Trait Complementarity Enhances Native Plant Restoration in an Invaded Urban Landscape ⧉

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ABSTRACT

Developing strategies to reintroduce native species in invaded landscapes is a major challenge for ecological restoration, particularly in urban areas. Although complete eradication of invasive exotics is a common restoration goal, an emerging approach in heavily invaded landscapes is to plant native species likely to persist, even in the presence of exotic competition. Functional traits may be used to inform restoration strategies by indicating whether native and exotic species are likely to occupy different niches (i.e., dissimilar traits indicate different resource strategies). We adopted a functional trait approach to test whether planting species with dissimilar, as opposed to similar, traits to exotic species enhanced native species cover and diversity for an urban restoration project that is heavily invaded by *Hedera helix* (English ivy) and *Hedera canariensis* (canary ivy). We conducted a trait screening of *Hedera* and 37 candidate native understory plants and used trait values to select three species that were functionally dissimilar and three that were functionally similar to *Hedera*. We then tested their survival and growth when planted in and out of competition with *Hedera* over two years. Species with dissimilar traits to *Hedera* had high survival and growth across time and competitive environments, whereas species with similar traits to *Hedera* had significantly reduced survival when in competition with *Hedera*. Our results suggest that, in heavily invaded landscapes, restoration projects that plant species with complementary resource strategies to exotics may be most successful and that functional traits are a useful tool to select these species.

Keywords: competition, functional traits, ivy, niche partitioning, resource-acquisitive

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🌿 Restoration Recap 🌿

- Exotic species such as ornamental ivy, which are pervasive and frequently cultivated, can pose a challenge to ecological restoration in urban environments. A potential strategy is to restore native species with complementary resource strategies to exotic species, with the goal of enhancing native abundance and diversity despite exotic presence.
- Functional traits of species may indicate species with different strategies than exotics. We used a trait screening approach to characterize native species as "dissimilar" and "similar" to ivy and planted these species in and out

of competition with ivy. We found that only species with dissimilar traits to ivy (which are likely to have complementary resource strategies to ivy) had high survival rates in competition with ivy.
- Our results support the idea that planting species that are functionally dissimilar to exotics is an effective strategy in heavily invaded, urban landscapes. In ivy-dominated habitats, taller native species with thicker tap roots are particularly successful.

A common goal in ecological restoration is to increase the diversity and abundance of native species (Suding 2011, Hallett et al. 2013a). Exotic invasive plants pose a key challenge to this goal via their competitive effects on native species (Pysek and Richardson 2010). This is of particular concern for restoration sites that are situated in invaded landscapes and are therefore likely to experience reinvasion (Ehrenfeld and Toth 1997, Buckley et al. 2007). Selecting

native species for restoration projects in heavily invaded habitats may require different approaches than does selecting species in more natural contexts (Seastedt et al. 2008, Hallett et al. 2013b). While restoration practitioners often apply local knowledge to select suites of species that will be successful in altered systems (Dickens and Suding 2013), broader predictive frameworks for assessing which species will persist in altered landscapes are a promising direction for urban ecosystem management (Lundholm and Richardson 2010, Van Mechelen et al. 2015).

An emerging paradigm of restoration in invaded landscapes is to plant native species with complementary niches to those of exotic species (Laughlin 2014). This approach aims to increase the probability of restored native species coexisting with invading exotic species. This approach contrasts with a second emerging paradigm based on the theory of limiting similarity (MacArthur and Levins 1967, Abrams 1983) that suggests that practitioners should plant native species whose niches overlap with exotic species in order to exclude potential invaders from the restored community (Funk et al. 2008, Laughlin 2014). Of the two approaches, limiting similarly has been more frequently tested, with most studies using a reduction in exotic species, as opposed to an increase in native species, as a metric of success (Price and Pärtel 2013). However, in urban landscapes where complete eradication of exotics is either infeasible or undesirable for aesthetic or social reasons, the more relevant metric may be whether restoration increases native species cover and diversity, regardless of exotic presence. In this context, predictive guidelines are necessary for the selection of species to restore at sites where the presence of exotic species is assumed.

A functional-trait approach provides a mechanistic way to predict how native and exotic species will interact (Díaz et al. 1998). Functional traits describe species based on their ecological roles, both how they respond to and affect the environment and other species (Díaz and Cabido 2001, McGill et al. 2006, Violle et al. 2007). Functional traits that reflect resource-use strategies can help to identify niche overlap between species (Mouillot et al. 2005, Kearney and Porter 2009, Violle and Jiang 2009). For example, species with similar root architecture (e.g., proportion of fine roots and diameter) may directly compete for below-ground resources, whereas species with dissimilar root architecture may access complementary pools of resources (Fargione and Tilman 2005). Consequently, contrasting the resource utilization traits of a focal exotic species against potential native species may help practitioners select and plant native species likely coexist with exotics (those with dissimilar traits to those of exotics) as opposed to species likely to directly compete with them (those with similar traits).

Here we take a functional-trait approach to develop and test restoration planting strategies for a heavily invaded, urban environment. We located our study along Strawberry Creek, an urban watercourse that runs through the campus of the University of California, Berkeley. The undergraduate community has initiated extensive volunteer efforts to remove invasive ornamental ivy from designated natural areas along the creek, but reinvasion rates remain high due to incomplete removal of root biomass and proximal use of *Hedera* in campus landscaping (Purcell et al. 2007). Consequently, active restoration of native species that can survive reinvasion is a central goal for natural areas management along the creek (Hans and Maranzana 2008). We conducted an extensive trait screening of two ornamental ivy species, *Hedera helix* (English ivy) and *Hedera canariensis* (canary ivy), and 37 candidate native understory species. We used multivariate analysis to select three native species that were functionally dissimilar and three that were functionally similar to *Hedera*. We then planted these trait groups (i.e., dissimilar and similar to *Hedera*) in and out of competition with *Hedera*. We compared the survival and growth of each group to test whether trait complementarity is an effective strategy to restore native abundance and diversity in the presence of a common exotic species.

Methods

Study System

Strawberry Creek is an urbanized watercourse that runs east to west through the campus of the University of California, Berkeley (Alameda County, CA, USA; 37°52′N, 122°15″W). Overstory vegetation at the creek consists predominantly of *Sequoia sempervirens* (coast redwood), planted by campus landscapers, and *Eucalyptus globulus* (blue-gum eucalyptus), a non-native species, with *Aesculus californica* (California buckeye), *Umbellularia californica* (bay laurel), and *Quercus agrifolia* (coast live oak) scattered throughout. Understory plant cover at Strawberry Creek is dominated by *H. helix* (English ivy) and *H. canariensis* (Canary ivy) (both ornamental ivy species) which have been cultivated in areas of the campus since at least the 1800s, although extensive removal efforts over the last two decades have reduced their extent (Purcell 2007). *Hedera* frequently reclaims areas from which it was removed, usually as a result of incomplete removal of root biomass. Natural recolonization by native plant species is minimal (Hans and Maranzana 2008).

Functional Trait Screening and Species Selection

We compared the functional traits of a regional pool of 37 native understory plants with those of the two invasive *Hedera* species. The regional pool included species that represented a mix of local habitat types (e.g., redwood forest, riparian, wetland, grassland), provided that they were native to Alameda County (Baldwin et al. 2012) or included in previous Strawberry Creek restoration plans (Charbonneau 1987, Purcell et al. 2007). We winnowed

this broad pool to 37 focal species based on availability and nursery survival rates (Table S1; Bickart 2013). In line with similar restoration projects we acquired plants through field cuttings and from local native plant nurseries; ages and propagation methods were standardized across functional groups to the extent practicable (Table S1). We replicated each of the species five times in a random-block design for a total of 195 individuals. We grew all individuals in an outdoor, on-campus nursery from June-July 2012 in American Soil & Stone's "Ultra Bedding Mix" (Richmond, CA) and conducted the trait-screening by block from August–October 2012. The nursery and out-planting sites experienced similar climate conditions (all were located with the UC Berkeley campus); the nursery was covered with a 20%-shade reduction cloth to parallel shade conditions in the out-planting environment.

There is a large debate in the functional trait literature as the whether it is appropriate to measure functional traits in a nursery/greenhouse setting (Poorter et al. 2012b). We chose to measure traits in the nursery because many restoration projects utilize nursery-grown plants, and consequently nursery trait measurements best reflect plant conditions at the start of restoration projects. To minimize pot-induced differences in plant traits between nursery and out-planting conditions we scaled pot size by plant size, with shrubs in gallon pots, forbs in 6-cm diameter × 12.7 cm deep and grasses in 5.1-cm diameter × 17. 8 cm deep pots (Poorter et al. 2012a). In addition, we focused on traits that are more likely to remain consistent between the nursery and out-planting environments (e.g., proportional traits such as specific leaf area [SLA] and specific root length [SRL]) (Cornelissen et al. 2003a).

We measured eight functional traits following protocols outlined in Cornelissen et al. (2003b). Aboveground traits included stomatal conductance, leaf chlorophyll content, plant height, and specific leaf area. Stomatal conductance, which is indicative of water acquisition ability (Chaves et al. 2003), was measured with a steady-state porometer (model LI-1600, Li-Cor, Lincoln, NE) with the plant in full sun, between 9:00 a.m. and 11:00 a.m. Chlorophyll content, which is correlated with tissue N and associated with photosynthetic capacity (Markwell and Blevins 1999), was measured with a Konica Minolta SPAD-502 and averaged across three young, fully-formed leaves per plant (Spasojevic and Suding 2012). Plant height, which is associated with overall size and competitive ability (Keddy and Shipley 1989, Westoby 1998), was measured from soil surface to the highest photosynthetically active tissue. Following non-destructive measurements, we collected two young, fully-formed leaves per plant, stored them in a cooler in sealed plastic bags with a moist paper towel, and scanned them within 2 h of collection. Images were processed with Image-J (Schneider et al. 2012) to determine leaf area. We dried (60°C for 48 h) and weighed the leaves and calculated specific leaf area (SLA), which is associated with leaf life

span and growth strategy (Reich et al. 1997), as leaf area (cm²) per unit of dry leaf mass (g).

Belowground traits included maximum root diameter, root/shoot, proportion of fine roots and specific root length. Maximum root diameter, associated with rate of nutrient uptake and root longevity (Roumet et al. 2006), was measured as the largest belowground root diameter, including rhizomes. Root-to-shoot ratio, which reflects plant resource allocation and drought tolerance (Mokany et al. 2006), was calculated as the total dried weight of belowground biomass divided by total dried weight of aboveground biomass (biomass dried at 60°C for 48 h). The proportion of fine roots, which is associated with resource allocation and root longevity (Roumet et al. 2006), was measured as the total dry weight of fine roots (i.e., those with a diameter < 2 mm) divided by total dry weight of all roots (protocol following Roumet et al. 2006, Butterfield and Suding 2013). Finally, specific root length (SRL), which represents investment in fine roots and root turnover and reflects the ability to rapidly acquire belowground resources (Roumet et al. 2006), was measured as fine root (< 2 mm) sample length divided by dry weight. We measured SRL on a representative sample of 10 fine roots per plant, the majority of each was secondary or tertiary roots and likely associated with absorptive capacity (McCormack et al. 2015). The length of each root was measured and summed, and the 10 roots were dried (60°C for 48 h) and weighed collectively.

We assessed species trait similarity using principle component analysis (PCA); species with similar traits were grouped together in ordination space. Prior to analysis, we averaged trait values within a species and standardized trait values around the mean across species. We used the PCA to select three available species with similar traits to those of *Hedera* (i.e., small Euclidean distances) and three available species with dissimilar traits (i.e., large Euclidean distances), see results section for species similarity scores. "Similar" species were *Asarum caudatum* (wild ginger), *Symphyotrichum chilensis* (California aster), and *Polystichum munitum* (western sword fern); "dissimilar" species were *Ceanothus thyrsiflorus* (blue-blossom ceanothus), *Mimulus aurantiacus* (sticky monkeyflower), and *Ribes sanguineum* (pink-flowering currant). All analyses were conducted in R (v 3.1.2, R Foundation, Vienna Austria); the PCA was conducted using "rda" in the vegan package (Oksanen et al. 2015).

Restoration Out-Planting

In August 2013, we established nine replicates in a random block design in *Hedera*-dominated sites along the south fork of Strawberry Creek, for a total of 18 plots. The majority of *Hedera* cover was *H. canariensis*. *Hedera* were removed by hand from one randomly-selected plot in each block, which resulted in nine "with *Hedera*" and nine "without *Hedera*" plots. Each plot was 2.4 m × 1.8 m. The

"without *Hedera*" plots were monitored for encroachment and maintained by hand over the course of the experiment. Two individuals of each of the six species (corresponding to 12 individuals: six with similar and six with dissimilar traits to *Hedera*) were planted in every plot for a total of 216 individuals across all plots. Plants were acquired from the same nurseries and were of approximately the same age as those used in the trait screening. Plants were evenly spaced at least 60 cm from the edge and randomly ordered within plots. Because our study took place during a drought, we reduced mortality by hand-watering each plant weekly with approximately 0.75 liters of creek water throughout the study period.

To assess restoration success, we focused on two key metrics: survival and growth rates. We quantified survival by conducting an annual census over two years (March 2014 and 2015). We quantified growth non-destructively by counting the number of leaves on each plant at the start of the experiment (August 2013) and at the peak of the growing season over the next two years (March 2014 and 2015). We used these leaf count data to calculate relative growth rate as $(\ln(Leaf_2)–\ln(Leaf_1))/(t_2–t_1)$, where Leaf is the total number of leaves and t is the year.

We characterized patterns of survival by first calculating percent survival within species, plot and year. Second, we analyzed percent survival each year using ANOVA with *Hedera* treatment (with, without), species trait group (similar, dissimilar), a treatment × trait group interaction as fixed effects and block and species as random effects using library, package "nlme" (Pinheiro et al. 2015). This analysis allowed us to test whether planting species with dissimilar traits to those of *Hedera* led to higher survival rates. To test differences in growth responses we used similar ANOVA with relative growth rate (RGR) as the response variable.

Results

Functional Trait Relationships

The cumulative variance explained by the first two axes of the PCA was 49.2% (Figure 1). The first axis, which explained 28.1% of the variance, was correlated with lower SLA and SRL and greater leaf chlorophyll content, proportion of fine roots and plant height. The second axis, which explained 21.1% of the variance, was correlated with lower root/shoot ratios and higher stomatal conductance and maximum root diameter. Both *Hedera* species loaded in the middle of axis 1 and very low on axis 2 (Figure 1). Based on this ordination, we selected three commercially available species that were similar to the two *Hedera* species (i.e., small Euclidean distances), notably *Asarum caudatum* (distance to *H. canariensis* = 0.33)*, Symphyotrichum chilensis* (distance to *H. canariensis* = 0.32), and *Polystichum munitum* (distance to *H. canariensis* = 0.61) (Figure 1). Dissimilar species were selected as commercially available

species with high values along both axis 1 and 2, specifically *Ceanothus thyrsiflorus* (distance to *H. canariensis* = 1.71), *Mimulus aurantiacus* (distance to *H. canariensis* 1.94), and *Ribes sanguineum* (distance to *H. canariensis* = 0.91; Figure 1). Mean trait values for all species are in Table S2.

Restoration Success by Trait Group

Survival differences appeared in the second year, following 100% survival in 2014. Restoration success, as characterized by percent survival, was significantly affected by a trait group by competitive environment interaction in 2015 (treatment × trait group; $F_{1,49}$ = 8.0, p = 0.007). Species with similar traits to those of *Hedera* had high survival out of competition with *Hedera*, comparable to dissimilar species in competition with *Hedera*, but the survival of similar species was significantly reduced when in competition with *Hedera* (z-value = 6.8, p < 0.001; Figure 2). Among species with dissimilar traits to those of *Hedera*, percent survival was high and only slightly reduced by competition with *Hedera* (z-value = 2.88, p = 0.02; Figure 2). Patterns within species mirrored trait group patterns (Figure S1).

Plant relative growth rates were lower when grown in competition with *Hedera* in both years (2014: $F_{1,140}$ = 4.6, p < 0.0001; 2015: $F_{1,101}$ = 13.4, p = 0.0004). In 2014 there was a significant interaction (treatment × trait group, $F_{1,140}$ =3.5, p = 0.0007) in which relative growth rates were pronouncedly higher for functionally dissimilar species in the absence of competition than for all other trait group and treatment combinations (z-values ≥ 3.2, p < 0.008; Figure 2). In 2015 there was no significant interaction effect, but there was a trait group effect in which similar species had very low growth rates compared to dissimilar species regardless of competitive environment (z-values ≥ 4.9, p < 0.001; Figure 2). Patterns within species generally mirrored trait group patterns, although *C. thyrsiflorus* had markedly lower growth rates than the other dissimilar species (Figure S2).
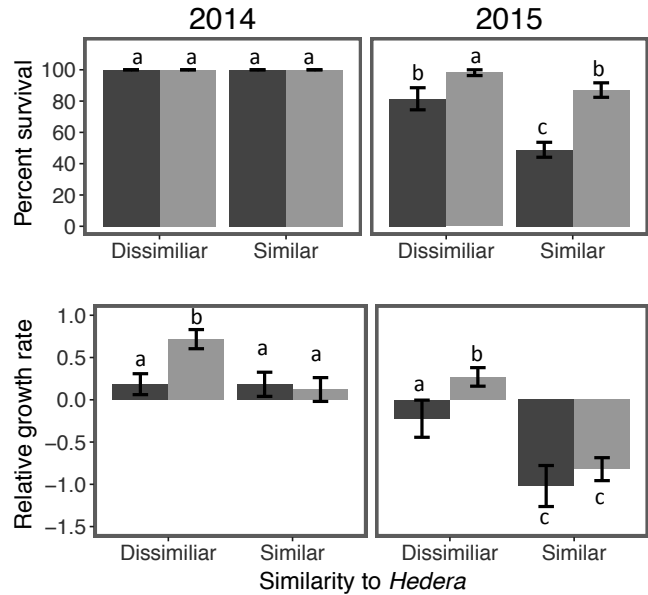
Discussion

Developing strategies to enhance native cover and diversity is a major challenge for ecological restoration, especially in heavily invaded and urban landscapes. A trait-based approach may provide general insights about how native species are likely to interact with exotic species (Pywell et al. 2003, Brudvig and Mabry 2008, Sandel et al. 2011, Clark et al. 2012). By pairing a trait screening and out-planting experiment, we tested the hypothesis that restoration success, measured as native species cover and diversity, is enhanced by planting species with complementary traits to prevalent exotic species (Laughlin 2014). Our results support this hypothesis in the context of invasion by *Hedera*: species with dissimilar traits to those of *Hedera* had higher survival when in competition with *Hedera* than did species with similar traits. In heavily invaded
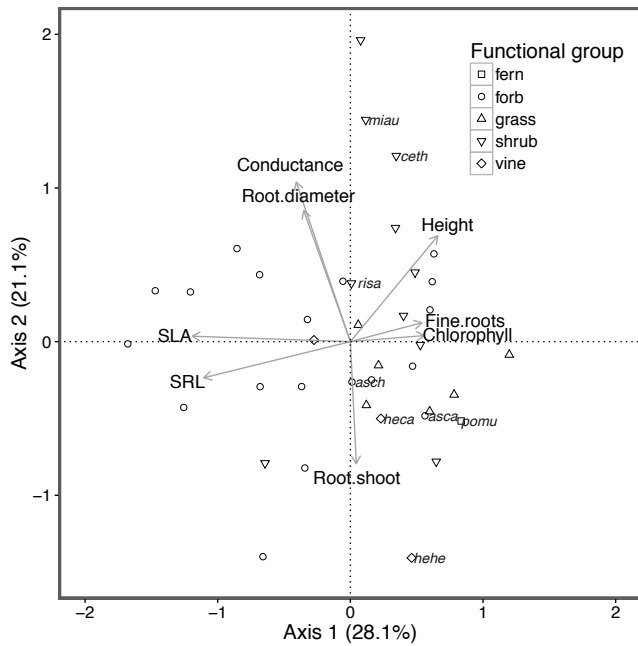
Figure 1. PCA ordination of nine functional traits for 37 native understory plants and two exotic ornamental ivy species, *Hedera canariensis*, *Hedera helix* (heca, hehe). Focal species with similar traits to *Hedera* are labeled *Aster chilensis*, *Asarum caudatum*, *Polystichum munitum* (asch, asca, pomu) as are those with dissimilar traits to *Hedera*, *Ribes sanguineum* var. *glutinosum*, *Ceanothus thyrsiflorus*, *Mimulus aurantiacus* (risa, ceth, miau). See Table S2 for mean trait values for all species.

Figure 2. Percent survival and relative growth rates for species with dissimilar and similar functional traits to those of *Hedera* within different competition treatments (dark indicates with, and light indicates without *Hedera*) and across years (± SE). Letters denote significant differences between treatment groups.

landscapes, restoration projects that adopt a trait-based approach focused on native-exotic coexistence may provide an alternative to those focused on exotic exclusion.

Niche complementarity may help native species persist in heavily invaded restoration sites (Laughlin 2014). Complementary functional traits typically enable niche differentiation between species (Mouillot et al. 2005, Violle and Jiang 2009). For example, species with dissimilar root architecture may access different water sources; a classic example of resource partitioning among coexisting species (Parrish and Bazzaz 1976, Cody 1991, Fargione and Tilman 2005). Our study indicates that functional traits relationships may be leveraged to enhance native species cover and abundance in invaded landscapes. We found that native species with functional traits dissimilar to those of exotic *Hedera* had high survival rates when in competition with *Hedera*, whereas species with similar traits did not. By filling niches not occupied in exotic *Hedera* monocultures, dissimilar species are likely able to take advantage of resources not exploited by *Hedera*. For example, dissimilar species to *Hedera* were typically taller, reflecting different light-acquisition and -use strategies compared to the groundcover *Hedera* species. Planting native species with complementary strategies may be particularly effective when it is unrealistic to expect that the exotic species

will be totally eradicated, as is the case for ornamental species that are valued and cultivated in other areas of the landscape (Shackelford et al. 2013) or for species in which complete removal (e.g., *Hedera* root biomass) is very difficult (Biggerstaff and Beck 2007).

In our study, species that were dissimilar to *Hedera* also tended to have trait patterns associated with competitive abilities in high-resource environments (Laughlin 2014). Dissimilar native species in our study had a cluster of traits associated with rapid resource acquisition and growth, such as greater height, lower root/shoot ratio, and higher stomatal conductance (Keddy and Shipley 1989). Resource-acquisitive traits may be especially important in urban sites like ours which often have high soil nutrient concentrations due to adjacent fertilizer use and nitrogen deposition (Foley et al. 2005). These results are in line with a series of studies that suggest that trait hierarchies can predict the outcome of competition (Keddy and Shipley 1989, Kunstler et al. 2012, Laughlin 2014, Funk and Wolf 2016). For example, Funk and Wolf (2016) also found that trait hierarchies based on resource acquisition, but not limiting similarity, increased planting success in competition with an invasive annual grass. Notably, in our study, dissimilar species exhibited very high potential growth rates when not in competition with *Hedera*, likely because of their resource-acquisitive traits. For these species, competition with *Hedera* primarily reduced relative growth rates and not survival. This suggests that, although permanent *Hedera* exclusion is unrealistic in sites like ours, temporary

Hedera removal may still be a useful tool for restoration. For example, planting dissimilar species in cleared areas may allow an initial period of rapid growth, and that could bolster success in face of subsequent *Hedera* reinvasion.

The concept of limiting similarity has inspired recent work in restoration ecology (Funk et al. 2008, Abella et al. 2012, Li et al. 2015), but its utility may depend on the landscape context. Planting species with similar traits to those of exotic species should be most effective when the restored community can completely assemble before facing reinvasion. For restoration sites situated in urban and disturbed landscapes, however, reinvasion pressure may occur before the restored community becomes fully established (Vidra and Shear 2008). In these situations, selecting species based on limiting similarity may have the perverse effect of reducing restored populations due to immediate competitive interactions with widespread invasive species. Our experiment, which planted species directly in competition with *Hedera*, mirrored this situation, and we observed a concordant decrease in the survival of species with similar traits to *Hedera*. We expect this effect would be general to restoration sites situated in landscapes dominated by aggressive invasive species. In this context, it is not surprising that the strongest evidence that limiting similarity increases site resistance to invasion has come from pot (Byun et al. 2013, Li et al. 2015) and field (Dukes 2002, Cleland et al. 2013) experiments in which natural (i.e., non-experimental) reinvasion was prevented (Price and Pärtel 2013). Studies situated in invaded landscapes (Emery 2007, Thompson et al. 2010) or in conjunction with disturbance events (Collinge et al. 2011) and ongoing species-environment feedbacks (Hulvey and Aigner 2014) have found less evidence for exotic exclusion via limiting similarity.

Trait-based approaches have gained traction in restoration ecology, but in practice they may be difficult to employ due to the time and financial costs associated with trait-screening. The rise in trait databases, such as TRY (Kattge et al. 2011), may alleviate this constraint for some sites. Further, the principles highlighted by our study, to plant functionally dissimilar, resource acquisitive species in nutrient enriched, invaded landscapes, may provide a starting-point for planning restoration projects in enriched, urban environments. Finally, although urban landscapes pose unique challenges to restoration, they provide opportunities for community engagement with environmental stewardship. For example, over 500 undergraduate students each year participate in restoration efforts along Strawberry Creek. These volunteers enabled us to conduct this trait screening and maintain and assess out-planting treatments. Similar community engagement programs in urban environments may allow additional trait-based restoration studies that may be unfeasible in remote areas.

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