Conservation and Resource Studies, Alumni, Class of 2013
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Managing the Weed-Shaped Hole: Improving Nitrogen Uptake and Preventing Re-invasion in Urban Riparian

Keywords: restoration ecology, invasive species control, trait-based filtering, limiting similarity, stable isotope tracer analysis, native plants, riparian restoration, Strawberry Creek, nitrogen pollution, volunteer-based restoration.

Abstract

As the field of ecological restoration grows, novel methods to improve the effectiveness of restoration projects are being advanced and tested. Here, measured plant functional traits are used to select a native planting palette for the restoration of riparian habitat at Strawberry Creek, a heavily invaded urban ecosystem in Berkeley, CA. I partnered with an active restoration program and together we focused on methods to prevent re-invasion by a dominant non-native understory species and reduce nitrogen pollution of the riparian ecosystem. A ^{15}N uptake study revealed a marginally significant ($0.05<p<0.10$) result suggesting that shrubs may be more proficient at taking up nitrogen, though further research is needed to clarify this finding. This work points to the potential benefits that ecosystem science research and on-the-ground restoration efforts can offer one another.

Figure 1. Evidence for the weed-shaped hole near Strawberry Creek on the UC Berkeley campus: Ivy (Hedera helix, right) previously covered this site. After the ivy was removed from this area, another invasive species, panic veldtgrass (Ehrharta erecta, left), quickly colonized the niche vacated by the ivy.

Introduction

The field of ecological restoration is growing rapidly in response to increasing humaninduced degradation of the Earth's ecosystems (1, 2). Despite this growth, there is still much to learn regarding how best to carry out ecosystem restoration (2, 3, 4). Realistic and tangible goal setting (5, 6), scientifically supported restoration techniques (3), and novel theoretical frameworks (7) have all been suggested as mechanisms to improve the success of restoration projects in achieving desirable outcomes.

Rivers, creeks, and streams are often at the epicenter of restoration work (8, 9). Along the West Coast of the United States, efforts to improve fish habitat, particularly for salmon, have directed significant restoration efforts towards these waterways (10). While dense human settlement near creeks may lead to their degradation, human proximity also facilitates connection with these natural spaces and interest in restoring the ecosystem. The restoration of urban creek ecosystems is tremendously challenging: human community needs (e.g. public safety), heavy pollutant inputs (e.g. nitrogen deposition due to combustion processes; see (11)), hydrologic alterations, and frequent disturbance (e.g. trampling) complicate management and make many noble restoration goals infeasible (12).

One significant challenge that many restoration projects face is that of invasive non-native plant species (13), an issue that can be particularly pronounced in urban areas due to the connectivity of urban centers in an increasingly globalized world (14). Restoration of native flora is frequently cited as a goal in restoration projects (15), but can be exceedingly difficult.

Removing invasive species without effectively establishing other desired (typically native) species leaves a "weed-shaped hole" (a niche well-suited for non-native invasive species) that non-natives can quickly re-colonize (16), (Figure 1). Though the hope behind earnest non-native removal efforts is that native species will re-colonize the area once niche space becomes available, the evidence that this occurs without further intervention is limited (12, 17), particularly if the native species have been extirpated from the area and thus propagule material does not exist.

Funk et al. propose the concept of "limiting similarity" to reduce the possibility of re-invasion by non-natives (4). The idea is that non-invasive native species that have similar functional traits to non-natives (i.e. utilize a similar set of resources) are expected to be better competitors and prevent the re-invasion of non-native species (4). 'Functional traits' are species' attributes relating to how the species takes up resources and its effect on the resource pool in the ecosystem (4). The limiting similarity concept encourages practitioners to fill the 'weed-shaped hole' with native species that will prevent non-native invaders from accessing resources in the ecosystem. Nitrogen is a critically important resource in ecosystem management. Nitrogen deposition has been implicated in facilitating invasion of nutrient-poor California ecosystems by non-native plant species, particularly near urban areas with abundant fertilizer use and combustion-powered machinery (11, 18). Furthermore, nitrogen has the potential to cause eutrophication of downstream waterways if it is provided in excess by urban runoff (19). This work builds off of Cadenasso et al. (20) in that I suggest urban riparian restoration plantings as a method to preventnnitrogen pollution of the watershed.

In this article I operationalize limiting similarity in the context of a working, volunteer-based restoration project on the University of California – Berkeley (UC Berkeley) campus. Plant functional traits were measured to filter the regional species pool ('trait-based filtering, as suggested in (21)) to a set of native plant species best suited to achieve desired project goals, namely to prevent re-invasion by non-native ivy species (Hedera canariensis, canary ivy; and Hedera helix, English ivy), and to prevent nitrogen pollution of the creek and riparian habitat.

Within the broader trait-filtering framework, I hone in on the selection of native species with high rates of nitrogen uptake, as determined by a stable isotope tracer analysis. Enhancing riparian nitrogen uptake has the potential to both slow the rate of nitrogen delivery to the stream (alleviate downstream nutrient pollution) and help prevent re-invasion of riparian habitat by nonnatives (i.e. achieve limiting similarity). Finally, this research serves as an example of the sort of collaboration encouraged by Palmer (3), in which campus scientists inform the work of an 'onthe- ground' restoration program, which can then provide feedback with regard to the success of different approaches.

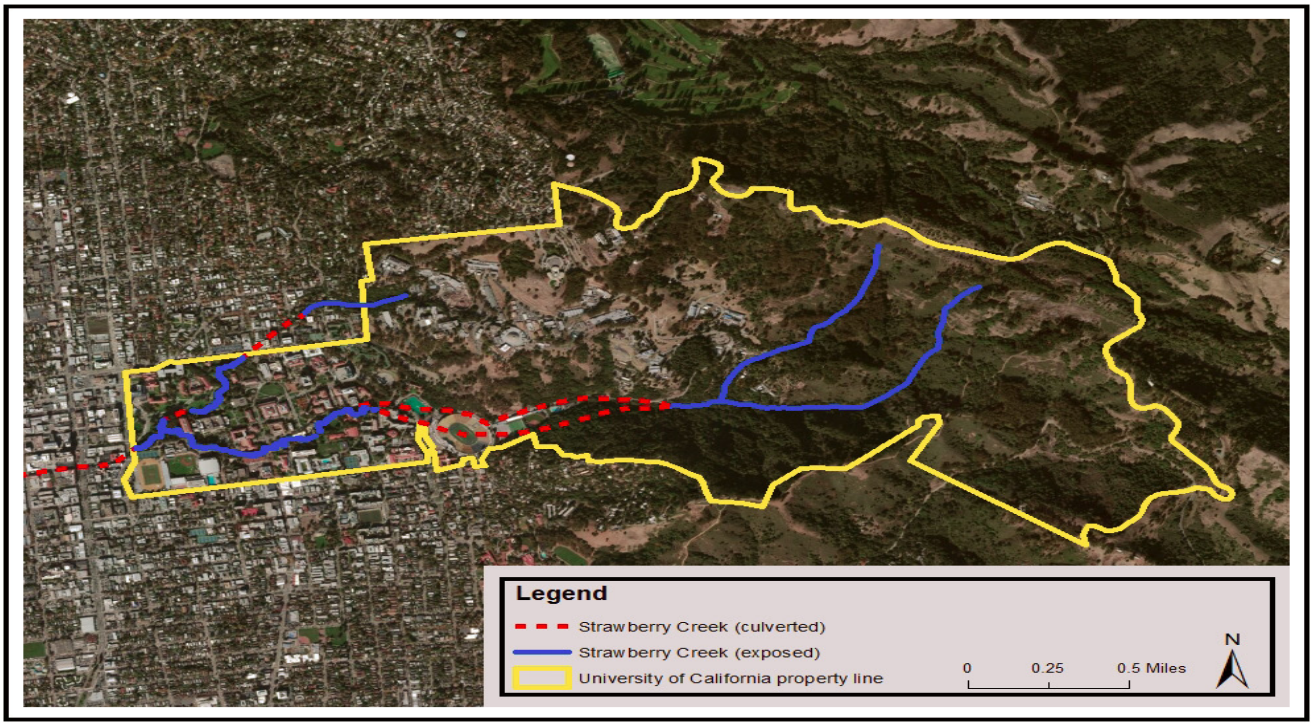
Methods

Project Site

Strawberry Creek (37°52'N; 122°15'W) is an urbanized watercourse that runs east to west through Berkeley (Alameda County), California, from the Berkeley Hills (immediately east of the UC Berkeley main campus) to the San Francisco Bay (Figure 2a). The creek has two forks North and South) that converge near the west entrance to the UC Berkeley campus (Figure 2b). The 4.7 km2 watershed drained by the creek is relatively undisturbed in the hills east of the campus, but is for the most part heavily urbanized, with impervious surfaces becoming the norm as the creek flows west through the flatlands of Berkeley (22, 23). The creek flows in underground culverts for the majority of its path, including immediately east and west of the UCB campus. This study focuses on the reaches of the creek within the confines of the UCB main campus, to match the spatial scope of the work done by the partner restoration program.

The establishment of the university along the banks of Strawberry Creek led to substantial degradation of its aquatic and riparian habitat. Trash dumping, sewage discharges, and campus lab waste made the creek a toxic site for most of the 20th century (24, 12). The creek's course and riparian habitat were substantially modified to prevent flooding of campus buildings, which has led to significant incision and channelization (12). In the late 1980s, the Strawberry Creek Restoration Program (SCRP) was born, which led to substantial water quality improvement and native fish reintroduction to the creek (22).

Understory habitat at Strawberry Creek is dominated by English (Hedera helix) and canary ivy (Hedera canariensis), both non-native, invasive species. In recent years, the SCRP has shifted its focus to student-led, volunteer-driven understory



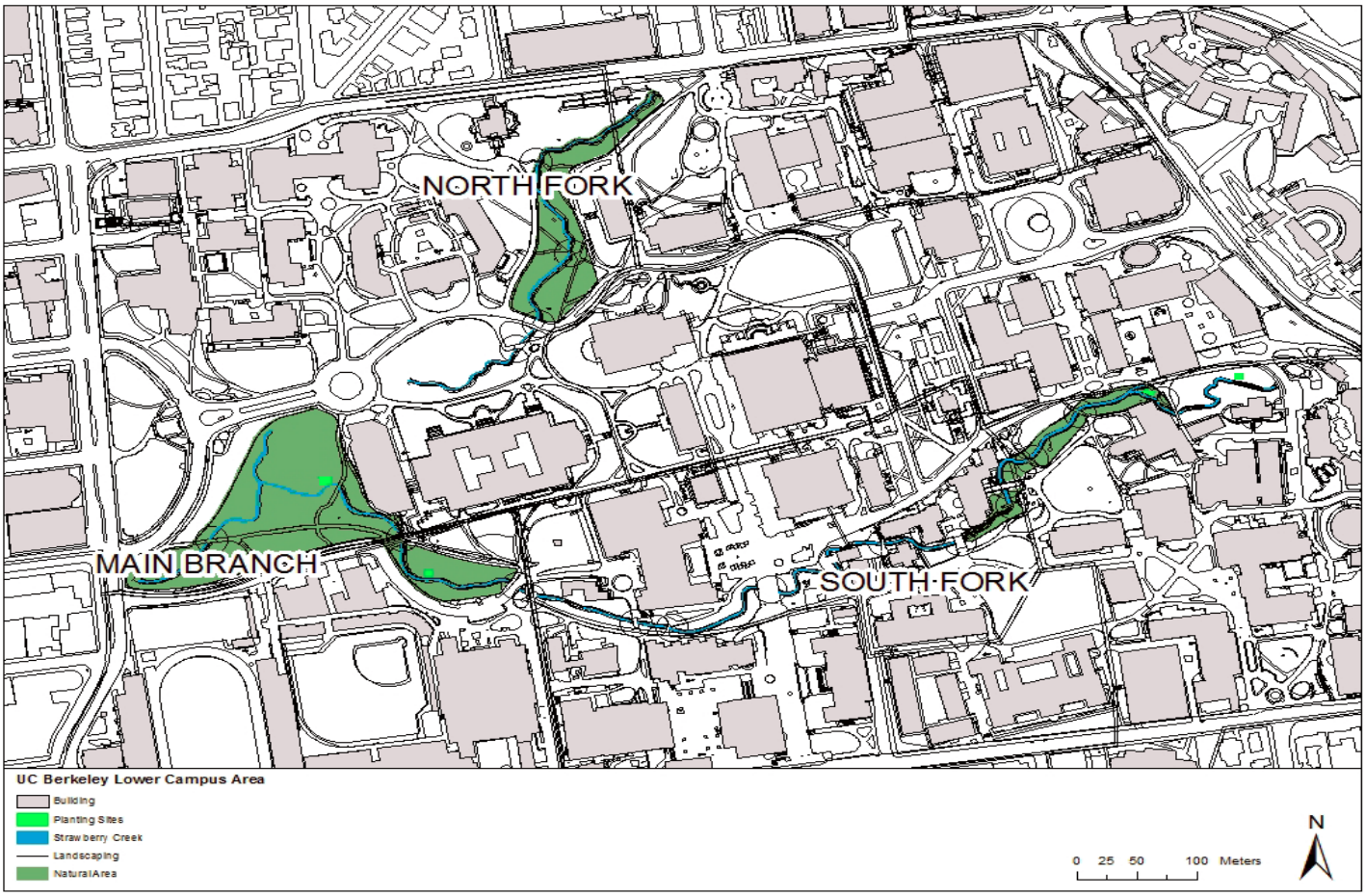


Figure 2. (a) Berkeley, CA, with the University of California's property and Strawberry Creek highlighted. The UC Berkeley main campus, referred to as the 'campus' in the document, is the small rectangle at the western-most point of the UC Berkeley property, west of Memorial Stadium (the Stadium can be seen near the middle of the picture, where the culverted line of the creek splits into two lines). The creek flows in a culvert for nearly the entirety of its trip from the west side of the campus (left edge of this image) to San Francisco Bay (approximately 2.5 miles). (b) The UC Berkeley main campus, with aboveground stretches of Strawberry Creek highlighted and labeled. Green areas represent the campus' 'natural areas,' in which the Strawberry Creek Restoration Program has permission to work. Sites where planting plans were implemented are also highlighted, in neon.

vegetation management; perhaps the program's biggest impact has been the removal of vast swaths of ivy from the shores of the creek. Other invasive species like periwinkle (Vinca minor) and panic veldtgrass (Ehrharta erecta) have also been removed, which has resulted in largely unoccupied understory habitat for substantial stretches of Strawberry Creek. To date, re-colonization of this habitat by native plant species has not occurred, and re-invasion of these habitats by weedy species (either that which was removed or a new species) occurs frequently (for example, see Figure 1). Ivy frequently returns to sites from which it was removed, usually as a result of incomplete removal of root biomass. The SCRP has recently increased its native plant output in an attempt to reintroduce native species to the banks of Strawberry Creek; the Program's interest in discovering which native plant species will do best in this urbanized ecosystem guides this research. Volunteers with the SCRP (both UCB students and members of the Berkeley community) helped clear nonnatives and plant native species at all of the sites mentioned below.

Trait-based filtering

Nine functional traits were measured on 38 plant species native to Alameda County, following from the methods in Cornelissen et al. (25). The regional species pool was narrowed to 38 species through a variety of considerations, most notably through the elimination of native species for which I did not have access to propagule material or species that did not grow well in the SCRP's on-campus nursery (for species list, see Appendix 1). The 38 species were almost entirely understory species, a function of the SCRP's focus on understory management. Species were selected from a variety of different habitat types (e.g. redwood forest, riparian, wetland, grassland) to minimize the possibility of 'pre-selecting' species assumed to do well at Strawberry Creek. In addition to the native species, functional traits were measured on two non-native species: canary and English ivy. These species were included to discern the relative differences in traits between the native and non-native species, an important prediction of limiting similarity. Ages and propagation methods were standardized across functional groups, to the extent practicable (Appendix 2); the SCRP's long-standing nursery program had some gaps in records, making it difficult to determine the exact age or geographic origin of some individuals.

The selected traits relate to diverse aspects of species morphology (Table 1). When possible, ratios were used instead of raw values (e.g. proportion of fine roots rather than mass of fine roots) to minimize the effect of any age differences. All trait measurements were taken on plants grown in nursery settings (e.g. in potting containers and a standardized potting soil). Trait measurements were taken on five replicate individuals for each plant species, then averaged across the replicates. The five replicates were spaced across five blocks in the nursery and species position within each block was randomized to minimize neighbor effects or the effects of divergent growing conditions.

Table 1. Leaf (a) and root (b) traits measured (with abbreviation in parenthesis), including the method (units in parenthesis), a brief description of the potential ecological relevance of the trait, and the source from which the measurement method was drawn, if applicable.

Trait (abbreviation)	**Measurement Method** (unit)	**Ecological relevance**	**Reference**
a. Leaf/shoot Traits			
Stomatal Conductance (cond)	LI-1600 Steady State Porometer. Measured on youngest fully formed leaf, with plant in full sun, between 0900-1100. ($mmol/m^2s$)	Shade tolerance, drought resistance, plant water relations	(26)
Chlorophyll Content	Chlorophyll meter: Konica Minolta SPAD-502. Average of three readings of young, fully formed leaves. (SPAD units)	Plant photosynthetic capacity, shade tolerance	(26)
Specific Leaf Area (SLA)	Fresh leaf (one-sided) area divided by dry leaf weight. Average of two young, fully formed leaves. Plant leaf area determined by scanning leaves and using Image J, an image processing	Drought tolerance, leaf longevity, shade tolerance, investment in leaf structures, potential relative growth rate	(25)

	program, while leaf was fresh and moist. Leaf was then dried and weighed. (cm^2/g)		
Plant Height	From soil surface to highest photosynthetically active tissue. (cm)	Competitive ability, facilitation	(25)
b. Root Traits			
Rooting depth	From soil line to lowest point of rooting structure, once plant had been removed from potting container and all soil had been washed from roots. (cm)	Drought tolerance, competitive relationships, niche differentiation	Adapted from (25)
Maximum root diameter	Largest belowground root diameter, including rhizomes. (mm)	Rate of nutrient uptake, water transport rates, root longevity, penetration force in soil	Adapted from (25)
Root-to-shoot ratio (rts)	Total dried weight of belowground biomass divided by total dried weight of aboveground biomass. (g/g)	Plant resource allocation, drought tolerance, disturbance response	
Proportion of fine roots (propF)	Total dry weight of fine roots (diameter less than 2 mm) divided by total dry weight of all roots (coarse plus fine, with coarse roots defined as those with a diameter greater than or equal to 2 mm, including rhizomes) (g/g)	Resource allocation in fine v. coarse, nutrient and water uptake capacity, root longevity	(27)
Specific (fine) root length (SRL)	Fine root sample fresh length divided by dry weight. A representative sample of 10 fine (<2 mm diameter) roots was taken from each plant. The length of each root was measured and summed, and the 10 roots were then weighed collectively. (m/g)	Resource allocation, investment in fine roots, resource availability, capacity for nutrient and water uptake, root turnover	(25)

^{15}N tracer analysis

Plant nitrogen uptake is a focal point of this research, but was treated differently from the traits listed above. I aimed to discover how nitrogen uptake rates vary across species of different growth forms (functional groups) and geographic origins (native/non-native). A nitrogen-15 stable isotope tracer analysis was conducted to address these questions. For this analysis, five species representing four functional groups were given ^{15}N-labeled ammonium chloride injections (Table 2). These species were also included in the broader trait-based filtering study. Individuals used for the nitrogen uptake analysis were all of the same age (approximately 6 months since propagation) and were all sourced from the Strawberry Creek watershed. Our interest in controlling these factors, in addition to cost constraints, motivated the choice to evaluate nitrogen uptake only on representative species from each functional group, rather than test all species. As above, propagation methods were standardized within functional groups. Inaddition to four native species, the nitrogen uptake rate of canary ivy (the more prevalent of the two ivy species at Strawberry Creek) was also analyzed, to allow for the comparison of native and non-native uptake rates. Five replicate individuals of each species were given ^{15}N injections.

This work follows from James & Richards (28) in terms of quantity of nitrogen delivered to the system. I assumed that in an urban setting, nitrogen will most likely be delivered to the riparian corridor in 'pulse' events carrying large amounts of nitrogen, e.g. rainstorms. However, Imodified the methods in James & Richards (28) to adjust for the size of the SCRP's planting containers (i.e. surface area and amount of soil) and different percent enrichment of ^{15}N (98% atom enrichment compared to 10% atom enrichment in (28)). In total, I added 2 mg of ^{15}N (as

Table 2. Species for the nitrogen-uptake analysis. All individuals of all species were approximately six months old at the time of the study, and all were sourced from the Strawberry Creek watershed. The non-native ivy is in bold.

Species name (alternate name)	Common name	Species code	Functional Group	Propagation Method
Aster radulinus (Eurybia radulina)	Rough-leaved Aster	AsRa	Forb	Field divisions
Clinopodium douglasii (Satureja douglasii)	Yerba buena	SaDo	Groundcover/ Vine	Field divisions
Hedera canariensis	Canary ivy	HeCa	Vine	Field divisions
Physocarpus capitatus	Ninebark	PhyCa	Shrub	Cutting
Ribes sanguineum var. glutinosum	Blood currant	RiSa	Shrub	Cutting

7.64 mg of $^{15}NH_4Cl$, molar mass 53.491 mg) in a 176.7 mL solution with de-ionized water (simulating a 10 mm rain event over the surface area of exposed soil, as in (28)) to each plant.

The labeled nitrogen solution was added to the soil via syringe injection. The solution was delivered via 18 injections in a circle around the base of the plant, to a depth of 10 cm. I attempted to label all parts of the soil column uniformly, injecting the solution into the soil at a slow and steady pace as I moved the syringe up through the soil column (29). The plants were harvested 13 days after injection. I chose to wait for a relatively long period of time between injection and harvest because this analysis was carried out in the non-growing season (injections on December 21st, harvest on January 3rd). The decision to perform the injections in the winter was pragmatic, based on this project's timeline. Plants were kept dry (not watered) for the week prior to injection and were not watered for the 13 days following injection.

After the 13 days had passed, the plants were harvested and all plant biomass was dried and weighed. Leaf samples (youngest fully formed leaves, as above) and root samples (a representative sample incorporating different root sizes) were collected for each plant; each sample was then ground and homogenized. Roots and leaves remained separate throughout this process. Approximately 5.5 mg of each sample was then weighed into tin capsules, yielding 50 samples: 5 species x 5 replicates x 2 samples/individual (1 leaf sample and 1 root sample). These samples were combusted in an elemental analyzer, and isotopic ratios were analyzed by a mass spectrometer, yielding leaf and root ^{15}N content for each individual plant.

Data Analysis

To visualize the interspecific differences in species' traits, a principal component analysis (PCA) was conducted for the nine traits (listed above) across forty species. Specifically, I looked to see how the native plant species would group, in terms of species traits, relative to the nonnative species and one another.

To evaluate how much labeled nitrogen each species had taken up in the 13-day study period, I examined the $\delta^{15}N$ (per mil) values for the roots and leaves of the five focal species, calculated relative to an ACM Peach standard sample according to Formula (1) below:

(1) $\delta^{15}N(\text{per min, compared to standard}) = [(R_{sample}-R_{standard})/(R_{standard})]*1000$
Where $R = (\text{Atom\% } ^{15}N)/(\text{Atom\% } ^{14}N)$

In addition to evaluating the $\delta^{15}N$ data by species, I also conducted of set of t-tests, for which I grouped the ^{15}N species into binary categories: shrub or non-shrub, and native or non-native. This allowed me to maximize the number of replicates in a group while still addressing the question at hand: how does nitrogen uptake vary across species of different growth forms (specifically, woodier versus less woody species) and geographic origins (native/non-native)? The $\delta^{15}N$ data was analyzed through a series of two-way t-tests assuming unequal variance: native shrubs (n=10, 2 species) v. all non-shrubs (including ivy, n=15, 3 species); native shrubs v. native non-shrubs (excluding ivy, n=10, 2 species); native species (n=20, 4 species) v. the non-native ivy (n=5); and native shrubs v. ivy. To compare total plant nitrogen uptake of each group, the $\delta^{15}N_{leaf}$ and the $\delta^{15}N_{root}$ values for each individual plant were summed and then averaged across the species or group in question. This method emphasizes total plant uptake of nitrogen, rather than the relative proportion of nitrogen taken up into roots or shoots. Upon noticing that most of the interspecific variation in $\delta^{15}N$ rates was a result of differences in leaf uptake rates, the same t-tests were conducted using only the $\delta^{15}N_{leaf}$ data, yielding 8 t-tests in total.

Results

Trait-based filtering

The first two axes of the PCA explained almost half of the trait variation in the dataset, with axis 1 explaining 25% of the variation, and axis 2 explaining 19.6% of the variation (Figure 3). Importantly, the two ivy species grouped together at very high root-to-shoot and chlorophyll values, and very low proportion of fine root values. These non-native species are also notably separate from the rest of the species within the trait space. Of the native species, Oxalis oregana (oxor, redwood sorrel) and Polystichum munitum (pomu, sword fern) appear to be the most similar, in terms of functional traits, to the non-native ivy species (heca and hehe, Figure 3).

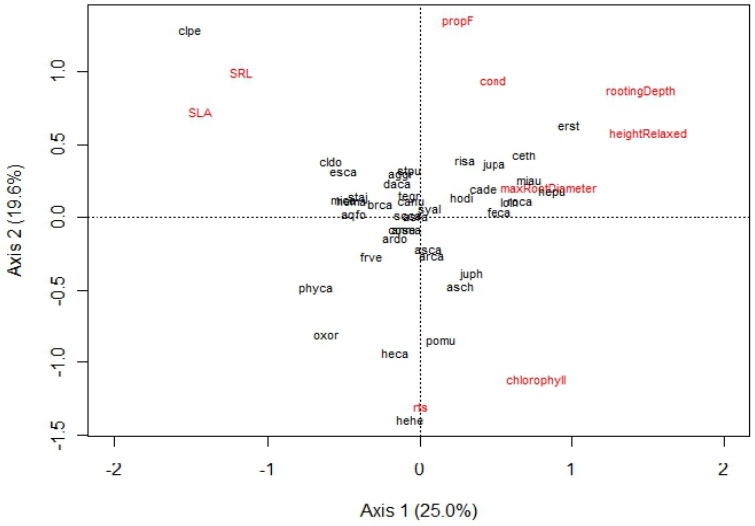


Figure 3. PCA for the 40 species and 9 traits studied. Species are in black, traits in red. Species codes correspond to the code names given in Appendix 1. Note that the ivy species (hehe and heca) group together at very high root-toshoot (rts) and chlorophyll values, and very low proportion of fine root (propF) values. Trait codes correspond to those given in Table 1.

^{15}N Analysis

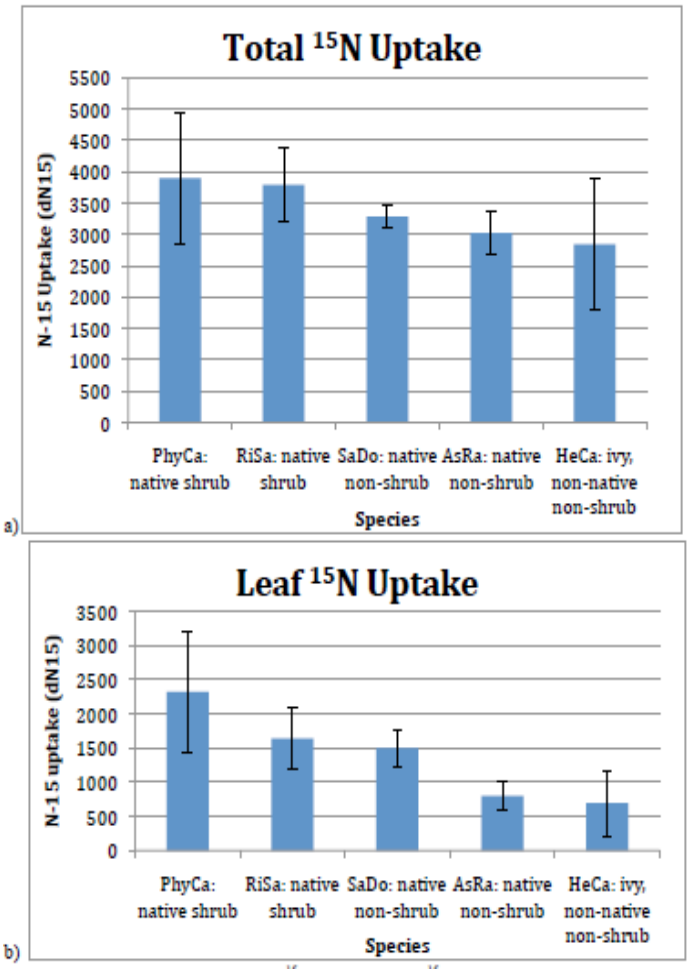
The combined root and shoot δ^{15}N values were not significantly different for any of the intergroupcomparisons conducted: native shrubs v. all non-shrubs (two-tail p=0.249, t=2.12, df=16),native shrubs v. native non-shrubs (p=0.272, t=2.2, df=11), native species v. the non-native ivy(p=0.57, t=2.57, df=5), or native shrubs v. ivy (p=0.425, t=2.36, df=7) (Figure 4a).

Figure 4. a) Combined root and leaf ^{15}N uptake rates (δ^{15}N, summed by individual plant, then averaged by species. Species codes correspond to those given in Table 2. No significant results were found for the pairwise t-tests between native shrubs and all non-shrubs, native shrubs compared to native non-shrubs, native species compared to the non-native ivy, or native shrubs compared to the non-native ivy. b) Leaf ^{15}N uptake rates (δ^{15}N), averaged by species. Marginally significant results (0.05<p<0.10) were found for the t-tests between native shrubs and all nonshrubs, and between native shrubs and the non-native ivy. The comparisons between native shrubs and native nonshrubs and between natives and the ivy showed no statistically significant differences.

Most of the interspecific variation in uptake rates appeared to come from differences in leaf uptake rates, but these differences in leaf uptake were only marginally significant at best. Two of the t-tests to discern differences in leaf uptake rates by group showed marginally significant differences (0.05<p<0.10), while the others were not significant (p>0.10) (Figure 4b). The comparisons of $\delta^{15}N_{leaf}$ between native shrubs and all non-shrubs (p=0.084, t=2.18, df=12) and between native shrubs and ivy (p=0.084, t=2.2, df=11) suggested that shrubs had marginally higher uptake rates. There were no differences in leaf uptake rates between native shrubs and native non-shrubs (p=0.136, t=2.18, df=12) and natives and the ivy (p=0.157, t=2.36, df=7).

Discussion

By measuring plant functional traits on the regional species pool, we now have a database of information to help 'filter' the pool to an appropriate list of species and guide restorative plantings. Below, I suggest a few ways to utilize this data and create planting plans to achieve the desired project goals: preventing re-invasion of riparian habitat by the non-native ivy species and reducing nitrogen pollution of the riparian corridor.



Trait-based planting plans

The PCA was analyzed in two ways to design planting plans in accordance with project goals. First, in an effort to achieve limiting similarity, species that grouped with the ivy species (and thus have traits similar to the ivy) were identified in the PCA and a planting plan was designed around these species. *Oxalis oregana* (oxor, redwood sorrel) and *Polystichum munitum* (pomu, sword fern) were both included in this planting plan. Full planting plans are shown in Table 3.

The second planting plan maximizes functional diversity in traits, in an attempt to fill all available niche spaces and thus prevent reinvasion by any non-native species. Species for this planting plan were selected from all around the PCA trait space; for example, *Claytonia perfoliata* (clpe, miner's lettuce), *Eriophyllum staechadifolium* (erst, lizard tail), and Juncus phaeocephalus (juph, brown-headed rush) were all included in this planting plan.

Nitrogen uptake

Statistically marginal evidence indicated higher nitrogen uptake rates in native shrub species, particularly for leaf uptake, when compared against non-shrubs and the non-native ivy. A third planting plan was developed based off this information, in which woodier species like *Cornus sericea* (creek dogwood) and *Mimulus aurantiacus* (sticky monkey flower) were prioritized in an attempt to maximize nitrogen uptake at these sites (Table 3). Each of the three planting plans was implemented four times, once at each of four similar sites along the South Fork of Strawberry Creek (Figure 2b). Over 100 SCRP-led volunteers, many of whom had earlier cleared ivy from the sites, planted the plans over two days in early February 2013.

Total plant biomass must be considered when evaluating the nitrogen uptake data. $\delta^{15}N$ values are effectively per gram values, such that if two individual plants have the same $\delta^{15}N$ as reported here, the plant with more biomass will have taken up more nitrogen, in total. With this in mind, a better way to evaluate $\delta^{15}N$ data in the future would be to scale the $\delta^{15}N$ by plant biomass (or by the biomass

Table 3. Planting plans established at 4 sites along the South Fork of Strawberry Creek. Each subplot was planted with 29 individuals according to the planting plans below, such that each planting plan (subplot design) was planted once at each planting site (four times total). The orientation of the planting plans with respect to one another within a site was randomized across the four sites to reduce neighbor effects. The location of each plant within each subplot was also randomized. Species not included in the trait-filtering analysis but included in the planting plans are asterisked.

Subplot 1: Limiting similarity		Subplot 2: Functional diversity		Subplot 3: N uptake	
Species	Number in subplot	Species	Number in subplot	Species	Number in subplot
Asarum caudatum	5	*Claytonia perfoliata*	4	*Rubus parviflorus*	1
Polystichum munitum	3	*Oxalis oregana*	2	*Physocarpus capitatus*	8
Aristolochia californica	2	*Juncus phaeocephalus*	2	*Ceanothus thyrsiflorus*	1
Aster radulinus	4	*Festuca californica*	2	*Holodiscus discolor*	3
Oxalis oregana	6	*Eschscholzia californica*	1	*Eriophyllum staechadifolium*	2
Juncus phaeocephalus	8	*Aquilegia formosa*	4	*Lonicera involucrata*	0
*Marah oregana**	1	*Mimulus cardinalis*	1	*Mimulus aurantiacus*	3
		Mimulus aurantiacus	3	*Rosa californica*	5
		Lonicera involucrata	1	*Cornus sericea*	2
		Cornus sericea	3	*Ribes divaricatum var. pubiflorum*	4
		Stipa pulchra	3		
		Rosa californica	3		

of the specific plant part being analyzed, e.g. total leaf weight). The data collected for this study was insufficient to properly scale up the $\delta^{15}N$ value to account for total plant biomass. Particularly because the (albeit marginally significant) differences in $\delta^{15}N$ values observed here occurred across functional groups, future research that explores shrub versus non-shrub species uptake, while scaling for biomass, could resolve some of the questions left unanswered by this research.

Also of note is that most of the interspecific or inter-group variation in uptake rates was observed in the leaf data, rather than the root data. While a representative sample of all root sizes was taken for the root $\delta^{15}N$-analysis, only the youngest fully-formed leaves were taken for the leaf analysis. This suggests that interspecific differences in uptake of nitrogen may be more pronounced in new growth: perhaps the trend of increased $\delta^{15}N$ in shrub species would become clear given more time to grow in the presence of the added nitrogen. However, the experimental framework used here related to a 'pulse' of nitrogen to the system, and thus was unable to address questions of nitrogen uptake operating over longer time scales.

Future directions

More detailed analyses should be completed in the future to uncover inter-functional group differences in nitrogen uptake. Here, coverage of several functional groups was prioritized over replication of individual species or functional groups; study with more than five replicates for each species, or with more than two or three species for each functional group, might be better equipped to evaluate inter-group differences.

Post-project monitoring will be the true test of the effectiveness of the trait-based framework in achieving project goals. In addition to collecting data on percent ivy reinvasion and nitrogen content in the soil surrounding Strawberry Creek, survivorship data on the native species outplanted will help us to determine which species do well in the unique urban ecosystems at Strawberry Creek, and which traits might predict this success.

Conclusion

This project serves as an example of a pragmatic collaboration between university scientists and on-the-ground, volunteer-driven restoration work. In this case, both parties benefitted from the collaboration: the restoration program received invaluable expertise and a quantifiable database on which to base the season's plantings, and the academic lab gained access to a nearby 'outdoor laboratory' that could serve as a testing ground for developing ecological theory. Though this approach had some limitations (e.g. limits to what species could be outplanted at Strawberry Creek), it also had extraordinary benefits, particularly in terms of outreach, as volunteers working on the creek were able to participate in and learn about the research being conducted. A transparent goal-setting and decision-making process for species selection engages volunteers and stakeholders in a way that is lacking in many restoration efforts (e.g. projects that plant natives just because they are natives, without further explanation).

In addition to serving as an example of research-informed restoration practice, this work also uncovered a marginally significant trend indicating higher nitrogen uptake in native shrub species when compared against a dominant non-native species or members of other understory functional groups. Though this trend needs to be confirmed in future research, it suggests a path forward for restoration work on Strawberry Creek in which native plantings both prevent reinvasion of a non-native species and enhance nitrogen uptake in the riparian corridor.

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Appendices

Appendix 1
Species on which functional trait measurements were taken. All species are native to California, except those bolded below. Species tested in the nitrogen tracer experiment are denoted with asterisks.

Species name	Common name	Functional group	Family	Code
Agoseris grandiflora	California dandelion	forb	Asteraceae	aggr
Anaphalis margaritacea	Pearly everlasting	forb	Asteraceae	anma
Aquilegia formosa	Western columbine	forb	Ranunculaceae	aqfo
Aristolochia californica	California pipevine	vine	Aristolochiaceae	arca
Artemisia douglasiana	Mugwort	forb	Asteraceae	ardo
Asarum caudatum	Wild ginger	forb	Aristolochiaceae	asca
Aster chilensis (Symphyotrichum chilense)	Pacific aster	forb	Asteraceae	asch
*Aster radulinus (Eurybia radulina)**	Rough-leaved aster	forb	Asteraceae	asra
Bromus carinatus var. carinatus	California brome	grass	Poaceae	brca
Calamagrostis nutkaensis	Pacific reedgrass	grass	Poaceae	canu
Carex densa	Dense sedge	grass	Cyperaceae	cade
Ceanothus thyrsiflorus	Bluebossom	shrub	Rhamnaceae	ceth
Claytonia perfoliata	Miner's lettuce	forb	Montiaceae	clpe
*Clinopodium douglasii (satureja douglasii)**	Yerba buena	groundcover	Lamiaceae	cldo
Cornus sericea	Creek dogwood	tree	Cornaceae	cose
Danthonia californica	California oatgrass	grass	Poaceae	daca
Eriophyllum staechadifolium	Lizard Tail	shrub	Asteraceae	erst
Eschscholzia californica	California poppy	forb	Papaveraceae	esca
Festuca californica	California fescue	grass	Poaceae	feca

Fragaria vesca	Woodland strawberry	groundcover	Rosaceae	frve
Hedera canariensis*	Algerian/Canary ivy	vine	Araliaceae	heca
Hedera Helix	English ivy	vine	Araliaceae	hehe
Helenium puberulum	Sneezeweed	forb	Asteraceae	hepu
Heracleum maximum	Cow parsnip	forb	Apiaceae	hema
Holodiscus discolor	Oceanspray	shrub	Rosaceae	hodi
Juncus patens	Common rush	forb	Juncaceae	jupa
Juncus phaeocephalus	Brown-headed rush	forb	Juncaceae	juph
Lonicera involucrata	Twinberry	shrub	Caprifoliaceae	loin
Mimulus aurantiacus	Sticky monkeyflower	shrub	Phrymaceae	miau
Mimulus cardinalis	Cardinal monkeyflower	forb	Phrymaceae	mica
Oxalis oregana	redwood sorrel	groundcover	Oxalidaceae	oxor
*Physocarpus capitatus**	ninebark	shrub	Rosaceae	phyca
Polystichum munitum	sword fern	fern	Dryopteridaceae	pomu
*Ribes sanguineum var. glutinosum**	blood currant	shrub	Grossulariaceae	risa
Rosa californica	California wild rose	shrub	Rosaceae	roca
Scrophularia californica	California bee plant	forb	Scrophulariaceae	scca
Stachys ajugoides	Hedge nettle	forb	Lamiaceae	staj
Stipa pulchra (Nassella pulchra)	Purple needle grass	grass	Poaceae	napu
Symphoricarpos albus	Common snowberry	shrub	Caprifoliaceae	syal
Tellima grandiflora	Fringe cups	forb	Saxifragaceae	tegr

Appendix 2.
Propagation methods, approximate age at time of trait-measurement, geographic origin, and method of acquisition (by the Strawberry Creek Restoration Program) for the forty species on which trait measurements were taken. All species are native to California, except those bolded below. Species tested in the nitrogen tracer experiment are denoted with asterisks. Data codes and acronyms are described below.

Species name	Common name	Functional group	Propagation method	age	Geographic origin of measured plants material	How acquired?
Agoseris grandiflora	California dandelion	forb	seed	6 months	RFS	Nursery
Anaphalis margaritacea	Pearly everlasting	forb	seed	1 year	Brisbane, CA	SBM
Aquilegia formosa	Western columbine	forb	seed	9 months	SC	OTN
Aristolochia californica	California pipevine	vine	seed	1.5 years	Lafayette, CA	NHN
Artemisia douglasiana	Mugwort	forb	seed	8 months	SC	Nursery
Asarum caudatum	Wild ginger	forb	seed	1 year	Wildcat Canyon, Richmond, CA	NHN
Aster chilensis (Symphyotrichum chilense)	Pacific aster	forb	seed	Adult, 2 years	Brisbane, CA	SBM
*Aster radulinus (Eurybia radulina)**	Rough-leaved aster	forb	field divisions	Adult plants, divided 6/21/12	SC	Nursery
Bromus carinatus var. carinatus	California brome	grass	seed	1 year	Brisbane, CA	SBM
Calamagrostis nutkaensis	Pacific reedgrass	grass	seed	adult, 2-3 years?	Brisbane, CA	SBM
Carex densa	Dense sedge	grass	seed	adult, 1.5 years	Brisbane, CA	SBM
Ceanothus thyrsiflorus	Bluebossom	shrub	seed	2 years	Brisbane, CA	SBM
Claytonia perfoliata	Miner's lettuce	forb	seed	4 months	Lamer	Nursery
*Clinopodium douglasii (satureja douglasii)**	Yerba buena	groundcover	field divisions	6 months	SC	Nursery
Cornus sericea	Creek dogwood	tree	cutting	5 months	Oakland Hills, CA	OTN
Danthonia californica	California oatgrass	grass	seed	1 year	RFS	Nursery
Eriophyllum staechadifolium	Lizard Tail	shrub	seed	2 years	Brisbane, CA	SBM

Eschscholzia californica	California poppy	forb	seed	6 months	RFS	Nursery
Festuca californica	California fescue	grass	seed	1.5 year	Brisbane, CA	SBM
Fragaria vesca	Woodland strawberry	groundcover	field division	1.5 years	Brisbane, CA	SBM
Hedera canariensis*	Algerian/Canary ivy	vine	Field divisions	6 months	SC	Nursery
Hedera Helix	English ivy	vine	field divisions	6 months	SC	Nursery
Helenium puberulum	Sneezeweed	forb	seed	1 year	Brisbane, CA	SBM
Heracleum maximum	Cow parsnip	forb	seed	1 year	SC	Nursery
Holodiscus discolor	Oceanspray	shrub	seed	2 years	Claremont Canyon, CA	NHN
Juncus patens	Common rush	forb	seed	8 months	SC	OTN
Juncus phaeocephalus	Brown-headed rush	forb	divisions	5 months	Brisbane, CA	OTN
Lonicera involucrata	Twinberry	shrub	cuttings	1 year	Brisbane, CA	SBM
Mimulus aurantiacus	Sticky monkeyflower	shrub	seed	1 year	Brisbane, CA	SBM
Mimulus cardinalis	Cardinal monkeyflower	forb	seed	6 months	Huckleberry Regional Park, Oakland, CA	Nursery
Oxalis oregana	redwood sorrel	groundcover	seed	Adult, unknown age	SC	Nursery
*Physocarpus capitatus**	ninebark	shrub	cutting	6 months	SC	Nursery
Polystichum munitum	sword fern	fern	field division	8 months	SC	Nursery
*Ribes sanguineum var. glutinosum**	blood currant	shrub	cutting	6 months	SC	Nursery
Rosa californica	California wild rose	shrub	seed	6 months	Brisbane, CA	SBM
Scrophularia californica	California bee plant	forb	seed	5 months	SC	Nursery
Stachys ajugoides	Hedge nettle	forb	seed; field divisions from SBM	4 months	Oakland Hills, CA	OTN
Stipa pulchra (Nassella pulchra)	Purple needle grass	grass	seed	10 months	RFS	Nursery

Symphoricarpos albus	Common snowberry	shrub	seed	1 year	SC	NHN
Tellima grandiflora	Fringe cups	forb	seed	10 months	Brisbane, CA	SBM

Notes:
'Geographic origin' codes give the location from which the genetic stock of the plant was collected originally:
RFS: Richmond Field Station, a UC Berkeley property, or surrounding areas within the same watershed.
SC: Strawberry Creek Watershed. Larner: purchased from Larner Seeds, with the precise origin of the genetic material unknown.

'How acquired' indicates whether the plant was propagated in the Strawberry Creek Native Plant Nursery (labeled 'Nursery'), or originally purchased from another nursery before being housed at the SCNPN. Nursery codes:

SBM: San Bruno Mountain's Mission Blue Butterfly Native Plant Nursery in Brisbane, CA.
OTN: Oaktown Native Plant Nursery, Berkeley, CA.
NHN: California Native Plant Society's Native Here Nursery, East Bay, Berkeley, CA.

The 'field division' propagation method implies that both aboveground and belowground plant parts were taken from a field site and then re-located to a container within the nursery. 'Cutting' implies that only aboveground shoot material was removed from an individual in the field. Cuttings were grown in a 3:1 perlite:vermiculite growing medium in the nursery, then transplanted to individual containers once new root growth emerged.