

THE CONSEQUENCES OF GENETIC DIVERSITY
FOR INVASION SUCCESS
IN POPULATIONS OF DANDELIONS

by

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ABSTRACT

Genetic variation is ubiquitous in natural populations, but very little is known about the ecological consequences of this variation. Recent interest in merging ecological and evolutionary studies has illustrated the potential for heritable trait variation to influence processes at the population, community or ecosystem level. In the few studies conducted to date, increased genetic diversity has been shown to increase the productivity and resistance to disturbance of populations of focal species and to increase the stability of plant communities. The objective of this study was to provide a test of the consequences of genetic diversity for the invasion success of populations of dandelions (*Taraxacum officinale*) under two sets of environmental conditions. We predicted that: (1) increasing genetic diversity in the invading population will increase average invasion success via a “selection effect”, whereby diverse populations have a higher probability of being dominated by a highly competitive genotype, or a “complementarity effect”, whereby niche differentiation or facilitation among genotypes results in mixtures having greater invasion success than expected from the performance of single genotypes; and (2) the strength of the diversity effect will be strongest in the most stressful environment. Replicate populations of three different genotypic richness levels were established in both environments (a mowed lawn and a fallow field) in June 2007. Individual plants were measured every month to determine plant size (as total leaf area) and all seed heads were counted. As predicted, plot productivity (as measured by plant leaf area or number of seeds produced) increased with plot genotypic richness, and plot productivity was greatest in the fallow field (no richness-by-environment interaction). Contrary to our second prediction, the diversity effect was strongest in the least stressful environment, the fallow field, as indicated by significant overyielding of genotype mixtures in this environment only. A positive selection effect drove the overyielding in the fallow field, while the balance of complementarity and a negative selection effect mediated the small (but non-significant) net effect in the mowed lawn. In conclusion, genetic diversity within invading populations can increase the probability of successful establishment, but the strength of this effect depends on habitat context.

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INTRODUCTION

The connection between biodiversity and ecosystem functioning has become a central issue in ecology. The consensus view, that humans are responsible for elevating extinction rates by several orders of magnitude above background rates (e.g. Pimm et al. 1995, Vitousek et al. 1997, Sala et al. 2000), predicts that ecosystems of the future will be highly depauperate compared to the ecosystems of today. Given that ecosystems provide key ecological services to people, such as nutrient cycling, water purification, soil formation and disease control, understanding the impact of species losses on the functioning of ecosystems and their ability to provide these services is of critical importance (Chapin et al. 2000). Both the number and the functional types of species present may influence ecosystem services, via their determination of organismal traits. It is organismal traits that mediate energy and material fluxes, either directly or indirectly by altering abiotic conditions. Hence, both species richness (the number of species) and composition must be considered when evaluating the consequences of species loss (Loreau 2000). Additionally, genetic diversity (within species) and genetic identity, especially within keystone or dominant species, may also influence ecosystem services (Whitham et al. 2003). However, as the vast majority of studies to date have considered only species diversity, I first provide an overview of key findings from the species diversity literature, in order to provide a conceptual framework for my study.

Background: Species diversity and Ecosystem Function

Species composition is often more important than the number of species in affecting ecosystem processes (Hooper et al. 2005). However, there is now substantial evidence, albeit mainly from small-scale experiments in plant communities, that species richness can affect many ecosystem functions. One recent review (Srivastava & Vellend 2005) found that of the 100 studies examined, 71% found a positive effect of biodiversity on at least one ecosystem function. Similarly, in a meta-analysis of 111 experiments (Cardinale et al. 2006), 88% of the studies found a positive effect of diversity on the abundance or biomass of a focal trophic group, which resulted in a more complete depletion of available resources. Ecosystem properties such as primary productivity (e.g. Hector et al. 1999, 2001; Schwartz et al. 2000; Tilman et al. 2001), nutrient retention

(e.g. Tilman et al. 1996, 1997), and resistance to disease (e.g. Power & Flecker 1996, Boudreau and Mundt 1997, Palumbi 2001) tend to increase with species richness in experimental ecosystems. As most of these experimental systems tend to contain relatively few species (10 or fewer), it remains unclear if these results apply to more speciose natural systems. However, a recent meta-analysis (Balvanera et al. 2006), which included 33 studies of experimental systems with greater than 20 species, found that biodiversity effects tended to be found more frequently in more speciose systems. This suggests that biodiversity effects may become stronger and more consistent as the number of species in a community increases. Although controversy remains (Kaiser 2000), most studies suggest that a large pool of species is required to maintain ecosystem functioning under changing environmental conditions (e.g. McGrady-Steed et al. 1997, Naeem & Li 1997, Norberg et al. 2001, Tilman et al. 2006).

One ecosystem property of particular concern is the biotic resistance of a community to invasion by exotic species. Human activities have accelerated the rate of biological invasions worldwide, and invasive species are now considered an important cause of extinction (Pimentel et al. 2000). According to the “niche hypothesis” (Stachowicz et al. 2002), more diverse communities should better resist invaders (compared to depauperate ones) because they reduce resource availability and increase competition. Consistent with this hypothesis, a number of recent experiments which manipulated species richness in small-scale communities have shown that as diversity increases, invasibility declines (e.g. Naeem et al. 2000, Hector et al. 2001, Fargione et al. 2003). However, the opposite pattern may also occur (i.e. more diverse communities are less able to resist exotics) if native species facilitate invaders. A growing body of evidence suggests that this may occur in a number of terrestrial and marine ecosystems (Bulleri et al. 2008). For example, on the rocky shorelines of Western Canada, native invertebrates protect the invasive oyster, *Crassostrea gigas*, from predation, thereby facilitating its survival in some cases (Ruesink 2007). At large scales, native and exotic species richness are positively correlated, owing to the influence of extrinsic factors such as resource availability (Fridley et al. 2007).

The effects of species diversity on ecosystem functioning (“biodiversity effects”) may be predictable based on the performance of each individual species when grown

alone (in “monoculture”), and knowledge of the relative abundance of each species in the community. If this is the case, the effect of biodiversity is considered additive, and the phenotype of individuals of a given species remains the same in monoculture and in mixture (i.e. a community of multiple species, a “polyculture”) (Hughes et al. 2008). The productivity of a mixture is then the average of the individual productivities of each constituent species, weighted by species’ relative abundances (Loreau & Hector 2001). In contrast, the performance of a diverse community may not be predictable based on the performance of individual species, when the effects of those species are non-additive (Loreau et al. 2001). Non-additive effects arise when inter- and intraspecific interactions are not the same (Fox 2005). These effects may cause the performance of a mixture to be higher or lower than expected based on the performance of individual species growing in monoculture (over- or underyielding, respectively).

There are two commonly discussed mechanisms for non-additive effects: selection, and complementarity (Loreau & Hector 2001). A selection effect arises from selective processes, such as interspecific competition, that cause dominance (high relative abundance) of species with particular traits. Communities containing multiple species, assembled at random from a pool of species, have an increased probability of containing (and becoming dominated by) a species with a strong effect on the ecosystem property of interest (e.g. productivity, invader-resistance). In this case, the performance of a mixture of species is, at most, equal to the performance of the best species when grown alone (Fargione & Tilman 2005). A selection effect may be positive, if communities are dominated by species with high values for a particular trait, or negative, if communities are dominated by species with low trait values. There has been some debate between ecologists as to whether these simple selection effects are relevant to natural ecosystems. Some ecologists view such effects as hidden treatments within diversity experiments (e.g. Huston 1997, Wardle 1999), arguing that they depend on the assumption that communities are randomly assembled from regional species pools, while much evidence suggests that communities are not random assemblages of species (e.g. Watt 1947, Whittaker 1956, Kershaw 1973). Other ecologists view selection effects as the simplest possible, but biologically very important, mechanism linking species richness to ecosystem functioning (e.g. Loreau 2000, Tilman et al. 2002). They argue that there are

many stochastic processes that can influence community composition (MacArthur & Wilson 1967, Roughgarden 1989), indicating that the random assembly of experimental communities resembles, to some extent, the assembly of communities in nature.

The second mechanism, complementarity, arises from niche differentiation or facilitation among species (Tilman et al. 2001). Positive species interactions lead to mixtures of species having higher performance than expected based on the performance of species grown in monoculture. Complementary interactions between species may occur if species use different types of resources (e.g. chemical forms of nitrogen), have different required ratios of needed resource types, or exploit the same resource at different times or in different spaces (e.g. variable phenologies or rooting depths) (e.g. Grime 1977, Tilman 1982). One notable form of complementarity occurs between legumes (which fix nitrogen) and non-nitrogen fixing plants (Loreau & Hector 2001). In theory, complementarity effects may also be negative, if individuals of different species inhibit one another to a greater degree than do individuals of the same species.

Selection and complementarity effects are not mutually exclusive, and both may play a role in the outcome of a biodiversity experiment (Cardinale et al. 2006). A recent review of 44 experiments which examined how plant species richness affects biomass production (Cardinale et al. 2007) found that mixtures of species produced an average of 1.7 times more biomass than the monoculture average. Although this positive net effect of diversity was partly attributable to the dominance of highly productive species, the contribution of species complementarity equalled or exceeded these selection effects. Furthermore, the magnitude of the complementarity effect increased with the duration of the experiment. In theory, the relative importance of selection versus complementarity effects should vary across ecosystems, depending on environmental conditions (Fridley 2001). Complementarity is expected to become more important as environmental heterogeneity (either spatial or temporal) increases, as heterogeneity promotes the ability of different species to partition resources (Tilman 1982). In a study examining primary productivity, parasitism rates, and coffee pollination in different natural ecosystems (Tylianakis et al. 2008), these ecosystem functions were found to be more strongly influenced by diversity where limiting resources were spatially heterogeneous, likely due to enhanced opportunities for complementarity. Selection effects should be more

important in small habitat patches (where stochastic processes have greater influence on extinction and immigration), and, similarly, in early successional communities (Cardinale et al. 2007).

Ecological Consequences of Genetic Diversity within Species

Although much progress has been made in understanding how species richness and composition may affect ecosystem-level processes, another important aspect of biodiversity has traditionally been ignored: the genetic diversity of species in the community. Genetic diversity, ubiquitous in natural populations, has been primarily of interest to evolutionary biologists in the past century (who study how it originates, what factors maintain it, its role in the evolution of sex, etc.) (Futuyma 1998), while being largely overlooked by ecologists. However, recent evidence suggests that the higher-level consequences of genetic diversity are analogous to the ecosystem functioning consequences of species diversity, and may be influenced by the same set of processes operating amongst genotypes. Surprisingly, the magnitude of genetic diversity effects can be similar to that of species diversity effects in comparable experiments (see Hughes et al. 2008 for examples). In one example, a study of plant genotypic diversity on arthropod community structure (Johnson et al. 2006), genotypic diversity within patches of *Oenothera biennis* explained 16% of the variation in associated arthropod community species richness. This result is comparable to the 15-23% of variation typically explained by plant species richness in natural communities.

Early interest in the ecological effects of genetic diversity occurred in the field of agronomy, with the goal of enhancing the productivity (yield) of crop species. Although the yield increase of mixtures compared to monocultures is usually small, increased genetic diversity of crops often decreases damage by insect herbivores and pathogens (Smithson & Lenné 1996). In one recent study (Zhu et al. 2000), rice blast (a costly fungal pathogen of rice) was effectively controlled by planting mixtures of common rice varieties. The severity of rice blast on disease-susceptible glutinous rice varieties planted in mixture (with disease-resistant varieties) decreased by 94%, while the yield of the glutinous rice varieties increased by 89%. The use of mixtures has also been shown to slow the spread of fungal pathogens of grains (e.g. Wolfe 1984, Ngugi et al. 2001, Mundt 2002), and there is some evidence that the use of mixtures may also help control plant

viruses (Power 1991). Given that pests and diseases are common in agricultural systems, the planting of genetically diverse crops is now widely accepted as a means of minimizing damage.

More recently, with the birth of the conservation genetics movement in the 1980s (Allendorf & Luikart 2007), the short-term ecological effects of genetic diversity, especially in small, endangered populations, have been highlighted. Small populations experience higher rates of inbreeding, and greater loss of genetic diversity due to genetic drift than larger populations (Lande 1995). This loss of genetic variation and expression of deleterious alleles (via inbreeding) can have negative consequences for fitness. In general, a 10% decrease in genetic variation is hypothesized to lead to a 10-25% reduction in the reproductive output of a population (Frankel & Soulé 1981). This reduction in fitness can lead to further decreases in population size, exacerbating the situation, and enhancing extinction risk (Frankham 2005). These results indicate that population viability, even in the short-term, is inextricably linked with population size and levels of genetic variation.

In the past two decades, the emergence of “community genetics” (Antonovics 1992), an attempt to merge community ecology with evolution, has highlighted the importance of understanding the interplay of evolutionary and ecological processes. This emerging discipline has sparked research programs spanning attempts to understand the mechanistic bases for evolution (in individual species) within a community context to studies of the role of genetic variation in generating community patterns (Agrawal 2003). These inquiries have revealed that evolutionary change can be sufficiently rapid to alter the dynamics of species interactions (Holt 2005), leading to faulty predictions of predator-prey and host-parasite dynamics when evolution is ignored (e.g. Hendry et al. 2000, Yoshida et al. 2003, 2007). Rapid evolutionary change is posited to be most common when communities are perturbed (as interaction strengths increase), an increasing phenomenon as more communities are exposed to anthropogenic disturbances (Neuhauser et al. 2003). Within communities at (or relatively close to) equilibrium, standing genetic variation, especially in dominant or keystone species, may influence processes at the population, community, or ecosystem level (Whitham et al. 2003).

At the population level, increased genetic diversity has been shown to enhance various fitness components (e.g. de Roode et al. 2005, Mattila & Seeley 2007), productivity (e.g. Bell 1991, Smithson & Lenné 1996, Crutsinger et al. 2006), and resistance to disturbance (e.g. Hughes & Stachowicz 2004). The increase in fitness can be substantial. In a study of *Oenothera biennis* (Johnson et al. 2006), genotype fitness (as measured by lifetime fruit production) increased by 27% when plants were grown in mixture versus monoculture. Productivity gains are similar to those seen in agricultural experiments, as described previously, and may result from selection effects (inferred in Bell 1991) or complementarity among genotypes (in Reusch et al. 2005, and Crutsinger et al. 2006). Additionally, genetic diversity may reduce variation in population performance (e.g. Jones et al. 2004). In amphipod populations exposed to perturbations (in the form of nutrient enrichment and desiccation), variance in the number of surviving individuals decreased with increasing diversity (Gamfeldt & Källström 2007). As with the conservation genetics results described previously, these demonstrations of enhanced fitness, and resistance and resilience to disturbance with increasing genetic diversity highlight the need to conserve genetic as well as species diversity.

Genetic variation may also have important population-level consequences for exotic species (Dlugosch & Parker 2008). In the initial stages of invasion, an exotic species will typically be rare locally (as a result of passing through a population bottleneck) and therefore prone to extinction. Increasing genetic variation in the founder population can improve responsiveness to natural selection (Holt 2005), as there are more “option values” for selection to choose from, and reduce fitness losses due to inbreeding depression. Natural selection can increase the growth rate of the founder population in its new range and thereby facilitate invasion. Many studies have documented rapid adaptation of exotic species to the novel conditions of their new range (e.g. Blair & Wolfe 2004, Huey et al. 2005, Vellend et al. 2007). This rapid evolution may be due in part to enhanced genetic diversity resulting from multiple introductions (Durka et al. 2005, Lavergne & Molofky 2007), although severe genetic bottlenecks do not preclude rapid adaptation (Sax et al. 2007). Therefore, the number of introductions may be indicative, to some degree, of an exotic species’ potential invasion success.

At the community level, genetic diversity has the potential to shape species interactions within a single trophic level, and across trophic levels. In competitive communities (of species on the same trophic level), genetic diversity may promote species diversity because it allows for the possibility of sorting among genotypes, enhancing coexistence (Vellend & Geber 2005). Coevolution of competitors generally promotes coexistence (MacArthur & Levins 1967, Pimentel 1968, Aarssen 1983), and requires genetic diversity in the coevolving species. Genetic diversity may also enhance population fitness, thereby decreasing extinction risk for each species individually (Frankham 2005). Several studies support the contention that genetic diversity enhances species diversity (e.g. Lankau & Strauss 2007, Whitlock et al. 2007). For example, in experimental communities of grassland plants, increasing the initial genetic diversity in each species in the community resulted in decreasing species losses over a period of five years (Booth & Grime 2003). In dominant species, genetic diversity may actually suppress the diversity of competing species in the community, via enhanced productivity or resource use of the dominant. Hence, as with the increased invasion-resistance of species rich communities, genetic diversity within species can enhance resistance to invasion (e.g. Crutsinger et al. 2007, 2008).

Additionally, a flurry of recent studies have shown that the genetic diversity of a plant species, reaching across trophic levels, can shape the dependent arthropod community. Insects can be sensitive to slight differences in phenotype between individuals of the same plant species, leading to differences in insect communities on different genotypes (which can vary in size, phenology, and resistance, etc.) (e.g. Dungey et al. 2000, Fritz et al. 2003, Johnson & Agrawal 2005). Typically, genetic diversity has a positive effect on the species richness and/or abundance of the associated arthropod species (e.g. Wimp et al. 2004, Reusch et al. 2005, Bangert et al. 2006, Crutsinger et al. 2006). Genetically diverse patches of *Oenothera biennis* hosted 18 % more arthropod species than monocultures; a greater abundance of omnivorous and predacious insects, but not herbivores, was also found in mixture (Johnson et al. 2006). The effect of genetic diversity on insect species richness was due to a combination of complementarity and selection effects, with the former responsible for the increased richness of omnivores, and the latter for that of predators. Consistent with observations on agricultural crops,

higher genetic diversity may also lower disease susceptibility in a variety of organisms (e.g. Schmid 1994, Hughes & Boomsma 2004, Pearman & Garner 2005).

At the ecosystem level, genetic diversity in dominant plant species can influence fluxes of energy, nutrients and matter (e.g. Madritch et al. 2006). Mixed stands of *Populus sp.* genotypes showed altered rates (by up to 57%) of immobilization of nitrogen and phosphorus compared to the null expectation based on genotypic means in monoculture (Schweitzer et al. 2005). The rate of decomposition also increased in mixed stands compared to monocultures. Similarly, in seagrass beds of *Zostera marina*, there was a negative correlation between genotypic diversity and the concentration of ammonium in sediment porewater, indicating enhanced nutrient uptake by diverse plots (Hughes & Stachowicz 2004).

The Environmental Context of Genetic Diversity Effects

The degree to which genetic variation will have important ecological consequences depends both on which traits are genetically variable, and the magnitude of this variation (Hughes et al. 2008). Evolutionary theory suggests that the environment may directly affect genetic variability in quantitative traits (Hoffmann & Merilä 1999). Several hypotheses predict that the expression of heritable genetic variation will increase in unfavourable (or stressful) conditions. These hypotheses include: (1) that stressful conditions (with limiting resources) increase phenotypic differences between genotypes; (2) a history of selection against low fitness alleles decreases trait heritability, but more so under favourable (common) conditions; and, (3) a history of selection for canalization decreases phenotypic differences among genotypes in favourable conditions, but not unfavourable (novel) ones. Some evidence from laboratory organisms (see examples in: Hoffmann & Merilä 1999), and crop plants (Ceccarelli 1994) support this contention. In contrast, other hypotheses (e.g. that stressful conditions increase environmental variance, thereby decreasing heritability) have predicted that the expression of genetic variation will be greatest in favourable conditions. This alternative hypothesis has support from studies of a variety of non-domestic, non-laboratory organisms (reviewed in Charmantier & Garant 2005).

Recent empirical work (e.g. Reusch et al. 2005) suggests that genetic diversity may be of particular ecological relevance under disturbance (i.e. stressful conditions). In

a study of the habitat-forming seagrass, *Zostera marina*, there was no detectable effect of seagrass genetic diversity during an initial period of expansion after planting (Hughes & Stachowicz 2004). However, after an extensive (and unanticipated) grazing event by migratory geese, the number of shoots remaining in experimental plots rose with increasing plot genotypic diversity, indicating enhanced resistance to the grazing disturbance in more diverse plots. While the differences in shoot density persisted for several months after grazing, a year later there was no longer any effect of plot genotypic diversity. Consequently, the effects of diversity might be expected to be magnified under more stressful conditions (the “stress hypothesis”).

Many questions remain concerning the ecological consequences of genetic diversity (Hughes et al. 2008). Sparse experimental data address basic questions such as: under what circumstances does genetic variation influence higher-level processes; what is the average magnitude of genetic diversity effects; and, what mechanisms underlie these effects? Here we present a study designed to address these questions in a novel experimental system. The objective of our study was to examine the consequences of genetic diversity for the invasion success of populations of dandelions, *Taraxacum officinale*. We tested the hypothesis (1) that genotypic richness of the invading population will affect average invasion success (individual plant survival and fitness), and predicted that increasing richness will increase average invasion success. If such an effect of diversity was detected, we then asked whether selection or complementarity effects were responsible for the observed pattern. We were also interested in how the magnitude of the genotypic richness effect might vary in different environments. Consequently, we replicated the entire genotypic richness experiment under two sets of environmental conditions, one more stressful than the other, to test the hypothesis (2) that the importance of genotypic richness in predicting dandelion invasion success will differ depending on environmental context. We predicted that the richness effect would be more evident in the more stressful environment, consistent with the stress hypothesis.

METHODS

Study System

The dandelion, *Taraxacum officinale*, is a tap-rooted, herbaceous perennial plant of the family Asteraceae. Its leaves sprout from a basal rosette above the tap-root and are oblong to oblanceolate, toothed to deeply divided in pinnate lobes (Holm et al. 1997). The commonly seen deep teeth of the leaves are thought to have given the plant its name in French, “dent de lion” (lion’s tooth) (Potter & Sargent 1973). Dandelions are easily recognized by their yellow, composite flower heads, borne singly on hollow stalks. Several flower heads may sprout at a time from a single rosette. The flower heads mature into the familiar, white spherical seed heads comprised of many individual single-seeded fruits, or “achenes” (Pojar & MacKinnon 2004). Each achene is attached to a hair-like pappus, a fluffy parachute that aids in wind-dispersal.

Considered a vexing weed by most gardeners, dandelions are capable of flourishing in a variety of human-dominated, disturbed sites. They are commonly found in agricultural fields, in pastures, along roadsides, in lawns and on disturbed banks of waterways, in addition to gardens (Stewart-Wade et al. 2002). Their prevalence in such diverse habitats may be related to their great adaptability; they can grow in a broad range of soils (Simon et al. 1996), climates (Holm et al. 1997), light availabilities and elevations (Longyear 1918). Other advantageous traits dandelions possess include: deep tap-roots (allowing access to resources out of reach for most plants), allelopathic properties, and the ability to regenerate from root fragments (Jackson 1982). They can also produce prolific numbers of highly dispersive seeds – up to 20 000 seeds per plant, under optimal conditions (Roberts 1936) - that may remain viable for years in the seed bank (Roberts & Neilson 1981).

Dandelions are native to Eurasia, where both diploid and asexual triploid individuals may be found (Lyman & Ellstrand 1984). They were introduced to North America in the 1600s, potentially as a food source for early European immigrants and imported honeybees (Schmidt 1979), and are now naturalized throughout the temperate regions of the continent (Stewart-Wade et al. 2002). Only triploid individuals have been found in North American populations; these are mainly obligate gametophytic apomicts,

producing seeds that are genetically identical to the parent plant (Solbrig 1971). Several studies have demonstrated that North American dandelion populations are often comprised of multiple distinct genotypes (genetically unique clonal lines) (e.g. Solbrig 1971, Vavrek 1998, Collier & Rogstad 2004). A survey of 22 North American dandelion populations found an average of five genotypes per population, with a range of one to thirteen genotypes (Lyman & Ellstrand 1984).

Genotypes can show variation in ecologically important traits, such as phenology, competitive ability, and tolerance to disturbance. Vavrek (1996) established mixed-genotype populations of dandelions in natural field sites, and measured several fitness components (e.g. growth, leaf area, seed production) for each genotype in each season. Differential genotypic responses to season were observed, with some genotypes growing best in warm seasons and others in cool seasons. Ford (1981) demonstrated that different dandelion genotypes are best suited to different habitats, and hence the rank order of genotypes (based on productivity) changes with habitat. Additionally, some genotypes were more competitive at a given density than others, and came to dominate established mixed-genotype populations. Solbrig and Simpson's (1977) garden experiment with two dandelion biotypes revealed differential tolerance of disturbance (either clipping or tilling) between biotypes. Biotype D dominated the population in undisturbed control plots, while biotype A was more prevalent in both types of disturbed plots. The differential response of dandelion genotypes to environmental heterogeneity (either spatial or temporal) may maintain these diverse types within a population.

Provenance of Dandelion Genotypes

Prior to the establishment of our field experiment, ripe seed heads from more than 60 "clonal families" were collected in the Vancouver area of BC, Canada by Mark Vellend. Based on leaf traits measured on 30 of these in a greenhouse trial, and microsatellite DNA analysis, seven candidate genotypes were identified from the original clonal families. These genotypes were selected to represent as broad a range of trait space as possible. One of the seven genotypes selected had red achenes, which some authors consider a separate species (*T. laevigatum*), although genetic evidence indicates that *T. laevigatum* and *T. officinale* share the same evolutionary lineage (Taylor 1987). All seed stock used in our experiment originated from the first generation plants used in

the greenhouse trial. These greenhouse plants flowered in the spring of 2006, and a stock of several thousand ripe seeds per genotype was collected.

Experimental Design

Our field experiment was designed to compare the relative invasion success of dandelion populations of low, medium and high genetic richness under two sets of environmental conditions. As initially planned, the experiment would be fully factorial with equal numbers of replicates for each treatment combination. A total of thirty replicates would be of low richness (1 genotype populations), thirty of medium richness (2 genotype populations) and thirty of high richness (5 genotype populations) in each environment. As described previously, a total of five genotypes corresponds to a realistic expected richness for a North American dandelion population. This design allows us to test for richness effects with replication at each level exceeding that of most studies. Additionally, owing to the inclusion of monocultures (and from taking data on individual plants), we can identify the underlying mechanism(s) by partitioning the richness effect, *sensu* Loreau and Hector (2001).

Six putative genotypes were selected for use in our experiment, but a microsatellite genotyping error, discovered after the experiment had already started by Mark Vellend (personal communication), revealed that two of our six genotypes were in fact the same. Essentially, the alleles for one locus (msta 53) used in the genetic analysis (described in Vellend et al. 2009) were initially scored as 221 and 225 bp for the offspring from one seed head (initially genotype 33 in our experiment). However, in a follow-up analysis, the alleles were later confirmed as 223 and 227 bp, identical to the scores of another genotype (genotype 16). As described below, this discovery had effectively no influence on our ability to test for effects of genotypic richness in the two environments.

As originally planned, six unique combinations of genotypes were to be planted for each richness level with five replicates per combination (Table 1). For plots with k genotypes, chosen from a pool of n genotypes ($n = 6$ in this case), the number of unique combinations is $n!/(k!(n-k)!)$, giving 15 possible combinations of two genotypes, and six combinations of five genotypes. All possible single genotypes and all possible combinations of five genotypes were used, while six of the 15 possible combinations of

two genotypes were selected randomly, with the constraint that each genotype be represented an equal number of times (in this case, twice). Given the genotyping error, the actual design was not fully balanced (see Table 2).

The described diversity treatments were fully replicated in two sets of environmental conditions, for a total of 180 experimental plots (90 per environment). These two environments simulate two different habitats where dandelions are commonly found growing around Vancouver BC, Canada (the location of our study). We will hereafter refer to the two sets of environmental conditions as “habitat types” for convenience. In the first habitat, a “Mowed Lawn”, dandelions were planted into a pre-existing mowed lawn, which was maintained by monthly clipping. In the second habitat, a “Fallow Field”, dandelions were planted into bare ground which was re-colonized by other species throughout the experiment.

The consequences of the genotyping error were as follows: an uneven number of plots with low, medium and high richness; all available genotypes (rather than a subset) in the highest richness treatment; and an over-representation of genotype 16 in the four-genotype plots. Importantly, this error had negligible impact on our ability to draw inferences from the results about the effects of genotypic richness and habitat on dandelion population performance. Replication was still relatively high at each diversity level, and the disproportionate abundance of genotype 16 in four-genotype plots could be accounted for by the partitioning methods (Loreau and Hector 2001) used to compare plant performance in monoculture and polyculture.

Experimental Layout

Plots were arranged in nine rows of twenty plots (0.5 m x 0.5 m) each (Figure 1). Each row had a 1 m border between it and adjacent rows or the perimeter, which was fenced to keep out grazing geese, and plots were adjacent within rows, with no space between them. Each plot was randomly assigned a habitat type, and each plot within a habitat type was randomly assigned a genotypic diversity treatment (i.e. a particular combination of genotypes at a given richness level).

A population of ten dandelion seedlings was planted in each plot, with all seedlings being of a single genotype in one-genotype plots, five seedlings per genotype in two-genotype plots, and so on. The seedlings were planted in random positions in a

triangular grid formation of 2 x 3 x 3 x 2 plants (see Figure 1 inset), so that each plant could be individually identified. Plants were 10 cm from each neighbour in the grid, for a density of about 185 plants per m². This density represents the high end of a spectrum of dandelion densities observed in the Vancouver area (personal observation).

Establishment of the Experiment

The field experiment was performed in Totem field, a 12 hectare research facility located on the UBC campus in Vancouver, BC Canada (Figure 2). The section of Totem used for our experiment was formerly maintained as a non-irrigated, regularly mown lawn. Species of *Poa*, *Plantago lanceolata*, and *Hypochaeris radicata* are dominant in this disturbed ecosystem. *Rhytidiadelphus squarrosus*, a lawn moss, *Medicago lupulina*, and *Trifolium* species are abundant in localized patches. *Taraxacum officinale* is also present in low abundance.

After laying out the experimental plots, but prior to establishment of the habitat type treatments, all plots were photographed and surveyed for initial vegetation composition. Vegetation composition was recorded for use as an environmental proxy, rather than recording soil moisture, soil depth, and so on. All species found within a given plot were recorded, and an estimate of their abundance was made. Species were categorized for each plot according to the following cover classes: 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75% and >75% cover. These estimations were made based on visual comparison with reference cards depicting the size of each category. Two separate observers first categorized species independently; final values are consensus values between both observers. Some species could not be identified beyond the genus level, and so were pooled with close relatives (e.g. *Poa sp.*).

Habitat type treatments were established in the first week of June 2007, approximately one week before “invading” dandelion seedlings into the plots. Mowed lawn plots were simply mowed as usual, to a height of about 5 cm above the litter layer. Fallow field plots were essentially “tilled” by shovel, in order to remove the sod layer. The sod in these plots was cut out down to about 15 cm, chopped into pieces, and then put back (root side up) into the plots. This had the effect of producing bare ground, largely free of other plants. This procedure was used, as opposed to removing the sod

entirely, so as to minimize differences in soil conditions between adjacent plots of different habitat types, and to retain the original seed bank.

Dandelion seedlings for this experiment were established individually from greenhouse-collected seed in 1 x 1 x 4.5 inch pots in partial shade at the field site (see Appendix A for details). Seeds were planted in April 2007, and by late June 2007 seedlings were large enough (3-7 leaves, with a 15 cm taproot) to survive transplantation into the field plots. The seedlings were acclimatized to full-sun field conditions for two weeks prior to planting.

Dandelion seedlings were planted mid-way through June 2007 over the course of three days (June 15th-17th). Holes were first punched into the ground in the desired grid pattern, and then seedlings were carefully transplanted into these holes from their pots. All plots were watered every 1-2 days throughout the summer to enhance survival, as seedlings are extremely sensitive to desiccation (von Hofsten 1954). Additionally, shade cloth was used to cover all rows for approximately one month in July 2007, as the plants were showing signs of severe sun-scorching. After one month the shade cloth was phased out by gradually uncovering the rows for longer and longer amounts of time. For the first month and a half, mortality was surveyed weekly and any dead seedlings replaced with a seedling of the same genotype. These seedlings were deemed to have died due to transplant shock.

Experiment Maintenance

Fallow field plots were hand weeded every 1-2 weeks until late August 2007, in order to minimize plot-to-plot variation in colonization of other species as dandelions established, after which there was no weeding. Mowed lawn plots were hand clipped with hedge shears to a height of about 5 cm above the litter layer, every 1-2 weeks throughout the summer of 2007. For the first two months the establishing dandelion seedlings were left untouched, to maximize early survival. Starting in September 2007, both the dandelions and the surrounding lawn were clipped once per month in the summer months. Aisles and perimeters surrounding the experimental plots were maintained with weekly mowing. Surrounding vegetation that started to overhang into plots was clipped on a biweekly basis.

Data Collection

We assessed individual plant performance over the course of the experiment, from planting in June 2007 to December 2008, in two ways. Firstly, we estimated plant size a total of eight times: four times in the growing season of 2007, and four times in the growing season of 2008. The four rounds of measurement were spaced at intervals of approximately one month in each growing season (see Appendix B for exact dates).

We estimated individual plant size as total leaf area (LA) using three measurements from each plant: the number of leaves greater than 4 cm long (N), the length of the longest leaf (L), and the maximum distance from the central leaf vein to a leaf lobe tip (measured perpendicularly to the central vein, this represents the maximum half width, W). These three measurements were previously determined to accurately predict total plant leaf area in a multiple linear regression. The regression model was parameterized with data taken from 56 plants collected around the UBC campus. Total leaf area was measured on a LICOR LI-3100C Leaf Area Meter. The final regression model was: $LA = 0.221 \times N \times L \times 2W$ ($R^2 = 0.95$).

Although plant size is usually a strong determinant of plant fitness (e.g. Gross 1981, Solbrig 1981, Samson & Werk 1986), we were also able to assess fitness more directly by recording the number of fruiting heads produced by each individual plant. Flowering commenced in August 2007 and continued until the end of the experiment, with peaks in October 2007, April-May 2008 and September 2008. During this period, all fruiting heads were counted and removed just prior to the release of seeds, after viable seeds had developed but before seeds could disperse to neighbouring experiments.

We converted the number of fruiting heads produced per plant into the number of seeds produced per plant, as the number of seeds per fruiting head can vary considerably (Ford 1981). The number of seeds per seed head was counted on field-collected, ripe fruiting heads for samples collected in the fall of 2007 and spring of 2008. In total, seeds were counted on 81, 98, 77, 44, and 92 fruiting heads for genotypes 2, 9, 16, 24, and 64 respectively. The number of seeds per fruiting head differed across genotypes and habitats. These effects individually varied by season (GLM with Poisson distributed data: genotype x season interaction, $p = 0.008$; habitat x season interaction, $p = 0.07$),

although the three-way interaction was not significant ($p = 0.06$). Therefore, we used genotype, habitat and season specific averages to make the conversion.

Seed Germination Trials

To assess the likely consequences across generations of genotypic differences in seed production, we conducted a second experiment on the establishment success from seed of each genotype, in each habitat type. A split plot design, with the whole plot completely randomized, was employed. Habitat (whether fallow field or mowed lawn) was randomly assigned to ten whole-plots, each with dimensions of 24 x 48 cm, for a total of five whole-plots per habitat type. Each whole-plot contained six sub-plots, with dimensions 8 x 18 cm (Figure 3). Next, each sub-plot within a whole-plot was randomly assigned a genotype (one of genotypes 2, 9, 16, 24, 64, or a control), for a single replicate of each genotype per whole-plot.

Whole-plots were established in a single strip along the eastern border of the main experiment at Totem field, on May 22nd 2008 (Figure 3). Habitat types were created as described previously. On May 23rd, 2008, fifty seeds of the appropriate genotype (or no seeds for the control) were sown into each sub-plot. In fallow field plots, seeds were loosely covered with a fine layer of soil (1-2 mm) to prevent seed movement. Seeds used for the germination trials originated from the fruiting heads previously collected in April and May 2008 for seed counting.

The number of dandelion seedlings was recorded for the first time on May 29th, 2008 (when germinants first appeared) and for the last time on October 21st, 2008. Between these two dates, germinants were counted regularly on a timeline commensurate with the rate of appearance of new seedlings. Roughly, seedlings were counted every two days for the first two weeks, then on a weekly basis for two months, and then on a monthly basis for the duration of the germination trials (as no new germinants were observed).

Data Analysis

Habitat and Richness Effects

To test for effects of genotypic richness, habitat type and their interaction on the invasion success of our dandelion populations, we performed an analysis of covariance (ANCOVA) on two measures of population productivity (covariate described below). The first was the summed leaf area of all dandelions in a plot, at a given measurement date, and the second, the total number of seeds produced per plot over the course of the experiment. Hence, there were seven ANCOVAs in total: one for seed number, and six for leaf area (one for each date starting two months after establishment of the experiment). Productivity data were transformed (Table 3) to meet the assumptions of the analysis: normality and homoscedasticity of the residuals. Post-hoc Tukey's HSD tests were conducted, but not included in the results as they were judged to be too conservative. With 15 comparisons, the adjustment to the p-values was severe, and the test results were not consistent with those of the ANCOVAs.

We included a covariate in our analyses to account for spatial variation in plot quality for general plant growth. The covariate was the first principal component, hereafter referred to as "prin1", from a principal components analysis on the vegetation composition data collected for each plot prior to the start of the experiment (see Appendix C for details). Prin1 explained 28% of the variation in vegetation composition, and was negatively correlated with dandelion productivity throughout the experiment. As this correlation was seen in both habitat types, even the fallow field (where all vegetation was removed), prin1 seemed to represent an inverse measure of soil quality for plant growth. Prin1 was only used as a covariate in the analyses after confirming that it did not interact with habitat or richness ($p > 0.05$ in all cases).

Richness was treated as a categorical variable with three levels: low richness for single genotype plots, medium richness for two genotype plots, and high richness for four or five genotype plots. We decided to transform richness into a categorical variable, rather than keeping it continuous, in part because of the large differences in sample size across richness treatments. Owing to the genotyping error, our design was no longer balanced, with many more replicates of single genotype plots than any other richness (Table 2). Pooling the four and five genotype plots resulted in greater evenness of

sample sizes across richness levels (low: $N = 35$, medium: $N = 25$, high: $N = 30$). Additionally, the relationship between plot genotypic richness (treated as continuous) and plot productivity was nonlinear, making analysis difficult.

Partitioning the Biodiversity Effect

We also tested for an effect of genotypic richness on plot productivity by comparing the performance of genotypes in polyculture (or mixtures: multiple genotype plots) to that in monoculture (single genotype plots), by applying the widely-used methods of Loreau and Hector (2001). For each genotype in a mixture, the expected yield (if there is no effect of richness) is the average yield of that genotype in monoculture multiplied by its initial proportion in the mixture. Summing these expected yields for all genotypes in a mixture gives the expected yield for the plot, Y_E . The difference between the observed yield of a mixture, Y_O , and the expected yield is the “net biodiversity effect”, $\Delta Y = Y_O - Y_E$. We further decomposed the net biodiversity effect for each mixture into complementarity and selection effects, using the additive partition of Loreau and Hector (2001).

As with the ANCOVA approach, we compared the yield of genotypes in monoculture and mixture for seven variables: seed number and leaf area at six sampling dates (September 2007 – August 2008). However, we first “corrected” the raw productivity data to account for variability in *prin1*. The correction was made by first regressing total plot productivity on *prin1*, and then taking the residuals from the regression. The corrected plot productivity values were then the plot residuals from the regression plus the mean plot productivity. The corrected productivity for a given plant, or genotype, in a plot was then the corrected plot productivity multiplied by the proportion of the total plot productivity that plant accounted for in the uncorrected data.

We performed separate regressions for each habitat, as average dandelion productivity was very different in the two habitats. Similarly, we calculated the net biodiversity effect, and its components, separately for polycultures in each habitat type. Next, we tested to see if the mean net, complementarity, or selection effects differed from zero (the null expectation – if genotypes perform identically in monoculture and mixture). Polycultures were pooled across richness levels, as there was no relationship between richness and effect size (as tested by linear regression; all slopes not

significantly different from zero, $p > 0.05$). Hence, we were able to use simple t-tests when the data were normally distributed or could be transformed to follow a normal distribution. In severe cases of non-normality, as with most cases of the selection effect, the more conservative, distribution-free sign-test was used.

Seed Germination Analysis

We analyzed only a single measure of seedling emergence, despite recording emergence over time. Genotypes germinated at different rates, but all genotypes eventually reached a plateau in the number of seedlings in a given habitat type. This number of seedlings was maintained for at least a month before declining, likely as a result of self-thinning. Therefore, we used the maximum number of seedlings for each sub-plot, minus the maximum number of seedlings observed in the control sub-plot of the whole-plot, as our estimate of seedling emergence. Similar results were found when using the number of seedlings at the date closest to most genotypes' peak values (July 2008).

The effects of genotype, habitat and genotype-by-habitat interactions on the maximum number of seedlings were determined using restricted maximum likelihood (REML), in a mixed model. While habitat and genotype were treated as fixed effects (as we selected habitat types and genotypes objectively for our experiment), the effect of whole-plots (to which habitats were assigned) was treated as random. The significance of the fixed effects was determined using an F statistic with the degrees of freedom approximated using the Satterthwaite method (Littell et al. 1996).

The majority of the statistical analyses were performed in SAS, version 9.1 (SAS Institute, Cary, North Carolina, USA). Some simple statistics were obtained using R, version 2.7.0 (R Development Core Team 2008).

RESULTS

Habitat and Richness Effects

The summed leaf area of all plants in a plot (“plot leaf area”) varied over time, with flushes of growth in the spring and fall, and die-back in between (Figure 4). However, the average plot leaf area was always highest in the fallow field, ranging from 2-5 times greater than the average plot leaf area in the mowed lawn. Consistent with our prediction that increasing genetic diversity will increase average plant fitness, plot leaf area increased with plot genotypic richness. In most cases, this richness effect did not depend on the habitat in which the plants grew (no habitat x richness interaction) (Table 3). One exception occurred in July 2008, when the habitat-by-richness interaction was significant, but the general trend showed no interaction. Many of our analyses involved multiple tests (e.g. for each habitat, and for each measurement date), and we did not correct p-values to control the Type I error rate. In our interpretation of analyses, we interpret only general trends, and not single p-values.

Although there was largely no richness-by-habitat interaction, the effect of richness was most evident in the fallow field. Average plot leaf area increased from the lowest richness level (single genotype plots) to the highest (4-5 genotype plots) by $52\% \pm 13\%$ (1 SE, where measurement dates are replicates) in the fallow field, but only by $20\% \pm 5\%$ in the mowed lawn. Within habitats, the effect tended to increase over time, reaching its maximum in July 2008 (for the fallow field) or August 2008 (for the mowed lawn). The shape of the relationship also changed slightly with time, with the productivity of high richness plots increasing compared to medium (2 genotype) richness plots. In terms of the rank order of the means for each richness level, at early measurement dates, means for the high and medium richness levels were roughly equal, and both greater than the mean of the low richness level. At later measurement dates, the high richness mean was greater than the medium richness mean, which exceeded the low richness mean.

The results for plant seed number closely resembled those for plant leaf area (Figure 5). Plots in the fallow field produced twice as many seeds, on average, as plots in the mowed lawn (a main effect of habitat). Plot total seed number increased with

increasing plot richness (a main effect of richness). Plots of medium and high richness produced significantly more seeds than plots of low richness (Tukey-Kramer test: $p = 0.02$ and $p = 0.0009$, respectively), but the medium and high richness levels were not significantly different from each other ($p = 0.8$). There was no interaction between the richness and habitat effects (see Table 3).

Variability within Richness Levels

Average plot leaf area was highly variable among genotype combinations within richness levels (Figure 6). Differences among genotypic combinations, within the same richness level, were more exaggerated in the fallow field than in the mowed lawn. For example, while the average leaf area of genotype 9 was only twice that of the second most productive genotype in the mowed lawn, it was more than three times greater in the fallow field. In the two genotype plots, treatments including genotype 9 had the greatest average leaf area, while the combination of genotypes 24 and 64 had the lowest average. Similarly, in the four genotype plots, the sole treatment lacking genotype 9 had the lowest mean leaf area. In neither habitat did the average leaf area of a polyculture exceed that of genotype 9 in monoculture (although some were nearly equal). This suggests that selection effects ought to dominate any observed biodiversity effects, rather than complementarity.

Net Biodiversity, Complementarity and Selection Effects

In the fallow field, mixtures produced more leaf area than expected based on monoculture yields ($\Delta Y > 0$). Thisoveryielding (positive net biodiversity effect) occurred for each measurement date (Figure 7a), and is consistent with a strong richness effect. Decomposition of the net effect (ΔY) into selection versus complementarity revealed that it resulted largely from a positive selection effect. The selection effect mirrored the net effect over time, and was significantly greater than zero at most dates (Table 4). This suggests that mixtures were dominated by highly productive genotypes, which enhanced the summed leaf area. The decomposition also hinted at some level of complementarity amongst genotypes, which could enhance individual plant productivity in mixture, even for genotypes with low monoculture productivity. The average complementarity effect was always greater than zero, although this difference was only

significant at two midsummer measurement dates. The seed number data also showed a significant positive net biodiversity effect (Figure 8) generated by a significant positive selection effect. As with the leaf area results, the average complementarity effect was also positive, but not significant (Table 5).

In the mowed lawn, effect sizes were much smaller than in the fallow field, reflecting the smaller relative size of the plants (Figure 7b). The average net biodiversity effect in the mowed lawn, while consistently positive, was not significantly greater than zero at any time (Table 4). The mean selection effect was significantly negative for the four earliest dates, meaning that genotypes with the least leaf area in monoculture derived the greatest benefit from growth in polyculture. This negative selection effect disappeared by the end of the experiment. The complementarity effect mirrored the net effect, and was always greater than zero, although not significantly so. Consequently, the complementarity and selection effects, having opposite signs, tended to cancel each other out at early dates (resulting in a small net effect). For seed production (Figure 8), the mean net effect was positive but not significant, in agreement with the leaf area results. However, the positive complementarity effect was significant, while the negative selection effect was not (Table 5).

Genotype Performance in Polyculture vs. Monoculture

In terms of per-plant productivity of individual genotypes, only genotypes 2 and 9 consistently performed better in polyculture than monoculture in the fallow field. These were the two genotypes showing the greatest average leaf area (Figure 9a), and seed production (Figure 10a). This is consistent with a positive selection effect, whereby these two highly productive genotypes came to dominate the mixtures. For leaf area production (Figure 9a), the three remaining genotypes (16, 24, 64) generally performed equally well in monoculture and polyculture, or better in monoculture. An exception occurred in the months of June and July 2008, when genotype 24 produced more leaf area in polyculture than monoculture. This explains the strong complementarity effect for these dates (Table 4); a majority of genotypes, of both large and small average leaf area, obtained a greater size in mixture versus monoculture. For seed production (Figure 10a), the three remaining genotypes performed better in monoculture than in polyculture.

In the mowed lawn, a different pattern of individual genotypic productivity emerged. Here, genotypes 16 and 64 consistently performed better in monoculture than polyculture, while the three remaining genotypes (2, 9, 24) typically grew larger in polyculture than monoculture, or at least performed equally in both (Figure 9b). Hence, genotypes that showed both high productivity (e.g. 9) and low productivity (e.g. 24) grew larger on average in polyculture than monoculture. The smaller genotypes (i.e. 2 and 24) actually derived greater benefit from growth in polyculture than the largest genotype (9), as can be seen from their greater vertical height above the 1:1 line. This is consistent with the negative selection effect observed at early dates (Table 4), which means that smaller genotypes obtained the greatest benefit in polyculture. When the selection effect became positive in July 2008 (Figure 7b), genotypes 2 and 24 had averages closer to the 1:1 line. Similarly, for seed production (Figure 10b), genotypes 16 and 64 performed better in monoculture, while genotypes 2, 9, and 24 performed better in polyculture.

Seed Germination Results

Genotypes varied in the maximum number of established seedlings in the fallow field, but not in the mowed lawn (Figure 11). There was a significant genotype-by-habitat interaction ($F_{4,32} = 3.47$, $p = 0.02$), and main effects of genotype ($F_{4,32} = 3.72$, $p = 0.01$) and habitat ($F_{1,8} = 15.9$, $p = 0.004$). The rank-order of genotypes, from highest to lowest production of seedlings, changed between habitats. In the fallow field genotypes 2 and 16 produced more seedlings on average than genotype 24, while all genotypes did equally poorly in the mowed lawn. Hence, genotype 24 produced relatively (in comparison with other genotypes) more seedlings in the mowed lawn than in the fallow field. The absolute number of established seedlings for any genotype was always highest in the fallow field.

DISCUSSION

Our study showed that the genotypic richness of an invading population of dandelions can influence the establishment success of all individuals in the population. Increasing genotypic richness tended to increase plant fitness, although the strength of this effect varied depending on the habitat type. Both selection and complementarity effects contributed to the richness effect, but the relative importance of the two mechanisms was quite different in the two habitat types, and also varied over time. We first discuss the role of genetic diversity in mediating invasion success, and the mechanisms responsible, and then we evaluate the relative importance of diversity effects in comparison with other factors that may influence invasion success. Lastly, we discuss the influence of environmental context on the strength of diversity effects, and make some general conclusions.

The Effect of Population Genotypic Richness on Invasion Success

Analyses on both of our measurements of plant fitness, total leaf area and seed production, were consistent, showing strong, significant main effects of richness and habitat type (Figures 4 & 5). Diverse plots had consistently higher productivity (as measured by leaf area or seed number) than monocultures, and the magnitude of this effect appeared to increase with time. Agricultural studies of crop yields generally show similar improvements in biomass, when multiple cultivars (of the same species) are grown together (Smithson & Lenné 1996). Additionally, experimental studies of terrestrial plants (e.g. Crutsinger et al. 2006, 2007), an alga (Bell 1991), a seagrass (Hughes & Stachowicz 2004, Reusch et al. 2005), a protozoan parasite (de Roode et al. 2005), and an invertebrate insect (e.g. Jones et al. 2004, Mattila & Seeley 2007) have found enhanced productivity of more genetically diverse populations. Prior to our study, studies of terrestrial plants had only measured productivity at a single time point, and so it was unknown whether the richness effects observed might have changed over time. In the seagrass, *Zostera marina*, evidence for changes in the richness effect over time is contradictory. In one study (Reusch et al. 2005), the effect remained strong over a single growing season, even appearing to magnify with time. In contrast, in another study

(Hughes & Stachowicz 2004), more diverse plots retained a greater number of shoots after a goose grazing event, but this effect was transient, disappearing after a few months. Hence, our results support the conclusion emerging from recent studies across a variety of systems that increasing genetic diversity can raise population productivity and suggest that these diversity effects may become stronger with time.

Averaged across both habitats, and all measurement dates, the mean total plot leaf area of polycultures was 36% higher than that of monocultures. (A similar increase of 27% was seen for seed number). This increase was quite variable, ranging from 5-103%, and generally was greatest in the fallow field and at later measurement dates. The magnitude of this difference is consistent with results from comparable studies of genetic diversity and productivity, which typically find an increase in productivity from monocultures to mixtures of about 30%. For example, 6-genotype and 12-genotype plots of *Solidago altissima* had 26% and 36%, respectively, higher aboveground net primary productivities than single genotype plots (Crutsinger et al. 2006). In another study of *S. altissima*, stem density, an estimate of biomass, increased by 45% from single genotype plots to 12-genotype plots (Crutsinger et al. 2007). Beds of seagrass with 8-genotypes had about 30% higher stem densities compared to single genotype beds (Hughes & Stachowicz 2004). At the low end of the spectrum, mixtures of the algae *Chlamydomonas reinhardtii* showed an increase of 10% in production compared to monocultures. The average productivity gain of mixtures of genotypes over monocultures in our experiment was only about half of that typically seen in comparable studies of species richness. Mixtures of species produce an average of 70% more biomass than species monocultures (Cardinale et al. 2007). In terrestrial and aquatic plant populations, it appears that genetic diversity may have a substantial, positive effect on productivity, but this effect is of lower magnitude than species diversity effects.

As very few studies to date have examined the consequences across generations of genetic diversity effects, we conducted separate seed germination trials to assess the likely next-generation consequences of our diversity treatments, at least as far as selection effects are concerned. The positive richness effect observed in our experiment, on first-generation plant fitness (as measured by seed production), does not necessarily translate into proportional differences in the number of individuals in the next generation.

Seeds of different genotypes might have different viabilities, germination rates, seedling survival, and so on. In the mowed lawn, seedling emergence rates were roughly equal for all genotypes (Figure 11). Hence, the observed differences in seed production between genotypes should translate into similar differences in seedlings in the next generation. In the fallow field, seed germination rates varied among genotypes, with modest differences between genotypes 2 and 16 (highest number of seedlings), genotype 9 (next highest) and genotypes 24 and 64 (lowest number of seedlings). By multiplying the average number of seeds per plant for each genotype (pooled across richness levels) with the mean genotypic seedling emergence (i.e. what proportion of seeds germinated), we obtained a rough estimate of the number of seedlings for plants of each genotype expected in the next generation (Table 6). The rank order of expected seedlings in the next generation (from most to least: 9, 2, 16, 64, 24) is nearly the same as the rank order of seed production in this generation (9, 2, 16, 24, 64). Therefore, differences in seed production should translate into differences in the number of seedlings, and the selection against genotypes 24 and 64 expected based on poor adult-plant fitness should be exacerbated by low seedling emergence rates.

Mechanisms Underlying the Richness Effect

Comparing observed polyculture yields to the null expectation based on monoculture yields (calculating ΔY , the net biodiversity effect) showed that there was significant “overyielding” ($\Delta Y > 0$) in the fallow field, but not the mowed lawn ($\Delta Y = 0$). This means that in the fallow field the average productivity of individual genotypes differed between monoculture and polyculture, being highest in polyculture. A zero net effect, as observed in the mowed lawn, could result from one of two reasons. One possibility is that all genotypes perform equally well in monoculture and polyculture. Alternatively, genotypes might perform differently in monoculture versus polyculture, but the differences cancel each other out. This could happen with a negative selection effect and a positive complementarity effect of equal magnitude, or if the distances between each genotype and the 1:1 line (in Figure 9) are non-zero but do not covary with monoculture yield, giving a zero selection effect and zero complementarity (equal differences above and below the line).

The positive net effect of diversity in the fallow field mainly resulted from a positive selection effect, although there was some evidence of complementarity as well (Figures 7 & 8). A positive selection effect indicates that the most productive genotypes in monoculture have come to dominate in the polycultures. This interpretation is confirmed for our experiment by looking at the performance of individual genotypes in polyculture versus monoculture: the two largest genotypes in monoculture, 2 and 9, derived the greatest benefit from growth in polyculture (Figure 9). These genotypes grew larger in polyculture than in monoculture, perhaps at the expense of the smaller genotypes. In the two months for which the complementarity effect was significant, genotypes 16 and 24 also performed better in polyculture than in monoculture. These were the two driest months of the experiment, and plants experienced considerable leaf loss. This could potentially have created temporary opportunities for these smaller genotypes, as light became less limiting. Genotypes 2 and 9 tended to form very dense stands at other times of the year, often completely covering the smaller genotypes. In the few studies that have inferred selection or complementarity effects for genetic diversity effects on productivity, both types of effects have been found (Hughes et al. 2008). Positive selection effects are typically inferred in agricultural studies (e.g. Smithson & Lenné 1996), while a number of studies in other experimental systems found complementarity (e.g. Jones et al. 2004, de Roode et al. 2005, Crutsinger et al. 2006).

A negative selection effect, indicating a greater degree of overyielding of genotypes with low productivity in monoculture, and a positive complementarity effect were found in the mowed lawn. These two effects nearly cancel each other out (the complementarity effect is slightly larger in magnitude), resulting in a net effect that is not significantly greater than zero. The selection effect was significantly less than zero for the leaf area data (Figure 7), but not for the seed number data (Figure 8), while the reverse pattern was observed for the complementarity effect. This discrepancy could be biologically meaningful, if the effect of plot genotypic richness had different effects on different fitness components, although a simpler explanation is more likely. Looking at the relative performance of each genotype in polyculture versus monoculture (Figure 9), both mechanisms fit with the observed patterns. Particular genotypes that were small (24), medium (2), and large (9) in monoculture all tended to perform better in polyculture

than in monoculture, creating a positive complementarity effect. As can be seen most clearly in the seed number results (Figure 10), the smaller genotypes (24 and 2) actually derived the greatest benefit from growth in polyculture, rather than the largest one (9), creating the negative selection effect. This suggests a limitation of the partitioning approach as applied to our data; slight changes in the polyculture versus monoculture performance of individual genotypes (such as the slight shift of genotype 24 above the 1:1 line) result in different mechanisms dominating statistically. A very similar partitioning of mechanisms was found in seagrass beds recovering from a climatic extreme (Reusch et al. 2005). In this system, a negative selection effect was found, but it was outweighed by complementarity among genotypes, resulting in a net positive effect of diversity. Hence, both types of mechanisms (positive or negative selection effects, and complementarity) play a role in the outcome of diversity experiments.

The dynamics of the mowed lawn differed from the fallow field, no doubt in part as the result of regular clipping, which may have contributed to the negative selection effect. In the mowed lawn, the largest genotypes would have suffered the greatest loss of leaf area from mowing, while small, compact genotypes remained largely untouched. Hence, the largest genotypes would not have had the same opportunity to dominate polyculture plots as in the fallow field.

In both habitats, there was some indication that genotypes might be differentiated on niche axes that result in complementary resource use or facilitation among genotypes, although this was not consistent. Although we have no direct evidence as to what form the positive interactions among genotypes might take, a few mechanisms are possible. Genotypes might differ in resource use in complementary ways (Tilman 1999); for example, different dandelion genotypes differ markedly in the timing of their flowering peaks (data not shown), and thus may exploit key resources (e.g. soil nutrients, moisture) at different times (see also Vavrek 1996). If genotypes varied in their susceptibility to common pathogens, genotypes in more diverse plots could benefit from the increased distance between individuals of the same genotype. This “dilution” of the pathogen reduces the inoculum received by susceptible individuals, and is considered to be the most important mechanism contributing to disease reduction in agricultural mixtures (Wolfe 1985). This mechanism was hypothesized to be partly responsible for the

reduction of rice blast in diverse plots, described previously (Zhu et al. 2000).

Dandelions are susceptible to a range of pathogens (Stewart-Wade et al. 2001), including a powdery mildew and a rust in our system. A related hypothesis is that dandelions may have benefited from “associational resistance” (e.g. Hamback 2000) to their herbivores. Further experiments are needed in order to distinguish which mechanism, or combination of mechanisms, was responsible for the complementary interactions between genotypes in our experiment.

Relative Importance of Genetic Diversity Effects

In our experiment, there was a strong effect of habitat type on plot productivity. Plot total leaf area (averaged across both habitats, and all time periods) (Figure 4) and plot seed number (Figure 5) were on average 3.9 times greater in the fallow field than in the mowed lawn. This result clearly confirms that the fallow field was the least stressful, and hence most productive, habitat for *T. officinale*. Plants were likely able to achieve a higher mean fitness in the fallow field for two reasons. Firstly, upon planting, seedlings faced little competition from other species (as they were planted into bare ground). As time passed, other species were allowed to colonize the plots, but the density of these species remained much lower than in the mowed lawn; bare ground was always in evidence in the fallow field, but never in the mowed lawn. Secondly, plants in the mowed lawn had leaves removed on a regular basis as part of the mowing treatment, prompting a faster rate of leaf turn-over, and presumably reducing whole-plant photosynthesis.

Surprisingly, there was only limited evidence that the relative performance among genotypes might vary by habitat. The rank-order of genotypes (from lowest to highest fitness) remained largely unchanged across the two habitats. This was surprising given that dandelion genotypes from several North American populations have been shown to vary in ecologically important traits (e.g. Vavrek et al. 1997), which might be suited to different environments, and the strong contrast between the growing conditions in our two habitat treatments. One study (Solbrig & Simpson 1977) directly demonstrated a genotype-by-environment interaction in dandelions, by showing that dandelion genotypes had differential tolerance to disturbance (environments had different disturbance regimes). Genotype-by-environment interactions are key to understanding the

maintenance of genetic variation, as they lead to heterogeneous selection pressures (Via & Lande 1985). Thus, it remains unclear how the different genotypes used in our experiment are maintained in the regional population.

Habitat type had a greater effect on plant productivity than plot genotypic richness. The 300% mean fitness increase of plants growing in the fallow field versus mowed lawn is ten times greater than the ~30% increase for plants in polyculture versus monoculture. This seems to indicate that the richness of an invading population, although of consequence, is of lesser importance for population success than which habitat is invaded. The relative importance of genetic diversity effects in comparison with other factors structuring ecological communities, such as variation in abiotic conditions, competition between species, and predation, is poorly understood (Hairston et al. 2005, Johnson & Stinchcombe 2007). In species diversity research, diversity effects uncovered in small-scale, controlled experiments may be overwhelmed by other factors at larger scales (Levine 2000). A well described example concerns the relationship between native and exotic species richness. At small scales this relationship is negative, indicating that more species rich communities are better at resisting invasion (e.g. Hector et al. 2001, Fargione & Tilman 2005). However, at larger, regional scales the observed relationship is positive, because the same environmental factors (e.g. resource availability, or heterogeneity) that favour native species also favour exotic species (e.g. Shea & Chesson 2002, Davies et al. 2005).

The few studies that address the relative importance of genetic identity or diversity effects give mixed results (Hughes et al. 2008). For example, in a study of *Oenothera biennis* and its associated arthropods, differences between genotypes accounted for 41% of the variation in arthropod diversity. This genotype effect explained more variation in the arthropod community than did environmental variation in microhabitat (blocked within habitat), but less than variation in habitat (Johnson & Agrawal 2005). Similarly, in populations of *Populus tremuloides*, variation in nutrient enrichment and genetic identity influenced leaf litter decomposition to a greater degree than did genetic diversity (Madritch et al. 2006). Therefore, other factors, such as environmental conditions, may be more influential to population performance than

genetic diversity. The magnitude of diversity effects seems to depend on the system under study, and on the magnitude of differences among habitats.

The Influence of Environmental Context on Genetic Diversity Effects

Although there was no significant interaction between genotypic richness and habitat in the ANCOVA models, two lines of evidence suggest that the richness effect was stronger in the fallow field habitat. Firstly, the increase in plot leaf area from monocultures to the highest richness plots averaged 52% in the fallow field, but only 20% in the mowed lawn (31% and 23%, respectively, in the seed number data). Secondly, there was significant overyielding in the fallow field, but not in the mowed lawn. These results suggest that, although the direction of the richness trend was the same in both habitats (increasing productivity with richness), the effect was more exaggerated in the fallow field. The reason that the ANCOVA models did not find a significant interaction between plot richness and habitat may have been a consequence of our data transformations. We analysed power-transformed data in order to meet ANCOVA assumptions. As with log transformations, power transformations can alter interaction strengths, by capturing multiplicative differences rather than additive ones. Hence, we might have observed an interaction between richness and habitat, if we had used the raw data.

In contradiction to the prediction that the most stressful habitat would show the strongest richness effect, based on previous work showing genetic diversity effects only after disturbance (Hughes & Stachowicz 2004, Reusch et al. 2005), our results showed the greatest effect in the least stressful habitat. Our interpretation of this result is that, in the fallow field, because the plants were so much larger, dandelions likely interacted mainly with other dandelions, resulting in strong intraspecific interactions. In the mowed lawn, plants remained small and interacted mainly with the surrounding matrix of vegetation, resulting in interspecific interactions that were stronger than intraspecific ones. Hence, populations with greater genetic variation may have higher colonization success and subsequent plant fitness, but this effect will be greatest when intraspecific interactions tend to dominate interspecific ones. To the extent of our knowledge, this is a

unique result, as our experiment represents the first explicit test of the stress hypothesis. This result contrasts with those of two studies on seagrass beds that did not manipulate environmental conditions directly (Hughes & Stachowicz 2004, Reusch et al. 2005). In these studies, the effects of genetic diversity were revealed only after an unanticipated stressful event (i.e. goose grazing, or a temperature extreme). Without further experimental work, we are unsure how to reconcile these two contradictory results. The influence of environmental context on the ecological effects of genetic diversity remains a largely unstudied topic.

Conclusions

Understanding the potential effects of biodiversity on processes at the population, community and ecosystem level remains an important topic in ecology (Hooper et al. 2005). Our results indicate that genetic diversity can have important ecological consequences for populations, enhancing vegetative productivity and seed production. However, the strength of this effect depended on habitat context, being stronger in the more productive environment. The effect of plot genotypic richness on fitness observed in our experiment supports other recent work showing a similar relationship (e.g. Johnson et al. 2006, Crutsinger et al. 2006, 2007). Greater invasion success of diverse populations could influence species diversity at the community level. For example, greater genetic diversity may positively influence species diversity, if it allows for more species to successfully establish in the community. Conversely, it may negatively influence species diversity, if genetic diversity in resident species tends to limit invasions. In terms of conservation applications, our study indicates that minimizing the number of genotypes introduced in an exotic species may help control its spread. The more genotypes that are introduced in an exotic species, the greater the chance that a very invasive genotype will be present, but also the greater the opportunity for complementarity among genotypes to enhance overall population fitness.

TABLES

Table 1. Outline of initially planned diversity treatments, including the number of unique combinations of genotypes used at each richness level (out of all possible combinations), and the number of replicates at each richness level.

Genotypic Richness	# Combos/(# Possible Combos)	Total Replicates
1	6/6	e.g. $6 \times 5 = 30$
2	6/15	30
5	6/6	30

Table 2. Description of diversity treatments as completed. The numbers in the composition column refer to specific genotypes.

Genotypic Richness	Genotypic Composition	No Replicates
1	2	5
	9	5
	16	15
	24	5
	64	5
2	2+16	10
	9+24	5
	9+64	5
	24+64	5
4	2+9+16+24	5
	2+9+16+64	5
	2+16+24+64	5
	9+16+24+64	5
5	2+9+16+24+64	10

Table 3. Results of ANCOVAs on two measurements of plant productivity, testing for effects of prin1, habitat, richness, and a habitat-by-richness interaction. Prin1 refers to the first axis of a principal components analysis, and is used as a covariate representing environmental conditions in each plot. Pwr(x) means that plot values were raised to the power of x, before analysis.

Variable	Date	Transformation	Effect	F	df	p	
Plot Leaf Area (cm ²)	Sept 07	pwr(0.16)	prin1	64.66	1, 173	< 0.0001	
			habitat	321.39	1, 173	< 0.0001	
			richness	2.98	2, 173	0.0534	
			habitat x richness	0.96	2, 173	0.3856	
	Oct 07	pwr(0.11)	prin1	59.52	1, 173	< 0.0001	
			habitat	310.00	1, 173	< 0.0001	
			richness	3.52	2, 173	0.0318	
			habitat x richness	1.72	2, 173	0.1816	
	Apr 08	pwr(0.10)	prin1	37.70	1, 173	< 0.0001	
			habitat	175.11	1, 173	< 0.0001	
			richness	4.50	2, 173	0.0124	
			habitat x richness	0.97	2, 173	0.3816	
	June 08	pwr(0.16)	prin1	24.45	1, 173	< 0.0001	
			habitat	174.81	1, 173	< 0.0001	
			richness	8.88	2, 173	0.0002	
			habitat x richness	2.45	2, 173	0.0895	
	July 08	pwr(0.18)	prin1	39.47	1, 173	< 0.0001	
			habitat	42.12	1, 173	< 0.0001	
			richness	13.07	2, 173	< 0.0001	
			habitat x richness	3.41	2, 173	0.0352	
	Aug 08	pwr(0.13)	prin1	20.52	1, 173	< 0.0001	
			habitat	42.02	1, 173	< 0.0001	
			richness	9.70	2, 173	0.0001	
			habitat x richness	1.36	2, 173	0.2587	
	Plot Seed Number	Total 2007 + 2008	sqrt	prin1	37.85	1, 173	< 0.0001
				habitat	308.07	1, 173	< 0.0001
				richness	7.68	2, 173	0.0006
				habitat x richness	1.51	2, 173	0.2229

Table 4. Results from one-sample tests on leaf area data, evaluating whether the mean net biodiversity effect and its two components, complementarity and selection, differed from zero. T-tests were used for all net and complementarity effects, and sign-tests were used for all selection effects. Pwr(x) means that the data were raised to the power of x, before analysis. P-values are shown to evaluate significance.

Habitat	Effect	Transformation	Measurement Date					
			September 2007	October 2007	April 2008	June 2008	July 2008	August 2008
Fallow Field	Net Effect	sqrt	0.0497	0.0007	0.0038	< 0.0001	0.0001	0.0005
	Complementarity	pwr(0.75)	0.1437	0.1201	0.0531	< 0.0001	0.0003	0.3152
	Selection	none	0.0027	< 0.0001	< 0.0001	0.0300	0.1048	0.0004
Mowed Lawn	Net Effect	sqrt	0.8432	0.7850	0.6467	0.5660	0.8268	0.1135
	Complementarity	sqrt	0.6355	0.4378	0.0841	0.1458	0.6675	0.1365
	Selection	none	0.0145	0.0065	0.0065	0.0300	0.5900	0.5900

Table 5. Results of one-sample tests on seed number data, evaluating whether the net, complementarity or selection effects differed from zero. T-tests were used for all analyses except the selection effect in the mowed lawn, where a sign-test was used. Pwr(x) means that the data were raised to the power of x, before analysis.

Habitat	Effect	Transformation	p
Fallow Field	Net Effect	none	< 0.0001
	Complementarity	none	0.0646
	Selection	none	< 0.0001
Mowed Lawn	Net Effect	sqrt	0.2096
	Complementarity	pwr(0.75)	0.0063
	Selection	none	0.2806

Table 6. The mean number of seedlings expected in the next generation for plants of each genotype, in the fallow field.

Genotype	Expected Seedlings
2	483
9	619
16	379
24	106
64	107

FIGURE CAPTIONS

Figure 1. Pictorial representation of the layout of the field plots within the experimental area. Rows of plots are labelled 1 through 9 from north to south. The inset (at top) shows that plots within rows are adjacent and that habitat types are intermixed. The layout of plants within plots in a triangular grid, with four rows, is also shown as dots within plots, in the inset.

Figure 2. Photo of the experiment in spring 2008, when the plants were in their spring flowering. Each plot is marked with wooden stakes. Both fallow field and mowed lawn plots can be seen.

Figure 3. Pictorial representation of the layout of the seed germination trials. Plots are arranged in a single column from north to south, and habitat types are randomly intermixed. The inset shows the layout of the six subplots within each plot.

Figure 4. (a-f) Mean plot leaf area (cm^2) \pm 1 SE at each of six dates from September 2007 to August 2008 by habitat and genotypic richness. The upper line is the fallow field (\bullet), the lower line the mowed lawn (\circ). Plot leaf area was corrected to account for variation due to the covariate prin1 (a measure of soil productivity), before the means were calculated (see text for details). There is a significant main effect of habitat and of genotypic richness for all dates (ANCOVA on transformed data, see p-values on figures). In July 2008 (e), there is also a significant habitat-by-richness interaction ($p = 0.04$). Richness was treated as a categorical variable with 3 levels: low (1 genotype), medium (2 genotypes) and high (4-5 genotypes).

Figure 5. Mean plot total seed number \pm 1 SE by habitat and genotypic richness. The upper line is the fallow field (\bullet), the lower line the mowed lawn (\circ). Plot seed number was corrected to account for variation due to the covariate prin1, before the means were calculated (see main text for details). There is a significant main effect of habitat and of richness (ANCOVA on SQRT-transformed data, see p-values on figure), but no

interaction ($p = 0.2$). Richness was treated as a categorical variable with 3 levels: low (1 genotype), medium (2 genotypes) and high (4-5 genotypes).

Figure 6. Mean plot leaf area (cm^2) \pm 1 SE in August 2008 for each combination of genotypes. Plot leaf area was corrected to account for variation due to the covariate prin1 before the means were calculated (see main text for details). Means are shown separately for (a) the fallow field and (b) the mowed lawn. Dotted lines separate means for plots of low (1 genotype), medium (2 genotypes) and high (4-5 genotypes) genotypic richness.

Figure 7. Mean net biodiversity effects (\bullet), complementarity effects (\circ) and selection effects (\blacktriangledown) \pm 1 SE for plant leaf area (cm^2) over time. Lines connect means of the same effect type across the six sample dates. Means are shown separately for (a) the fallow field and (b) the mowed lawn. The dotted line indicates an effect size of zero. A star (*) indicates that the mean is significantly different from zero (t-test for net and complementarity effects, data transformed if not normally distributed, $p < 0.05$; sign test for selection effects, $p < 0.05$).

Figure 8. Mean net biodiversity, complementarity and selection effects for plant seed number in each habitat. Error bars are 1 SE. A star (*) indicates that the mean is significantly different from zero (sign-test for selection in the mowed lawn; otherwise, t-tests, data transformed if not normally distributed, $p < 0.05$).

Figure 9. Dandelion genotype polyculture (plot genotypic richness > 1) versus monoculture (plot genotypic richness =1) means \pm 1 SE for leaf area (cm^2) at each of six dates from September 2007 to August 2008. Means are shown separately for (a) the fallow field and (b) the mowed lawn. Genotype leaf area was corrected to account for variation due to the covariate prin1 and log-transformed, before the means were calculated (see main text for details). The dotted line indicates a 1:1 relationship. Numbers refer to specific genotypes.

Figure 10. Dandelion genotype polyculture (plot genotypic richness > 1) versus monoculture (plot genotypic richness =1) means \pm 1 SE for total seed number. Means are shown separately for (a) the fallow field and (b) the mowed lawn. Genotype total seed number was corrected to account for variation due to the covariate prin1 and log-transformed, before the means were calculated (see main text for details). The dotted line indicates a 1:1 relationship. Numbers refer to specific genotypes.

Figure 11. Mean of the maximum number of emerged seedlings (minus the number of emerged seedlings in a control) \pm 1 SE for each genotype (genotypes are designated by numbers). Means are shown separately for (a) the fallow field and (b) the mowed lawn. There was a significant genotype-by-habitat interaction (Mixed Model with Satterthwaite correction, $p = 0.02$), and significant main effects of genotype ($p = 0.01$) and habitat ($p = 0.004$). Different letters indicate significant differences within a habitat (Tukey-Kramer test, $p < 0.05$).

FIGURES

Figure 1

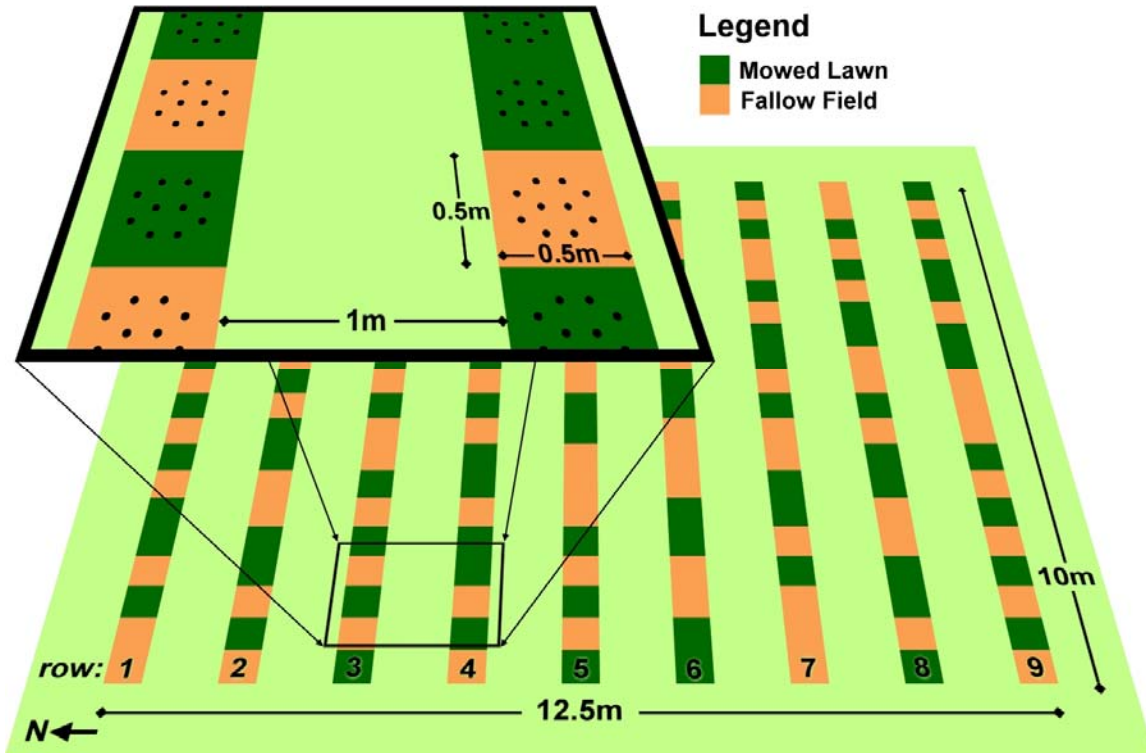


Figure 2



Figure 3

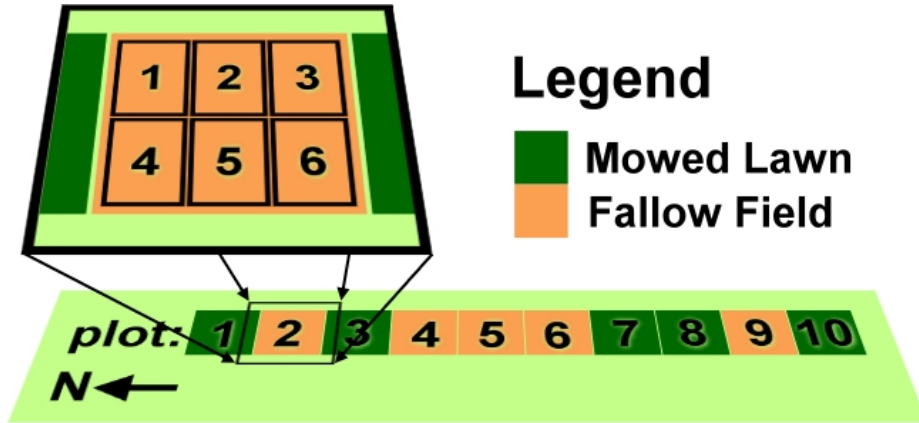


Figure 4

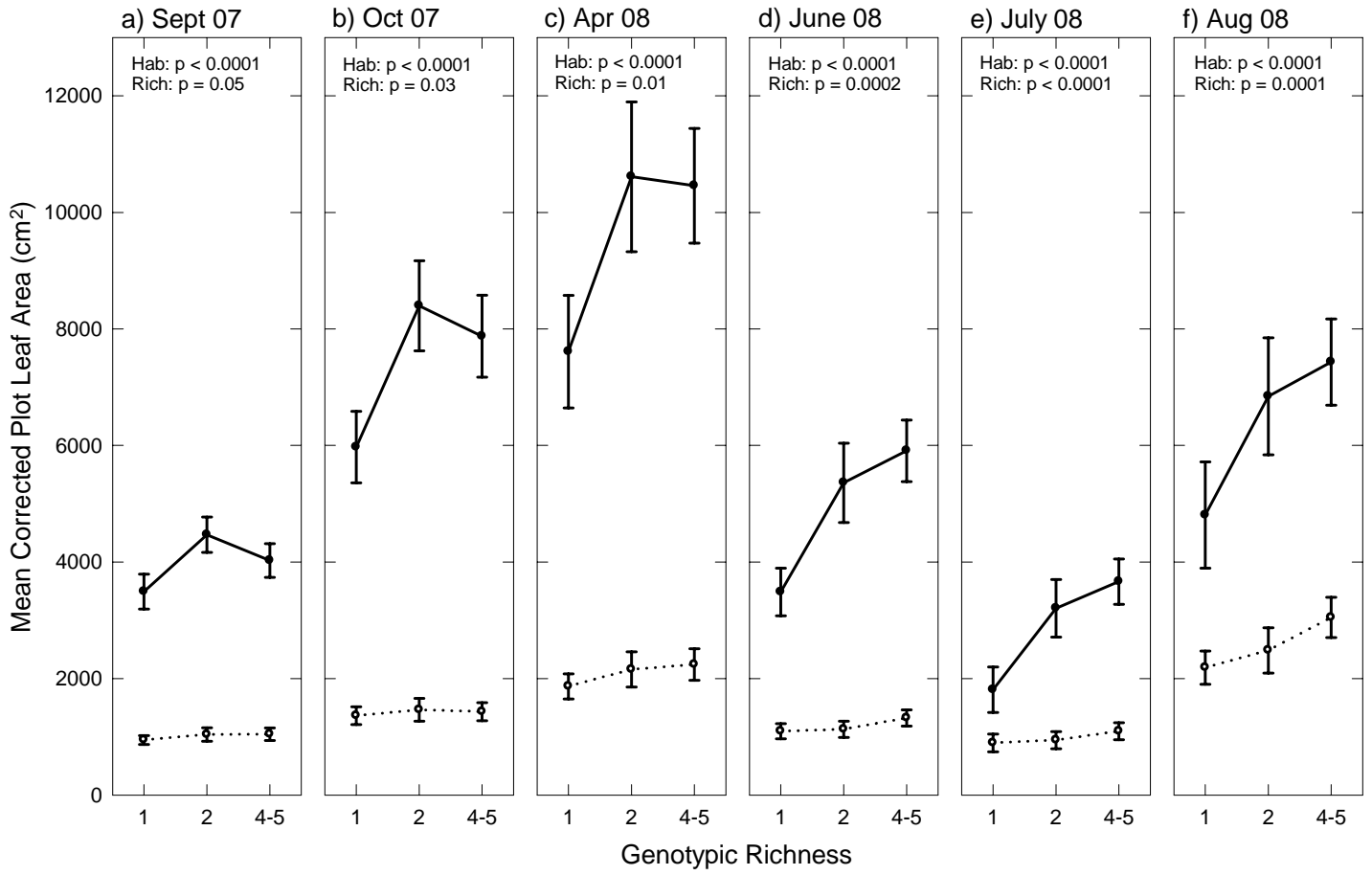


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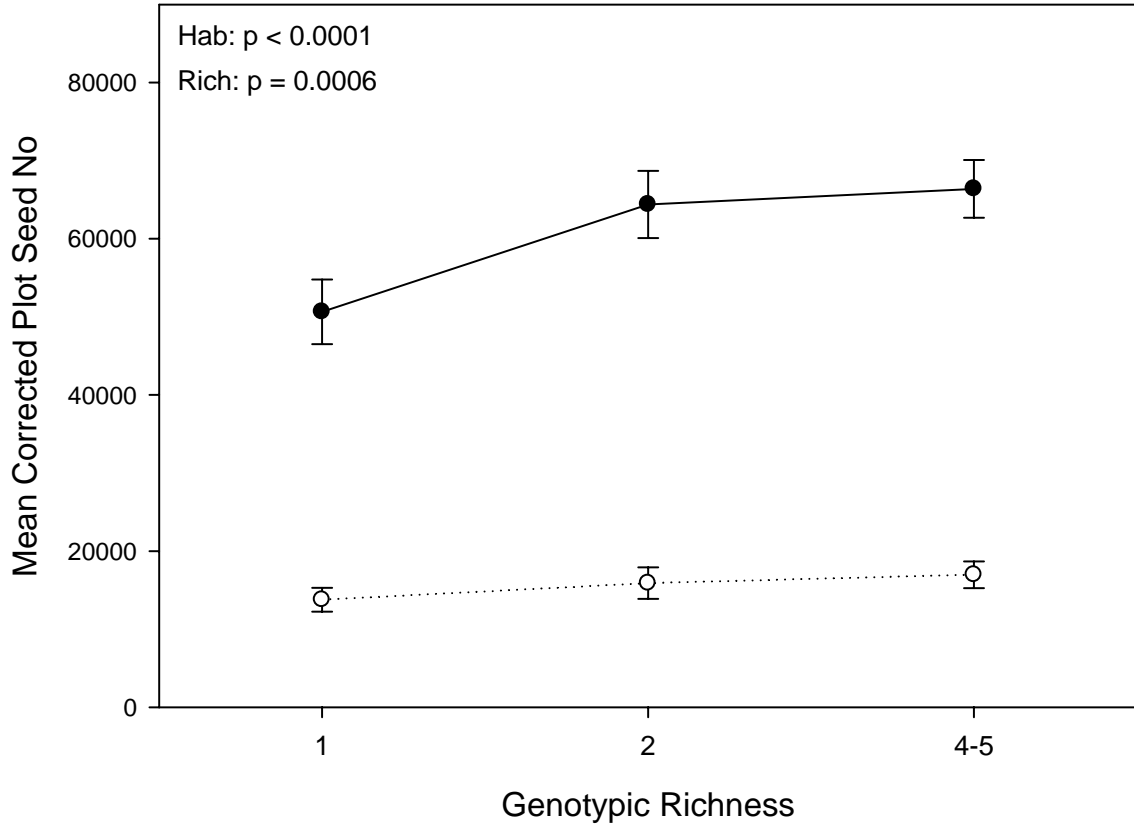


Figure 6

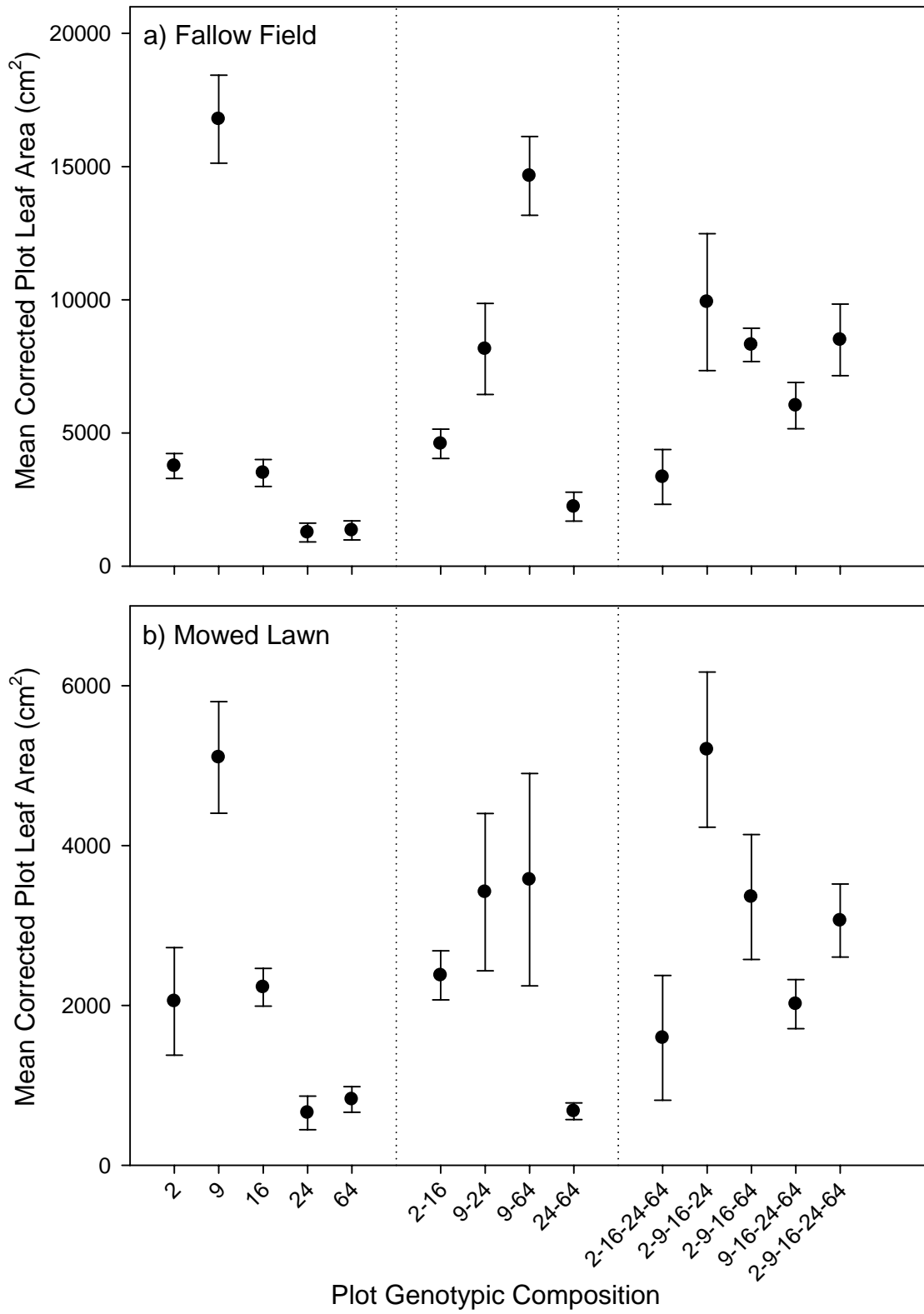


Figure 7

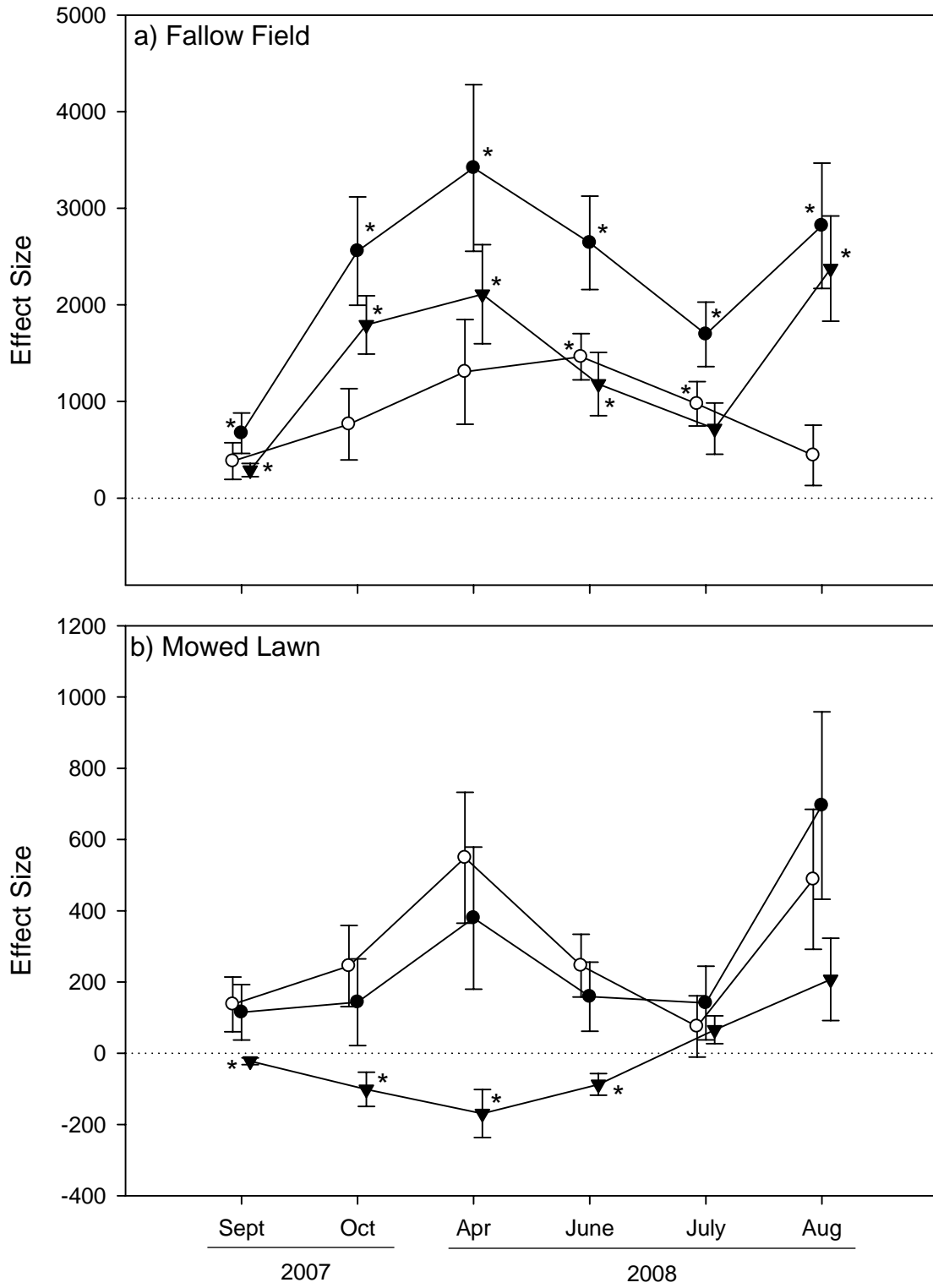


Figure 8

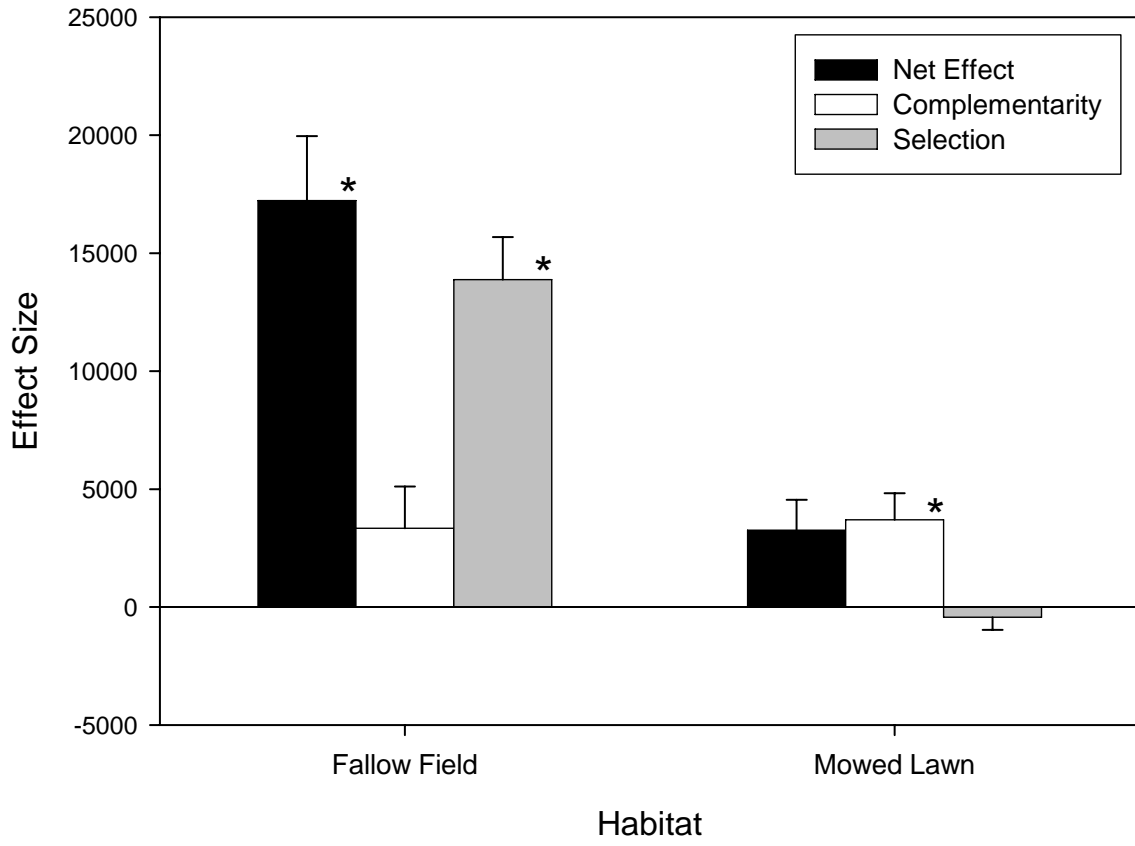


Figure 9

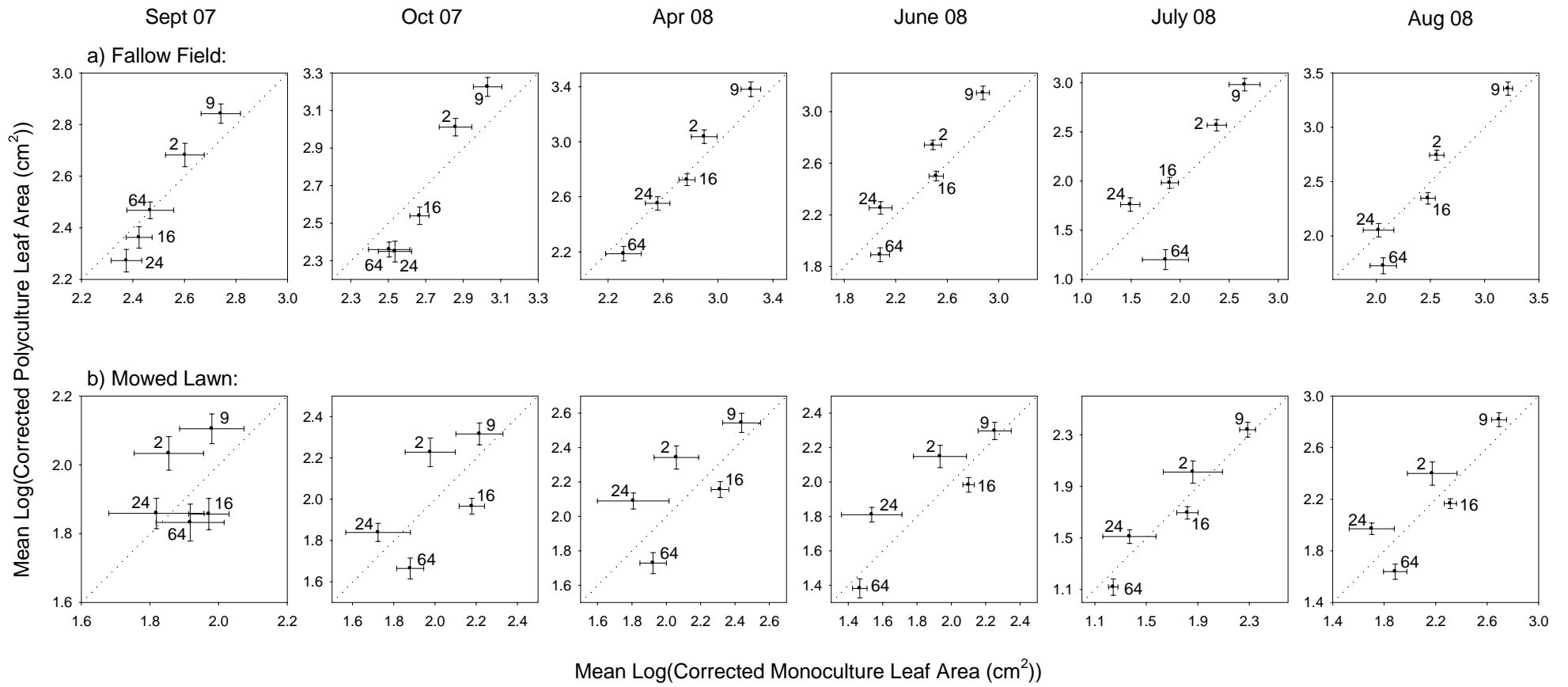


Figure 10

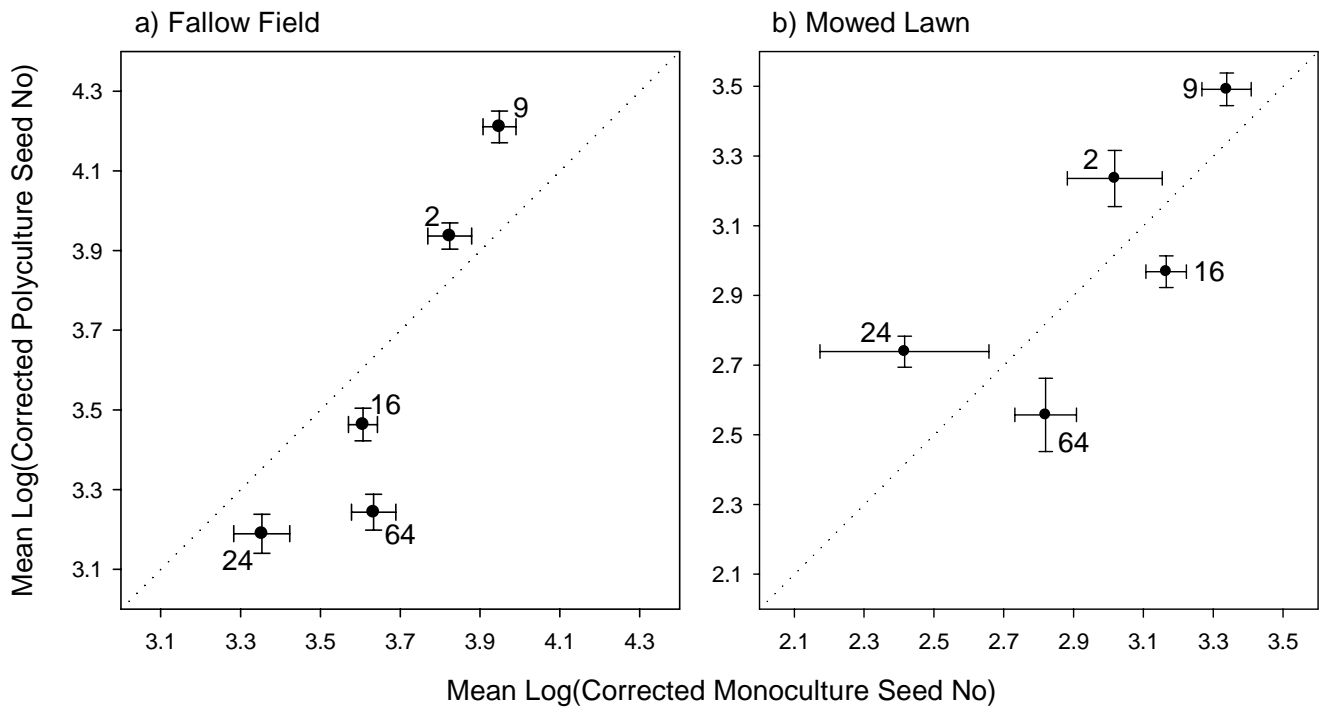
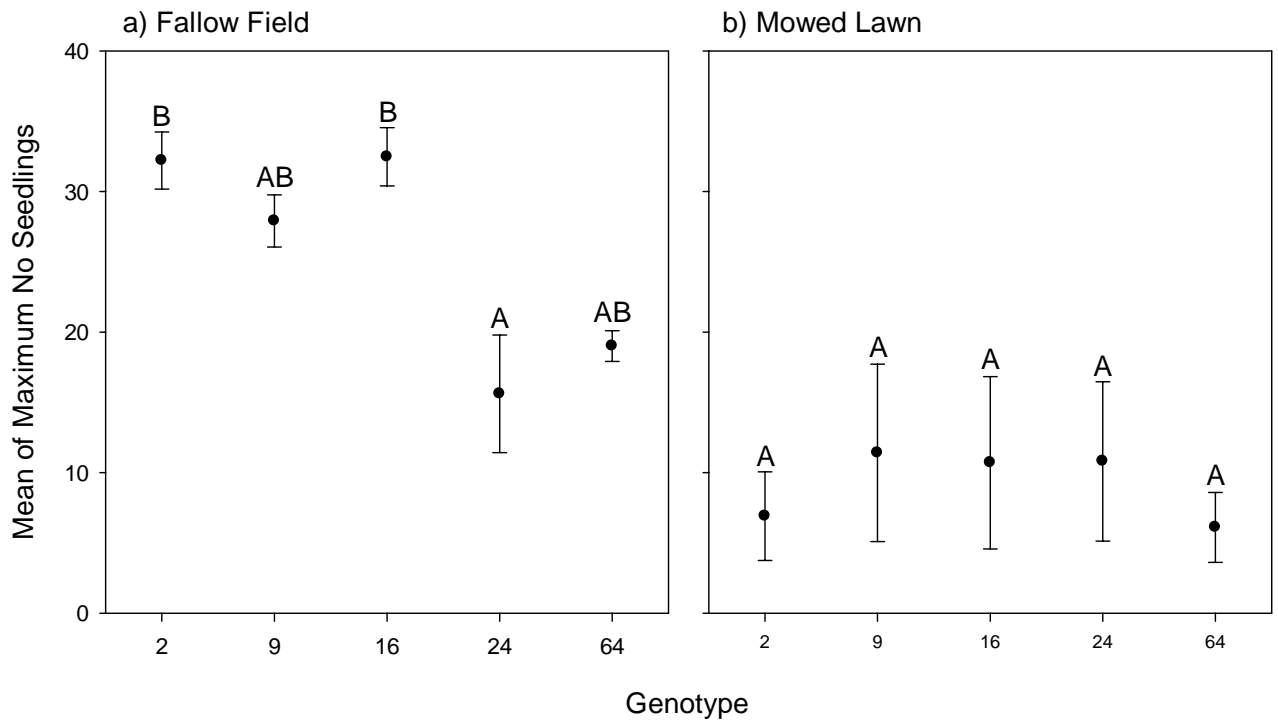


Figure 11



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APPENDIX A. Details of dandelion seed planting and seedling maintenance.

Dandelions of each of the genotypes included in the experimental design were established from seed stocks generated prior to our experiment (as described in the Methods). Multiple seeds were planted on April 11th, 2007 into individual “root-trainer” pots (1” x 1” x 4.25”): Spencer-Lemaire, Edmonton, AB) that allow easy separation of seedlings without root damage. Pots were filled with a pre-moistened lawn mix soil composed of peat, sand and subsoil (silt and fines) (Kutny’s Richmond Soils, Richmond, BC). Pots were watered daily, if needed, and fertilized on a weekly basis (Miracle Gro Quick- Start, NPK 4-12-4).

All pots were kept outdoors at the field site, in a partially enclosed shed. Although the shed roof limited the amount of light reaching the seedlings, it also protected the seedlings from wind desiccation, and heavy rainfall. Heavy rain could both cause seedling mortality, and cause seeds to “jump” between pots. It was absolutely essential that we knew the genotype of each seedling, so as to correctly implement our experimental treatments. The position of trays of pots was randomized, and trays were shifted on a regular basis.

Seedlings germinated from 2-6 weeks after planting. Germination was patchy between pots, and so seedlings were transplanted from pots with multiple seedlings to empty pots, as needed. Transplants were done while seedlings were small, before a significant tap-root had been established, and transplant success was very high (>95% survival). After transplanting between pots, seedlings in pots with high germination success were thinned to one individual.

Additional seedlings were grown up in a growth chamber (Conviron E15) as supplements to the outdoor stock. The following temperature regime was used: 10°C overnight, ramping up to 18°C from 7am to noon, and returning to 10°C from 5pm to 11pm. Full fluorescent lights were on for slightly less than 12 hours per day, from 7am to 6:40pm. These conditions mimic natural spring-time conditions in Vancouver. Because conditions varied slightly between the two growth chamber shelves (as one shelf is closer to the lights), trays of seedlings were randomly assigned to a shelf and switched periodically between shelves.

APPENDIX B. Dates for each round of leaf area measurements.

Table A1. Dates for each round of measurement, with accompanying short forms used in the text and figures.

Measurement	Exact Dates	Short Form
1	4-6 July 2007	July 2007
2	31 July – 3 August 2007	August 2007
3	27-31 August 2007	September 2007
4	24-29 September 2007	October 2007
5	21 April – 1 May 2008	April 2008
6	2-6 June 2008	June 2008
7	21-24 July 2008	July 2008
8	27 August – 5 September 2008	August 2008

APPENDIX C. List of species comprising the vegetation composition data used in the principal components analysis.

Table C1. Mean and standard error of cover classes for each species. Cover classes are described in the Methods, and have been numbered from 1 to 7 (from lowest to highest cover class). Prin1 denotes the value of the first axis from the principal components analysis for a given species.

Species	Mean Cover Class	Standard Error of Cover Class	Prin1
<i>Acer sp.</i>	0.006	0.006	0.0018
<i>Achillea millefolium</i>	0.017	0.012	-0.0005
<i>Agaricomycetes sp.</i>	0.061	0.020	-0.0097
<i>Aphanes arvensis</i>	0.039	0.016	0.0080
<i>Cerastium fontanum</i>	0.978	0.057	-0.0374
<i>Erodium cicutarium</i>	0.006	0.006	0.0022
<i>Geranium molle</i>	0.150	0.041	-0.0363
<i>Geranium dissectum</i>	0.233	0.043	-0.0727
<i>Hypochaeris radicata</i>	2.044	0.132	0.5819
<i>Lamium purpureum</i>	0.039	0.014	0.0056
<i>Medicago lupulina</i>	3.200	0.121	0.4551
<i>Montia linearis</i>	0.050	0.020	0.0218
<i>Myosotis discolor</i>	0.011	0.008	0.0046
<i>Plantago lanceolata</i>	0.928	0.107	0.1630
<i>Poa sp.</i>	5.944	0.060	-0.0745
<i>Ranunculus repens</i>	0.056	0.028	-0.0155
<i>Rhytidadelphus squarrosus</i>	1.233	0.110	0.2120
<i>Rumex acetosella</i>	0.122	0.037	0.0174
<i>Rumex obtusifolius</i>	0.011	0.011	0.0013
<i>Sonchus asper</i>	0.028	0.017	0.0052
<i>Spergularia rubra</i>	0.006	0.006	0.0019
<i>Stellaria media</i>	0.356	0.051	0.0571
<i>Taraxacum officinale</i>	0.911	0.073	0.0182
<i>Trifolium sp.</i>	1.344	0.128	-0.5888
<i>Veronica arvensis</i>	1.694	0.069	-0.1328