments on the importance and quantification of community similarity indices. K. McFarland graciously arranged for use of greenhouse space and provided pots, soil, and advice. Research was supported in part by the Dep of Ecology and Evolutionary Biology, Univ. of Tennessee. A preliminary draft of the manuscript was improved by comments from T. Fukami, M. Huston, P. Kover and D. Vázquez.

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