Occupation of bare habitats, an evolutionary precursor to soil specialization in plants

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Plant soil specialists contribute greatly to global diversity; however, the ecoevolutionary forces responsible for generating this diversity are poorly understood. We integrate molecular phylogenies with descriptive and experimental ecological data, creating a powerful framework with which to elucidate forces driving soil specialization. Hypotheses explaining edaphic specialization have historically focused on costs of adaptation to elements (e.g., nickel, calcium/magnesium) and accompanying tradeoffs in competitive ability in benign soils. We combine in situ microhabitat data for 37 streptanthoid species (Brassicaceae), soil analyses, and competition experiments with their phylogeny to reconstruct selective forces generating serpentine soil endemism, which has four to five independent origins in this group. Coupling ancestral state reconstruction with phylogenetic independent contrasts, we examine the magnitude and timing of changes in soil and habitat attributes relative to inferred shifts to serpentine. We find large changes in soil chemistry at nodes associated with soil shifts, suggesting that elemental changes occurred concomitantly with soil transitions. In contrast, the amount of bare ground surrounding plants in the field ("bareness"), which is greater in serpentine environments, is conserved across soil-type shifts. Thus, occupation of bare environments preceded shifts to serpentine, and may serve as an evolutionary precursor to harsh elemental soils and environments. In greenhouse experiments, taxa from barer environments are poorer competitors, a tradeoff that may contribute to soil endemism. The hypothesis of occupation of bare habitats as a precursor of soil specialization can be tested in other systems with a similar integrative ecophylogenetic approach, thereby providing deeper insights into this rich source of biodiversity.

ecological specialization | edaphic specialist | exaptation | ecological trade-off | *Streptanthus*

Ecological specialization is an important driver of biological diversity often associated with diversification through adaptive radiation, or with extinction due to evolutionary "dead ends." For plants, ecological specialization on geologically distinct parent soils (e.g., gypsum, gabbro, serpentine) contributes disproportionately to regional plant diversity, especially in the biodiversity hotspots of the South African Cape, California, and Cuba (1–3). In California, serpentine soils represent less than 1% of the area, but serpentine endemics comprise about 10% of the flora (1). Overall, two main approaches have been followed in the study of edaphic specialization. From a historical perspective, specialization has been placed in a phylogenetic context with the goal of inferring diversification rates associated with soil endemism either within or across groups (4–6). On the other hand, studies with a contemporary ecological perspective have, with experimental manipulations in either field or controlled conditions, tested hypotheses that address the drivers of edaphic specialization by focusing on plant performance in different microhabitats (7); along environmental gradients (8); when plants are grown on different substrates or with different elemental supplements (9–11); or in the presence of neighbors (12, 13), pathogens (14), or herbivores (15, 16).

The integration of molecular phylogenies with extensive clade-wide ecological data collections and experiments is greatly expanding our ability to test hypotheses and mechanisms generating diversity (17). Futuyma and colleagues (18, 19) and Armbruster and colleagues (20, 21) pioneered these approaches using experiments set in a phylogenetic context to identify exaptations and the adaptive significance of traits involved in radiations and ecological specialization. Common garden (*sensu lato*) experiments in which members of a clade are grown together to understand the ecological adaptive functions of traits have also been used (e.g., refs. 22–25). Experiments with an explicit phylogenetic framework can address aspects of trait evolution, niche conservatism, adaptation, historical contingency, exaptations, phylogenetic lag, and genetic constraints (20, 26–30). Here, we expand on these approaches by also incorporating extensive ecological data collections taken across field sites occupied by members of a whole clade, and integrating them with common garden greenhouse experiments and phylogenetic hypotheses. Using field data from 37 plant species of *Streptanthus* and close relatives (Thelypodieae, Brassicaceae) and greenhouse experiments involving 14 populations (seven species), we test hypotheses and reconstruct selective pressures involved with soil specialization in the context of phylogenetic history (31).

Understanding why some species become restricted to particular soils has challenged biologists for almost a century because most soil endemics are able to grow in more benign substrates (9, 32–36). Costs associated with adaptations to harsh environments are hypothesized to result in reduced competitive ability in zonal (regionally common) soils (9, 37), and have been the main paradigm to explain narrow soil endemism (9, 35, 36). Lately, tradeoffs in competitive ability associated with defense against herbivores and pathogens have also been implicated in the restricted distributions of soil specialists (4, 15, 16, 38, 39). For example, tissue replacement may cost more in stressful or poor nutrient environments, selecting

Significance

Integrating molecular phylogenies with clade-wide ecological data is expanding our ability to address classic ecological questions, such as the origins and maintenance of plant soil specialists, a global source of plant biodiversity. We reconstruct selective forces related to serpentine soil specialization using clade-wide microhabitat characterizations, soil physicochemical data, and phylogenetic hypotheses. Surprisingly, species' occupation of bare environments, not of chemically similar soils, preceded shifts to serpentine soils. Additionally, inhabiting bare environments traded off with competitive ability in multispecies greenhouse experiments, a relationship potentially contributing to soil endemism. We find that combining in situ detailed field ecological data, greenhouse experiments, and phylogenetic hypotheses can reveal underappreciated selective pressures and provide powerful tools to deepen our understanding of evolutionary pathways underlying biodiversity.

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for a higher investment in defense that, in turn, compromises growth rates (15, 40).

The bareness of habitats in which plants live may be an underappreciated selective force on soil specialists, and adaptations to bareness may also generate tradeoffs with competitive ability. Our recent work has shown that plants surrounded by bare ground experience greater rates of attack from herbivores owing to greater plant apparency (16). Bareness of habitat may not only make plants more apparent to enemies but may also expose them to greater UV radiation; increased drought stress (41) (Fig. 1); and, by definition, reduced densities of plant neighbors, which can be facilitators in harsh environments (42). Bareness may also be associated with soil texture (41) and rates of disturbance and erosion (43, 44), especially on rocky slopes (41, 43, 45). In studies of Mediterranean plant communities, soil endemics tended to occupy rocky substrates and steep slopes (46). Although the relative contributions of these different aspects of bare habitats are hard to tease apart, we suggest that the amount of bare ground (bareness) surrounding a plant integrates over many of these aspects, and thus we selected it a priori as one metric to capture selective regimes in harsh soil environments.

Here, we use the *Streptanthus* clade (*SI Appendix*, Fig. S1), an example of the "interplay between evolutionary radiation and edaphic endemism" (47), ancestral state reconstruction, and phylogenetic independent contrasts (PICs), to identify possible pathways leading to soil specialization, in particular to serpentine use. Members of the *Streptanthus* clade generally grow on rocky substrates like basalt, gabbro, rhyolite, shale, and granite, as well as in sandy substrates derived from various parent materials. Many species in this clade are soil endemics, with up to one-third restricted to serpentine soils (9), representing four to five independent origins of serpentine endemism (31). The wide range of soil affinities and specialization displayed by species in *Streptanthus* (now, and hereafter, *sensu lato*; *SI Appendix*, Fig. S1) make it an ideal group with which to investigate forces leading to adaptation to harsh soils.

Past investigators have identified challenges to plants specialized on serpentine soils as primarily the high Mg or low Ca/Mg ratio, the high concentrations of heavy metals usually toxic to plants (e.g., Ni, Cr, Co), and the low levels of essential plant nutrients [e.g., N, P, K (11, 41)] that are characteristic of these harsh soils. The vast majority of studies comparing serpentine and nonserpentine populations have focused on differences between serpentine outcrops and soils of adjacent nonserpentine habitats. However, to understand the evolution of soil use of edaphic specialists, which rarely occur on adjacent zonal soils, we believe the most pertinent comparisons lie between differences in serpentine and nonserpentine soils of clade mates.

To explore whether changes in chemical, textural, or microhabitat aspects of serpentine soils occur concomitantly or in a decoupled fashion from transitions in soil use, we used a combination of ancestral state reconstruction and PICs (48) based on our detailed soil and environment characterizations. Because serpentine and nonserpentine habitats and soils differ significantly in many elements and characteristics (e.g., ref. 9), we predict that there must be large changes in reconstructed soil attributes at some point in the evolutionary history of soil specialists. For example, because a low Ca/Mg ratio is identified as an important selective agent in serpentine soils (9), we might find that use of soils with low Ca concentrations precedes shifts to serpentine, and could facilitate serpentine use.

Surprisingly, we find that occupation of bare habitats, rather than any soil element characteristic of serpentine (e.g., Ni, Ca, Mg, K, P), preceded shifts to serpentine. With subsequent common garden experiments, we ask whether taxa from bare environments are, as the competitive exclusion paradigm would predict, poor competitors, a condition that might constrain their distributions to barer soils. A goal of this work was not only to deepen our understanding of pathways of edaphic specialization but also to expand a body of work that gains insights from combined descriptive and experimental ecological data collections within a phylogenetic framework (17).

Fig. 1. Microhabitat bareness, the amount of bare ground surrounding plants in the field, is highly variable and integrates many aspects of harsh environments, such as greater apparency to enemies, increased drought and exposure to UV light, and lower density of plant neighbors. (*Left*) *Streptanthus brachiatus* on serpentine soil. (*Right*) *Caulanthus anceps* on nonserpentine fine-texture soil.

Results

Characterization of Soils and Environments. Serpentine and nonserpentine soils used by streptanthoids are chemically and texturally different, as revealed by physicochemical analyses of 294 soil samples from 116 populations representing 45 species of *Streptanthus* and close allies (Fig. 2 and *SI Appendix*, Figs. S2 and S3 and Tables S1 and S2). Serpentine soils used by streptanthoids had lower levels of Ca (0.09×), K (0.20×), and P (0.28×), and higher levels of Ni (32×), Mg (5.63×), and Co (6.51×). Differences in other elements were not as pronounced. Texturally, serpentine soils had more coarse particles (>4 mm, 2×) and clay content (< 2 μm, 1.20×) but fewer overall fine particles (<1.7 mm, 0.67×).

Field surveys quantifying the percentage of bare ground surrounding plants across 37 species of *Streptanthus* (with replicate populations per species) revealed that these species typically occur in relatively bare microhabitats, and that those growing on serpentine habitats are surrounded by an even greater proportion of bare ground (1.2×; Fig. 2 and *SI Appendix*, Table S2). Many of the variables characterizing serpentine and nonserpentine soils are, not surprisingly, intercorrelated (*SI Appendix*, Table S3).

Microhabitat Bareness and Soil Texture Are More Strongly Conserved Than Soil Elements. With standard measures of phylogenetic signal, we explore if metrics of contemporary environments (bareness) and soils bear information allowing inferences about past growing regimes. Although there may be pitfalls in extrapolating from current conditions to past ones, the most parsimonious explanation of a strong phylogenetic signal in currently measured ecological characteristics is that current environments reflect past ones; such approaches have been applied in historical biogeography (49) and to test the adaptive significance of traits (17, 20).

Taking phylogenetic uncertainty into account, we find that serpentine affinity in the *Streptanthus* clade has strong phylogenetic signal (median Purvis's $D = -2.193$). The only habitat or soil attributes with K estimates higher than expected under the Brownian model of evolution (95% confidence interval of K estimates not overlapping with $K = 1$) were field microhabitat bareness and soil fine fraction ($K_{\text{Bareness}} = 1.292$, $P = 0.01$; $K_{\text{Fine}} = 1.443$, $P = 0.01$; Table 1 and *SI Appendix*, Fig. S4 and Table S4). Microhabitat bareness is more phylogenetically conserved (greater mean K) than most soil chemical elements (Table 1 and *SI Appendix*, Table S4), including elements with which it was correlated (*SI Appendix*, Tables S3 and S5), although distributions of K estimates overlap in some instances (*SI Appendix*, Table S4). Soil elements considered

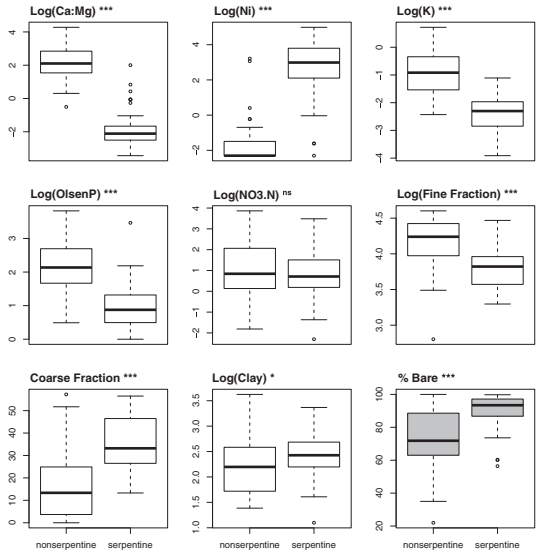

Fig. 2. Serpentine and nonserpentine soils and microhabitats used by streptanthoids are different in soil chemistry, soil texture, and bareness. ***$P \leq 0.001$; *$P \leq 0.05$ (*SI Appendix*, Figs. S2 and S3 and Table S2).

important indicators of serpentine that exhibit significant phylogenetic signal do not depart from expectations under the Brownian model of evolution ($K = 1$; e.g., $K_{Ca/Mg} = 1.151$, $P = 0.01$; $K_{Ni} = 0.955$, $P = 0.01$; $K_{Co} = 0.829$, $P = 0.01$; Table 1 and *SI Appendix*, Table S4). Interestingly, many chemical elements that differ between serpentine and nonserpentine soils show no or weak ($K < 1$) phylogenetic conservatism (e.g., $K_{Clay} = 0.771$, $P = 0.12$; $K_{Mn} = 0.563$, $P = 0.22$). In contrast, macrotextural soil fractions exhibit a very strong phylogenetic signal (Table 1 and *SI Appendix*, Table S4).

Transitions to Serpentine Are Accompanied by Concomitant Large Changes in Chemical Soil Composition; Changes in Habitat Bareness Preceded Serpentine Shifts. For each of 5,000 randomly selected postburnin trees from a study by Cacho et al. (31), we reconstructed the history of serpentine use and identified nodes associated with soil transitions. We then compared PIC absolute values of soil chemistry and microhabitat attributes at nodes ancestral to soil shifts with values at the rest of the nodes that are not associated with soil transitions (*Methods*; Fig. 3). For a given attribute, similar PIC values between these two kinds of nodes would indicate that its change is not associated with soil shifts. Because we know how the two soil types differ with respect to each of the attributes studied, it is possible to make inferences about the direction of the changes observed. We find that contrasts associated with chemical elements considered diagnostic of serpentine soils (e.g., Ca/Mg, Ni, Co) show large changes between nodes with and without inferred shifts in soil use (e.g., Ca/Mg mean $PICs_{NO\text{-}SHIFT} = 28.24$; Ca/Mg mean $PICs_{SHIFT} = 72.09$; t test median P value across 5,000 trees = 0.05; Fig. 4 and Table 1).

In contrast to soil elemental characteristics, changes in bareness (%Bare) at nodes associated with shifts to serpentine soils are significantly smaller than changes at nodes not associated with inferred edaphic shifts (%Bare mean $PICs_{NO\text{-}SHIFT} = 326.20$; %Bare mean $PICs_{SHIFT} = 169.4$; median $P = 0.04$; Fig. 4 and Table 1). In other words, nonserpentine habitats ancestral to serpentine shifts were already very bare. These results imply that occupation of bare environments may be a precursor enabling transitions to barer serpentine soils. A similar but weaker pattern is observed in organic matter (OM mean $PICs_{NO\text{-}SHIFT} = 15.18$; OM mean $PICs_{SHIFT} = 10.06$; median $P = 0.15$). For the rest of the soil chemical and textural characteristics, there were no significant differences among contrasts at nodes preceding shifts in soil use and the rest of the nodes in 5,000 postburnin trees we analyzed (Table 1). Even excluding from the analysis the outgroups and the *Streptanthus* clade II, in which there are no serpentine-using species, we still recover these patterns, although they are weaker (PIC $P_{Ca/Mg} = 0.06$; $P_{\%Bare} = 0.11$; *SI Appendix*, Fig. S5 and Table S6).

Could Occupation of Bare Habitats Trade Off with Competitive Ability and Contribute to Soil Specialization? In lath-house assays with raw field soils, we related the average competitive ability of *Streptanthus* species to their average microhabitat bareness surrounding plants in replicate field sites (*Methods*). We found that competitive ability of streptanthoid species is negatively related to species mean field microhabitat bareness ($n = 10$; estimate = −1.33, $P = 0.039$; Fig. 5) and marginally significant when phylogeny is taken into account [phylogenetic generalized least squares (PGLS) estimate = −1.093, $P = 0.087$]. The relationship is stronger when comparing only populations with estimates of both bareness and competitive ability rather than species averages ($n = 14$; estimate = −1.324, $P = 0.004$; PGLS estimate = −0.931, $P = 0.016$; *SI Appendix*, Table S7). The interaction bareness * serpentine was not significant (species-level PGLS $P = 0.25$, population-level PGLS $P = 0.11$).

Discussion

Plant soil specialists contribute greatly to global plant diversity, especially in arid and Mediterranean regions (2, 44, 50, 51). By integrating extensive contemporary microhabitat data collections and common garden experiments with phylogenetic history, we

Table 1. Phylogenetic signal and means of absolute values of PICs (absPICs) at nodes associated and not associated with inferred soil shifts, over 5,000 postburnin randomly sampled trees

	Phylogenetic signal		abs(PICs)		
Variable	Median K	Median P	NO-SHIFT node	SHIFT node	Median P
%Bare	**1.292**	**0.009**	**326.20**	**169.40**	**0.044**
Log (Ca/Mg)	**1.151**	**0.009**	**28.24**	**72.09**	**0.050**
Log (Co)	**0.829**	**0.009**	**16.25**	**44.91**	**0.074**
Log (Ni)	**0.955**	**0.009**	**40.81**	**93.48**	**0.085**
Log (OM)	0.578	0.287	15.18	10.06	0.150
Log (Na)	**0.694**	**0.050**	17.93	11.70	0.160
Log (Mg)	**0.910**	**0.009**	21.78	42.06	0.193
Log (P)	**0.881**	**0.009**	16.20	27.85	0.209
Log (K)	**0.949**	**0.009**	15.96	24.15	0.297
Log (Ca)	**0.960**	**0.009**	22.65	32.46	0.310
Log (B)	**0.650**	**0.050**	18.26	12.39	0.316
Log (CEC)	**0.677**	**0.030**	17.72	13.81	0.320
Log (NO_3N)	0.632	0.149	25.80	36.18	0.370
Log (Mn)	0.563	0.218	18.17	21.66	0.403
Log (Cu)	0.487	0.564	19.04	15.03	0.414
Log (SP)	0.571	0.119	4.85	4.25	0.440
Log (C)	0.583	0.158	14.29	12.17	0.481
Log (Fe)	**0.748**	**0.009**	18.49	17.57	0.583
Log (N)	0.512	0.485	13.18	12.08	0.598
Log (Cr)	0.570	0.327	3.12	2.21	0.606
Log (pH)	**0.630**	**0.030**	2.49	2.44	0.666
Log (Zn)	0.582	0.139	17.93	18.42	0.671
Log (clay)	0.771	0.119	12.06	16.12	0.370
Log (silt)	0.581	0.188	11.72	8.52	0.385
Coarse fraction	**1.117**	**0.009**	286.50	271.10	0.463
Fine fraction	**1.443**	**0.009**	5.39	5.19	0.562
Sand	0.572	0.347	291.80	281.10	0.618

Variables are ordered by significance of difference in PICs within category (bareness, chemistry, and texture). The 95% confidence intervals for K are provided in *SI Appendix*, Table S4. CEC, cation exchange capacity; OM, organic matter; SP, saturated paste. Boldface denotes $P < 0.10$.

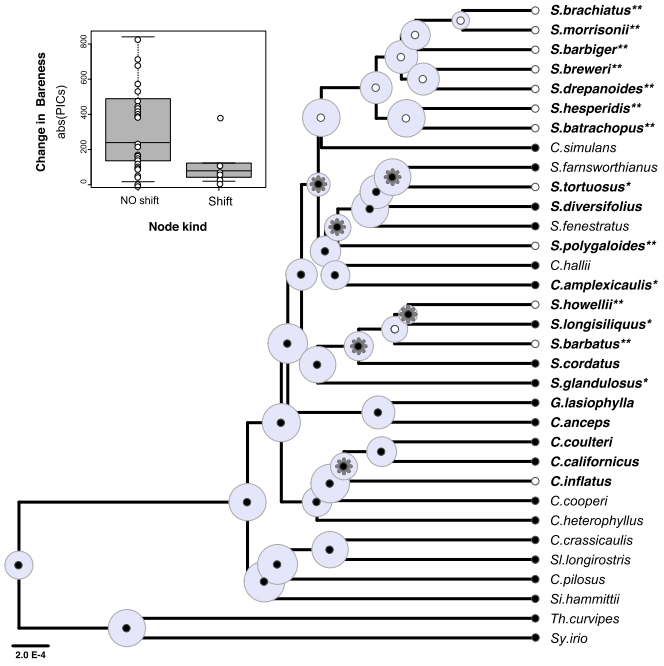

Fig. 3. Single realization [1 of 5,000 randomly sampled postburnin trees (31)] of serpentine and bareness evolution in the *Streptanthus* clade. Small circles represent serpentine states, assigned with a probability equal to the proportion of records on serpentine (PRS) for a given species (white indicates serpentine). Stars represent selected nodes, because they precede soil shifts. Gray circles show size proportional to the absolute value of PICs [abs(PICs)]. Species with PRS > 0 are shown in boldface, serpentine endemics (PRS > 87%) are indicated by two asterisks, and bodenvags (defined as PRS > 11%) are indicated by one asterisk. (*Inset*) Bareness PICs (absolute value) for this particular realization.

suggest a new hypothesis: the importance of habitat bareness as a driver of soil specialization. We show that shifts onto serpentine soils likely took place not from chemically similar soils (e.g., with a low Ca/Mg ratio or high Ni content), as has been previously hypothesized (9), but from ancestrally bare microsites. Adaptations to bare habitats may, per se, enable adaptation to harsh soils like serpentine. Batten et al. (52) had similar ideas on forces maintaining rare plant species found in different soils (greenstone, limestone, shale, and others) along the Yukon River in Alaska: "...factors other than the chemical nature of the substrate are responsible for the persistence of these supposed relic species.... [T]hese slopes provide a habitat for species adapted to dry unstable conditions, but intolerant of competition" (also ref. 53).

We point to three lines of evidence suggesting that elemental composition may be an easier evolutionary hurdle than bareness in soil specialization by streptanthoids. First, members of the *Streptanthus* clade use a huge number of parent soils with highly variable elemental composition (*SI Appendix*, Table S2), including three southwestern limestone specialists that, by definition, tolerate high soil Ca (in contrast to low-Ca serpentine). Second, microhabitat bareness tends to be more conserved across the clade than elemental features of soils previously identified as important selective agents in serpentine soils [e.g., Mg, Ni, Ca/Mg ratio (35, 41, 43, 54)]. Third, our ongoing experiments in this clade and work of many others demonstrate that harsh soil-adapted species can grow on zonal soils (32, 33, 35, 43, 53), suggesting more lability in the fundamental niche of soil use than in the realized niche. The main paradigm to reconcile edaphic endemism with the ability of many soil endemics to grow on alternative soils relies on hypothesized tradeoffs between the ability to tolerate peculiar substrate chemistry and the ability to withstand competition in zonal soils [competitive ability tradeoff hypothesis (36, 39–41, 44, 52)]. We show, in addition, that ability to live in bare habitats might contribute to this tradeoff.

Multiple, nonmutually exclusive sources of selection arising from bare environments might result in tradeoffs in competitive ability. Abiotically, life in bare microhabitats might require adaptations to increased disturbance (45), rockiness, drought (55), and exposure to high levels of UV light (36). Adaptations like the production of heat-shock proteins and UV-absorbing phenols and flavonoids may have costs that reduce competitive ability (56, 57). Likewise, adaptations to disturbance, which are associated with a lack of vegetation cover in serpentine and other bare soils (45, 52) and which may perpetuate a lack of vegetation (58), may also have costs. Bare environments were rockier, and macrotextural aspects of soils (coarse and fine fractions, which are not included in "off-the-shelf" analyses) were highly conserved across this clade.

Bare habitats also differ in their biotic selective regimes; by definition, they have a lower biomass of plant neighbors. Other studies have provided evidence for positive, facilitative effects of plant neighbors in a variety of harsh abiotic environments (42, 59), suggesting that a lack of neighbors (bareness) could impose abiotic challenges for plants. However, using both experimental and descriptive approaches, we found the net effect of neighbors measured over the lifetime of two serpentine *Streptanthus* species in the field was negative, not facilitative (16). Low levels of plant competition in bare environments might select for different suites of plant traits than those traits favored in more vegetated and competitive environments (60), as outlined in Grime's plant strategies (61) and in other studies (62).

Our previous work, and that of others, has shown that bareness or low neighbor density can increase plant apparency to enemies (16, 63). Bareness, both naturally occurring and manipulated, was associated with increased levels of damage from herbivores in the field, and a concomitant reduction in plant fitness, in *Streptanthus breweri* and *Streptanthus hesperidis*. Apparency in bare or open environments might increase the need for enemy defense (64, 65), an investment that could also trade off with competitive ability (15, 16; but also ref. 39). Species of *Streptanthus* exhibit various forms of antiherbivore defense; notably, several species have brown or gray leaves that match the color of their soil outcrop (16). This potentially costly crypsis defense is found only on bare habitats, both serpentine and nonserpentine. Ni hyperaccumulation (66) and mimicry of herbivore pierid butterfly eggs that reduces oviposition by butterflies (67) provide additional evidence that herbivory and bare environments may represent historical selective forces in this

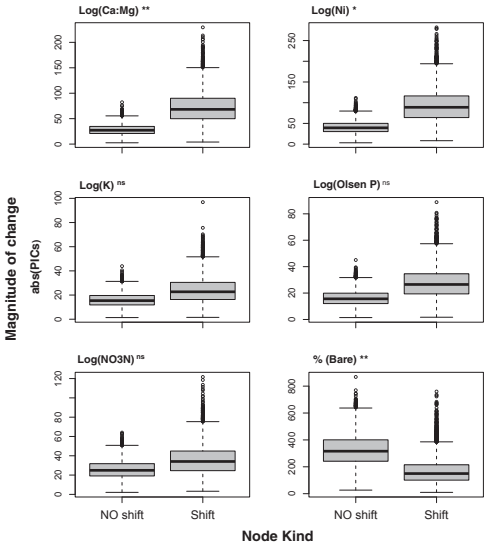

Fig. 4. absPICs at nodes with and without inferred shifts to serpentine soils. Points are mean PICs for each node category (Fig. 3) for each of 5,000 postburnin trees (31). $^{**}P \leq 0.05$; $^{*}P < 0.1$. Estimates and *P* values are provided in Table 1. ns, not significant.

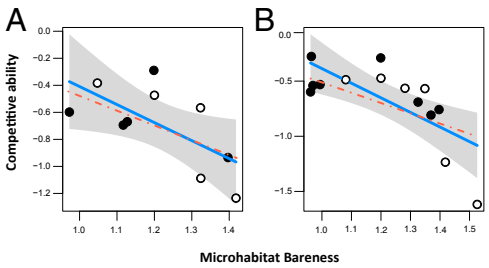

Fig. 5. Field microhabitat bareness [percentage of a 0.25-m^2 quadrat not occupied by plants; arcsinsqrt(%Bare)] is negatively correlated with competitive ability (log response ratio) against a native grass, as measured in a greenhouse experiment. Serpentine populations are denoted ○, and nonserpentine populations are denoted ●. Fits for linear (solid lines) and PGLS models (dashed lines) are depicted. (*A*) Species-level analysis; serpentine and nonserpentine populations of bodenvag species are treated separately (PGLS lnRR = −1.093 × + 0.614; $P = 0.08$, adjusted $R^2 = 0.24$). (*B*) Population-level analysis (PGLS lnRR = −0.932 × + 0.419; $P = 0.02$, adjusted $R^2 = 0.34$). Details are provided in *SI Appendix*, Table S7.

clade. Thus, tradeoffs between competitive ability and bareness might arise from adaptations to a variety of nonexclusive selective forces.

Combined historical and contemporary approaches can point to potentially underappreciated forces shaping biodiversity, but reconstructing past selective forces, sequences of events, and trait changes is challenging. Alternative hypotheses might explain our results. For example, bareness may be a surrogate for a correlated, as yet unmeasured, factor. Disentangling the relative importance of bareness, nutrients, elements, enemies, and competition in pathways leading to soil specialization will require the expansion of experimental and descriptive approaches, for example, a design incorporating specific nutrient and elemental manipulations with varying competition intensity in a phylogenetic context. Additionally, measurement and phylogenetic reconstruction of plant traits and abilities associated with elemental uptake, competition, and drought tolerance may shed light on the sequence of selective forces and trait evolution contributing to soil specialization.

Soil endemism contributes disproportionately to regional floras and to overall global plant diversity (2, 44, 50, 51). Our integrative ecophylogenetic approach can be extended to test the generality of adaptation to bare habitats in other plant groups; in other regions with high levels of soil endemism; and in other bare soil substrate types like gypsum (5, 68), limestone (33, 69), ironstone (70), and dolomite (71). More broadly, ecophylogenetic approaches applied to a variety of systems and questions in evolutionary ecology continue to be an important means through which we can explain the origins and maintenance of biodiversity.

Methods

Species and Phylogenetic History. To integrate over phylogenetic uncertainty, we performed analyses over a random sample of 5,000 postburnin trees of a 50-million–generation Bayesian analysis (31). Due to lack of monophyly in the well-supported *Streptanthus glandulosus* complex (31), which also uses a variety of soil types, we collapsed it to a single lineage in all our evolutionary analyses, sampling tips (with their soil affinities) at random across our 5,000 iterations (a full explanation of methods used is provided in *SI Appendix, Methods in Full*).

Soils and Environments. Soil samples (one to three samples per population, 116 populations, 45 species) were collected from the rhizosphere (top 30 cm of soil) immediately below randomly selected focal plants within each population, dried, and stored. Soils were sifted into three fractions (fine, <1.7 mm; medium, 1.7–4 mm; and coarse, >4 mm) using standard soil sieves. Physicochemical analyses were done at the University of California, Davis Analytical Laboratory (http://anlab.ucdavis.edu). Microhabitat bareness was quantified at the time of flowering in 2011 and 2013 for 71 populations of streptanthoids (37 species; *SI Appendix*, Table S1) as the percentage of bare ground in a 0.25-m^2 quadrat centered on focal plants naturally occurring in the field. Plants are patchily distributed in expansive habitats, so we identified focal plants with a combination of targeted and random sampling, first identifying areas where plants occurred, then selecting some areas at random, and then randomly selecting focal plants within selected patches. When possible, we measured replicate populations per species and 15 focal plants per population (a minimum of five plants per site in low-density populations). We investigated the potential effect of year in our estimates using sites measured in both years. We found that bareness estimates between years were variable but correlated ($r = 0.6$, $P = 0.02$ after removing one outlier; $n = 14$) and not significantly different ($P = 0.29$; $n = 30$), justifying our use of data collected across years.

Statistical Analyses. We compared serpentine and nonserpentine soils with Welch's *t* tests to account for unequal variances in R version 3.1; when necessary, soil elemental data were log-transformed to meet normality assumptions. Using only the populations for which we had both field bareness and soil chemical data (*SI Appendix*, Tables S1 and S5), we also analyzed the relationship between bareness and individual soil elements using univariate linear models and correcting for multiple comparisons (Bonferroni).

Phylogenetic Signal and PIC Analyses. We incorporated phylogenetic uncertainty by analyzing 5,000 randomly selected postburning trees (31). We evaluated phylogenetic signal using Blomberg's *K* (72) or Purvis's *D* (73). All analyses were done in R (details and functions used are provided in *SI Appendix, Methods in Full*). For our PIC analyses, we first inferred soil use history to identify soil transitions in each tree. Then, for a given habitat attribute, we compared the PIC absolute values at nodes ancestral to transitions to serpentine, which reflect the magnitude of change associated with soil shifts ("SHIFT" nodes), with the rest of the nodes ("NO-SHIFT" nodes) using a Welch's *t* test that accounts for unequal variances (Fig. 3).

Tradeoffs Between Competitive Ability and Bareness. We explored the relationship between competitive ability [log response ratio (lnRR)] measured in lath-house experiments and field microhabitat bareness using linear models (JMP Pro version 10, SAS Institute Inc.) and PGLS (74) based on the maximum credibility tree of a 50-million–generation Bayesian analysis (31). Competitive ability was estimated as the response ratio of the performance (biomass) of *Streptanthus* plants grown with (B_W) and without (B_{WO}) a grass neighbor (*Bromus laevipes*), calculated as $\text{lnRR} = \ln(B_W/B_{WO})$ (75). *B. laevipes* is native to California and occurs at many *Streptanthus* sites. Competition assays were performed under natural light and temperature conditions in natural raw soils also from *Streptanthus* sites. Focal plants and their grass neighbors were collected for dry biomass analyses at the onset of first flower. Full details on germination and growing conditions are provided in *SI Appendix, Methods in Full*. For a species-level analysis, we used species averages of both lnRR and bareness. Three of the seven species measured can be found on and off serpentine (*Streptanthus glandulosus, S. tortuosus, Caulanthus amplexicaulis*), and because serpentine and nonserpentine sites differ in bareness, serpentine and nonserpentine populations were analyzed as separate data points. For an analysis at the population level, we included 14 populations for which we had estimates of both field bareness and lnRR.

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SUPPLEMENTARY FIGURES

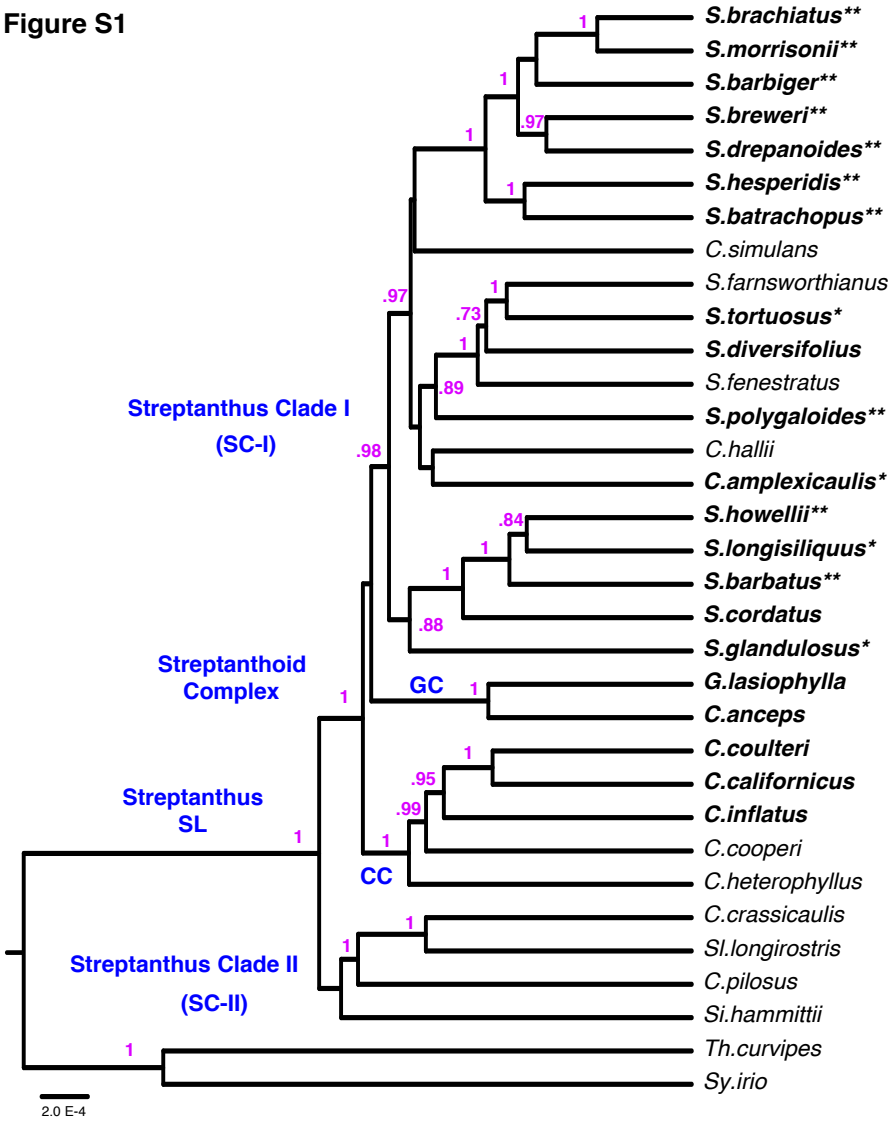

Figure S1. Relationships and clade support values in *Streptanthus* and close relatives. In bold, species with proportion of records in serpentine (PRS) > 0 are in bold; serpentine endemics (PRS > 87%) are noted with two asterisks, and bodenvags (PRS > 11%), with one asterisk. Genera abbreviations are as follows: *Streptanthus* (S), *Caulanthus* (C), *Guillenia* (G), *Sibaropsis* (Si), *Streptanthella* (Sl), *Sisymbrium* (Sy), *Thelypodium* (Th).

Figure S2.

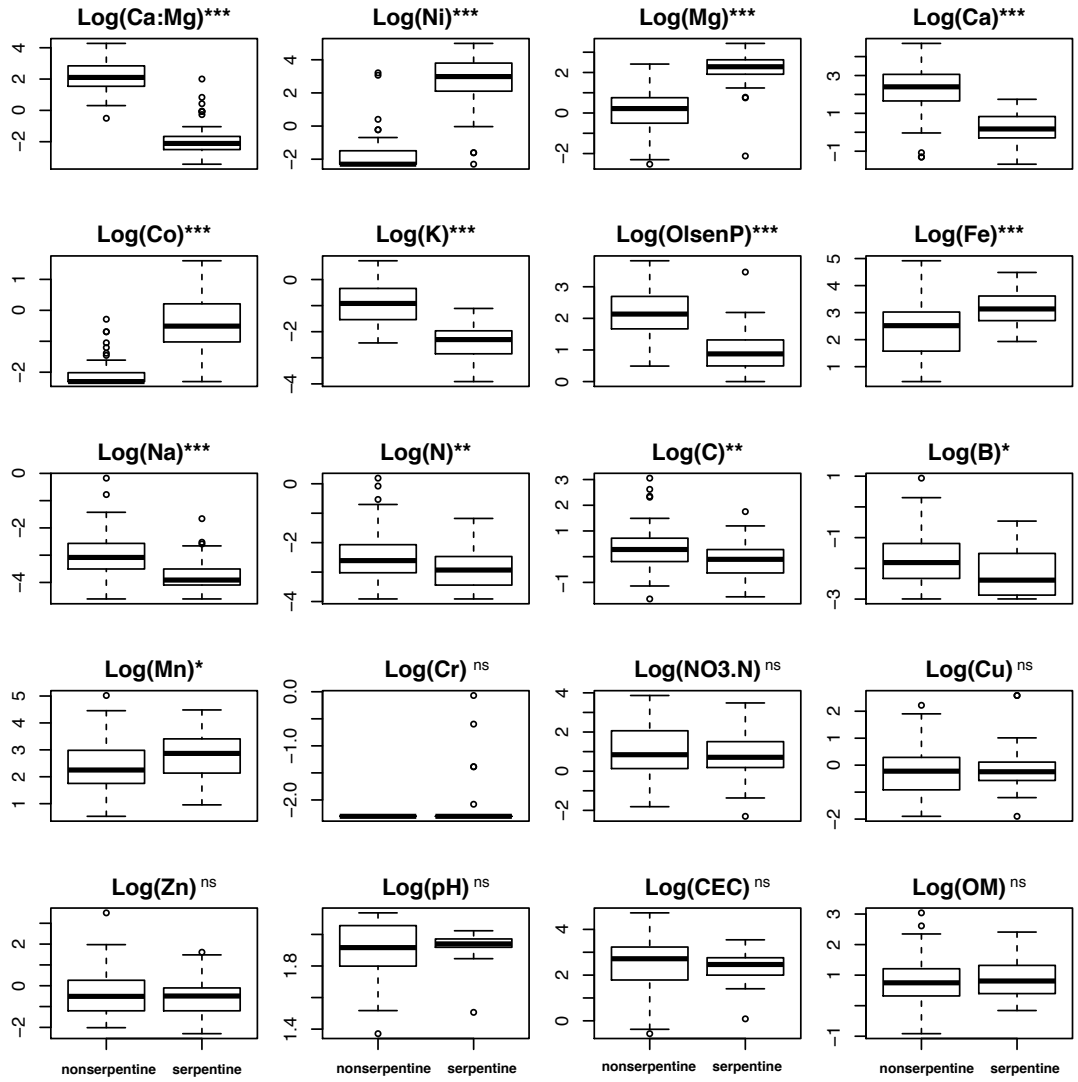

Figure S2. Chemical characterization of serpentine (S) and nonserpentine (NS) soils inhabited by species of the Streptanthoid complex and allies. For p-values, estimates of means and units, see Table S2.

Figure S3.

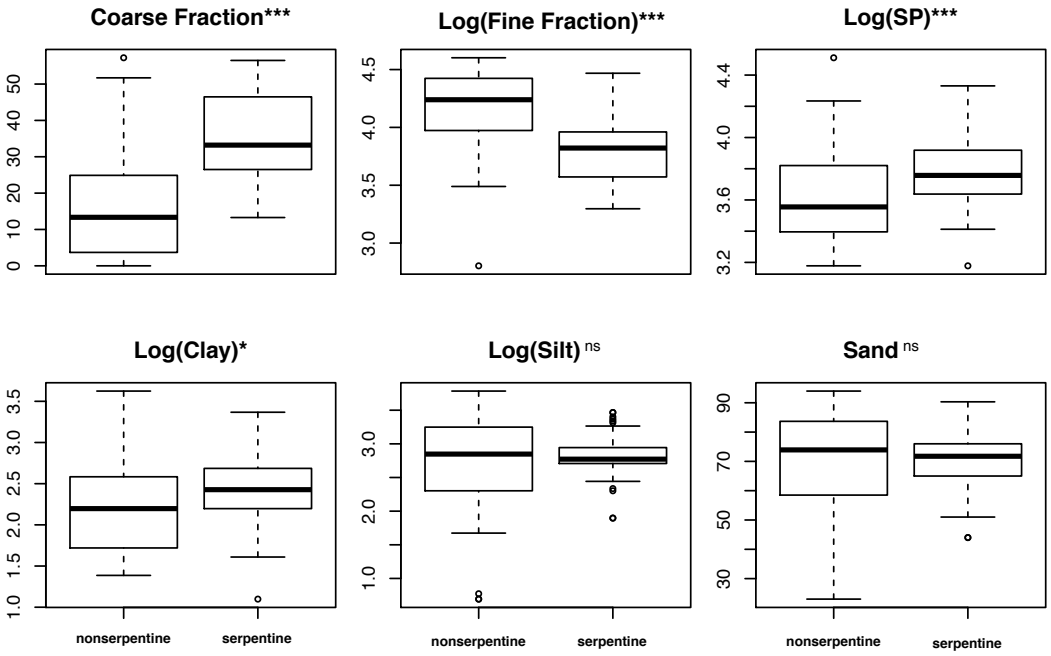

Figure S3. Textural characterization of serpentine (S) and nonserpentine (NS) soils inhabited by species of the Streptanthoid complex and allies. For p-values and estimates, means and units, see Table S2.

Figure S4.

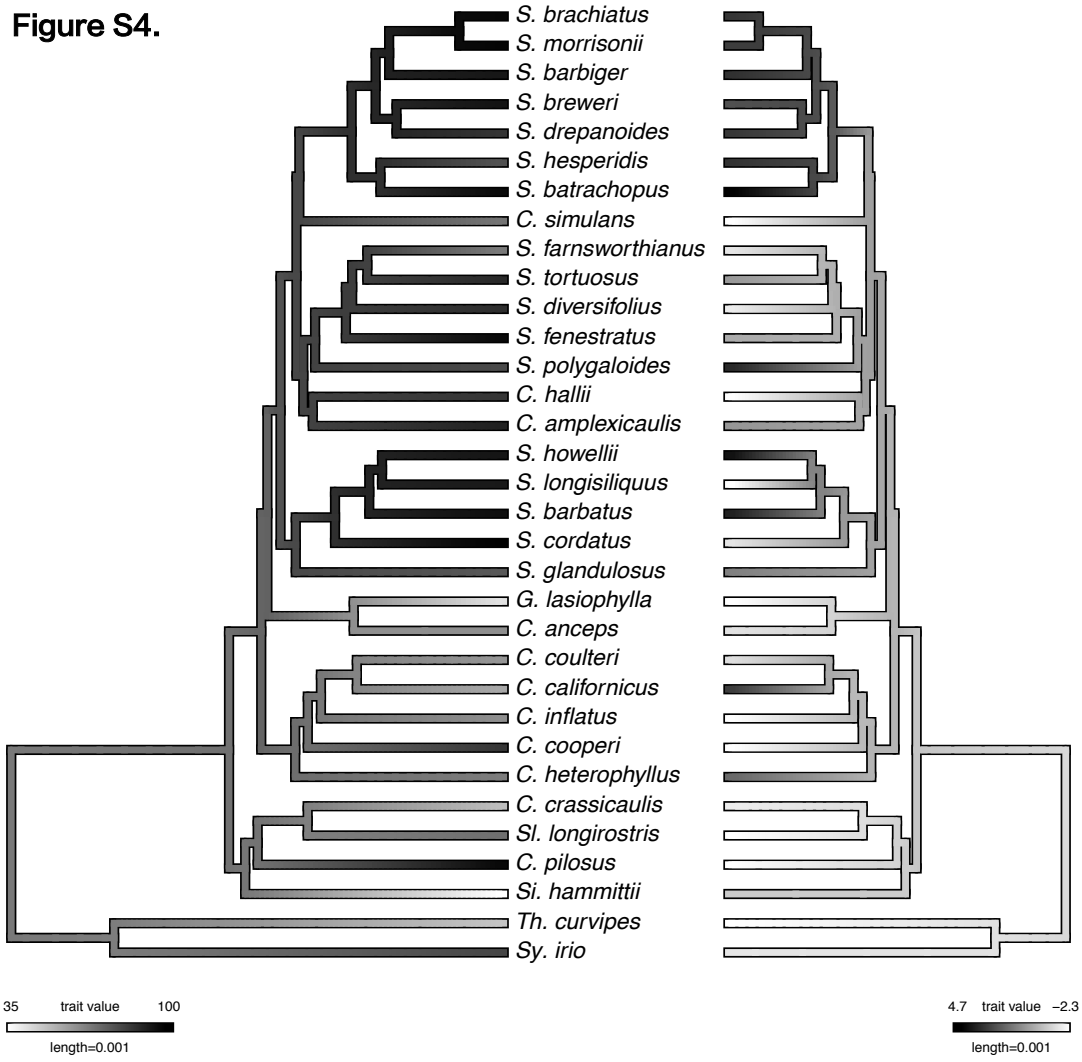

Figure S4. Habitat bareness measured in the field is more phylogenetically conserved than chemical elements of soils used by the Streptanthoid complex. Left: microhabitat bareness. Right: soil nickel.

Figure S5.

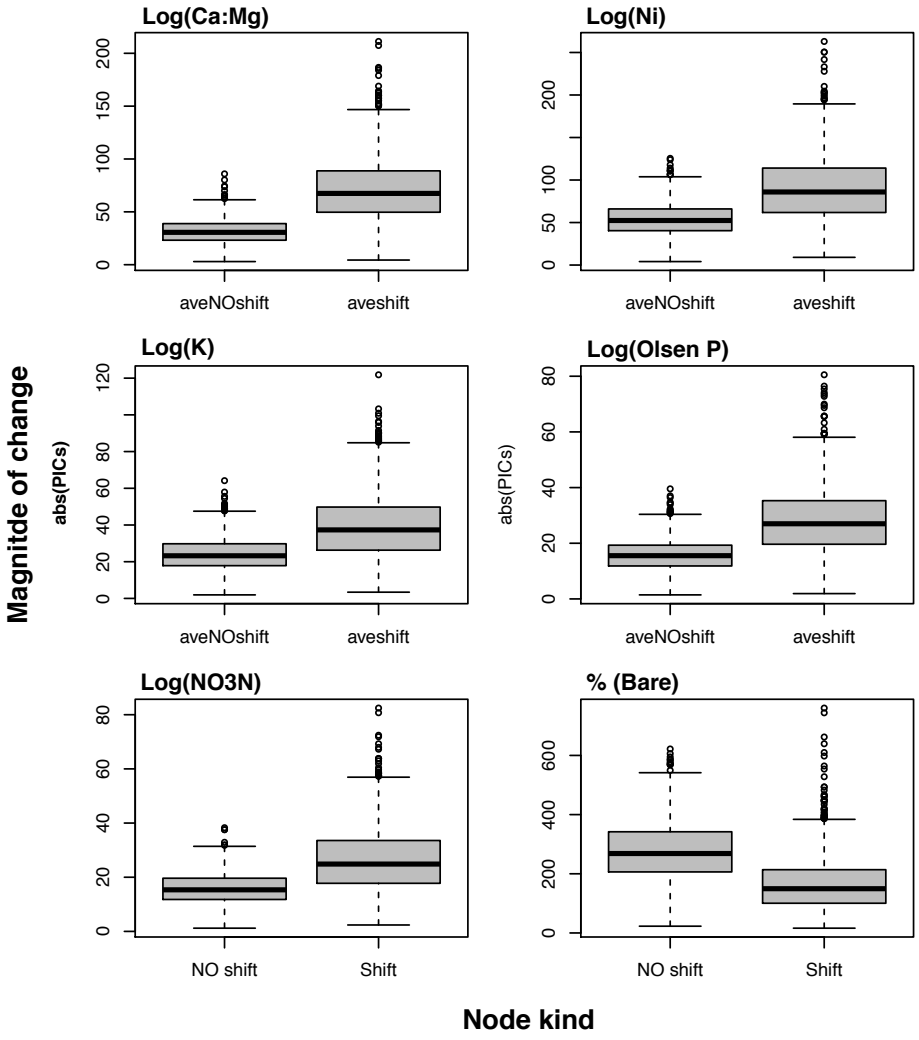

Figure S5. Phylogenetic independent contrasts (absolute values) at nodes with and without inferred shifts to serpentine soils when considering the Streptanthoid Complex only (clades SC-I, GC, CC). Each point represents the mean value of nodes with/without inferred soil shifts for each of 1,150 post-burnin trees (1). For values and p-values see Table S6.

SUPPLEMENTARY TABLES

Table S1. Populations included in the study. The bareness dataset consisted of 71 populations, representing 37 species (33 tips when considering the *S. glandulosus* complex (SGC) as a single lineage –marked by an asterisk*). The soils dataset consisted of 116 populations, representing 45 (40*) species. Competitive ability (lnRR) was measured in a total of 19 populations, representing 9 (7*) species.

N	Population	Soil kind	Soils	Bare	lnRR	Species	Species collapsed
1	AirQuality_gland	serpentine	X	X		*S.glandulosus**	*S.glandulosus**
2	AirQuality_hesp	serpentine	X	X		*S.hesperidis*	*S.hesperidis*
3	Ballinger_anceps	nonserpentine	X	X		*C.anceps*	*C.anceps*
4	Ballinger_coulteri	nonserpentine	X	X		*C.coulteri*	*C.coulteri*
5	Ballinger_inflatus	nonserpentine	X	X		*C.inflatus*	*C.inflatus*
6	Ballinger_stanleya	nonserpentine	X			*St.pinnata*	*St.pinnata*
7	BartlettSprings	nonserpentine	X	X	X	*S.glandulosus**	*S.glandulosus**
8	BidwellBridge	nonserpentine	X	X		*S.tortuosus*	*S.tortuosus*
9	BigSandy	nonserpentine		X	X	*S.diversifolius*	*S.diversifolius*
10	brew_ROD	serpentine	X		X	*S.breweri*	*S.breweri*
11	BuraMtRd_brach	serpentine	X			*S.brachiatus*	*S.brachiatus*
12	ButtCyn_hesp	serpentine	X			*S.hesperidis*	*S.hesperidis*
13	CalciteMine	nonserpentine	X			*Sl.longirostris*	*Sl.longirostris*
14	Caliente-Bod_coulteri	nonserpentine	X	X		*C.coulteri*	*C.coulteri*
15	Caliente-Bod_glasio	nonserpentine		X		*C.lasiophyllus*	*C.lasiophyllus*
16	Carinaz_orpipe1	nonserpentine	X			*S.carinatus*	*S.carinatus*
17	CasaLoma_kyle	serpentine	X			*S.polygaloides*	*S.polygaloides*
18	Cattleguard_calif	nonserpentine	X	X		*C.californicus*	*C.californicus*
19	Cedars_gland	serpentine	X			*S.glandulosus**	*S.glandulosus**
20	Cedars_morrisoni	serpentine	X			*S.morrisonii*	*S.morrisonii*
21	ClearCrk	serpentine	X			*S.insignis**	*S.glandulosus**
22	CordatusDickOD	nonserpentine	X			*S.cordatus*	*S.cordatus*
23	CoyoteCyn_sisym	nonserpentine	X			*Sy.irio*	*Sy.irio*
24	CoyoteCyn_stella	nonserpentine	X			*Sl.longirostris*	*Sl.longirostris*
25	CrawleyLake	nonserpentine	X	X		*C.pilosus*	*C.pilosus*
26	DavisRd	nonserpentine	X	X		*C.coulteri*	*C.coulteri*
27	Davycamp	serpentine	X	X	X	*C.amplexicaulis*	*C.amplexicaulis*
28	DeathValley_cord	nonserpentine	X	X		*S.cordatus*	*S.cordatus*
29	DeathValley_elata	nonserpentine	X			*St.elata*	*St.elata*
30	DeathValley_pinn	nonserpentine	X			*St.pinnata*	*St.pinnata*
31	DelvinoCt	nonserpentine	X			*C.heterophyllus*	*C.heterophyllus*
32	Devils_hesp	serpentine	X			*S.hesperidis*	*S.hesperidis*
33	DrumPwr_poly	serpentine	X			*S.polygaloides*	*S.polygaloides*
34	DrumPwr_tort	serpentine	X			*S.tortuosus*	*S.tortuosus*
35	Elsinore	nonserpentine	X	X		*Si.hammitii*	*Si.hammitii*
36	ForbesTown_tort	serpentine	X			*S.tortuosus*	*S.tortuosus*
37	ForbesTownDam_poly	serpentine	X			*S.polygaloides*	*S.polygaloides*
38	FredoynerPk	nonserpentine	X			*C.major*	*C.major*

N	Population	Soil kind	Soils	Bare	lnRR	Species	Species (collapsed)
39	FremontPk	nonserpentine	X	X		*C.inflatus*	*C.inflatus*
40	GiantGland	nonserpentine	X			*S.glandulosus**	*S.glandulosus**
41	Gorge_drep	serpentine	X			*S.drepanoides*	*S.drepanoides*
42	Gravesck	serpentine	X			*S.barbatus*	*S.barbatus*
43	Graywacke_insig	serpentine	X			*S.insignis**	*S.glandulosus**
44	GreenValleyRd-Fulker	nonserpentine	X		X	*C.amplexicaulis*	*C.amplexicaulis*
45	HayesRanchTX	nonserpentine	X			*S.bracteatus*	*S.bracteatus*
46	hesp_ROD	serpentine	X			*S.hesperidis*	*S.hesperidis*
47	HetchHetchy	nonserpentine	X			*S.tortuosus*	*S.tortuosus*
48	HighLSprings_bbiger	serpentine	X	X		*S.barbiger*	*S.barbiger*
49	Highway03_barbatus	serpentine	X	X		*S.barbatus*	*S.barbatus*
50	Highway299_tort	nonserpentine	X			*S.tortuosus*	*S.tortuosus*
51	Highway74	nonserpentine	X	X		*C.heterophyllus*	*C.heterophyllus*
52	HinkeySummit	nonserpentine	X			*C.major*	*C.major*
53	HolidayCamp_pil	nonserpentine	X	X		*C.pilosus*	*C.pilosus*
54	HuntingCrk_breweri	serpentine		X		*S.breweri*	*S.breweri*
55	HuntingCrk_morris	serpentine	X	X		*S.morrisonii*	*S.morrisonii*
56	Hwy175_bbig	serpentine	X			*S.barbiger*	*S.barbiger*
57	Hwy29_hesp	serpentine	X			*S.hesperidis*	*S.hesperidis*
58	IowaHill_tort	nonserpentine	X	X	X	*S.tortuosus*	*S.tortuosus*
59	JadeMill	serpentine	X			*S.insignis**	*S.glandulosus**
60	KBR32_breweri	serpentine	X			*S.breweri*	*S.breweri*
61	KingsCyn_div	nonserpentine	X	X		*S.diversifolius*	*S.diversifolius*
62	KingsCyn_farns	nonserpentine	X	X		*S.farnsworthianus*	*S.farnsworthianus*
63	KingsCyn_fen	nonserpentine		X		*S.fenestratus*	*S.fenestratus*
64	KramerJct_glasio	nonserpentine	X	X		*G.lasiophylla*	*G.lasiophylla*
65	KramerJct_inflatus	nonserpentine	X	X		*C.inflatus*	*C.inflatus*
66	KreyConglom	nonserpentine	X		X	*S.insignis**	*S.glandulosus**
67	KreyShale	nonserpentine	X			*S.insignis**	*S.glandulosus**
68	LagunaMtn_brew	serpentine	X			*S.breweri*	*S.breweri*
69	LimeSaddle_drep	serpentine	X	X		*S.drepanoides*	*S.drepanoides*
70	LimeSaddle_polyg	serpentine	X	X		*S.polygaloides*	*S.polygaloides*
71	LlagasCastle	serpentine	X			*S.albidus**	*S.glandulosus**
72	LowDivideRd305	serpentine	X	X		*S.howellii*	*S.howellii*
73	MadRiverRd_drepROD	serpentine	X			*S.drepanoides*	*S.drepanoides*
74	Magalia	serpentine	X			*S.polygaloides*	*S.polygaloides*
75	MarinWD_gland	serpentine	X	X	X	*S.glandulosus**	*S.glandulosus**
76	Mayacamas_brach	serpentine	X	X		*S.brachiatus*	*S.brachiatus*
77	Mayacamas_gland	nonserpentine		X	X	*S.glandulosus**	*S.glandulosus**
78	McL_CorreaHouse	nonserpentine		X	X	*S.glandulosus**	*S.glandulosus**
79	McL_CoyoteHill	serpentine	X	X		*S.breweri*	*S.breweri*
80	McL_LomHill	serpentine	X	X		*S.breweri*	*S.breweri*
81	McL_QuarryView	serpentine	X	X		*S.hesperidis*	*S.hesperidis*
82	MetcalfRd	serpentine	X	X		*S.albidus**	*S.glandulosus**
83	MillarRd_het	nonserpentine	X	X		*C.heterophyllus*	*C.heterophyllus*
84	MineWash_coop	nonserpentine	X	X		*C.cooperi*	*C.cooperi*
85	MineWash_hallii	nonserpentine	X	X		*C.hallii*	*C.hallii*
86	MonitorValley_olig	nonserpentine	X			*S.oliganthus*	*S.oliganthus*
87	morr_ROD	serpentine	X			*S.morrisonii*	*S.morrisonii*

N	Population	Soil kind	Soils	Bare	lnRR	Species	Species (collapsed)
88	MtBaldy	nonserpentine	X	X	X	*C.amplexicaulis*	*C.amplexicaulis*
89	MtDiablo_hispidus	nonserpentine	X	X		*S.hispidus**	*S.glandulosus**
90	MtHam_callistus	nonserpentine	X	X		*S.callistus**	*S.glandulosus**
91	MtHam_gland	nonserpentine	X			*S.glandulosus**	*S.glandulosus**
92	NormaFowler	nonserpentine	X			*S.bracteatus*	*S.bracteatus*
93	phyllis	nonserpentine	X			*S.hyacinthoides*	*S.hyacinthoides*
94	NewIdria	serpentine		X		*S.insignis**	*S.glandulosus**
95	Oakglen	serpentine			X	*S.albidus**	*S.glandulosus**
96	PanocheHills_insig	serpentine		X		*S.insignis**	*S.glandulosus**
97	PetersonRd	nonserpentine		X	X	*S.farnsworthianus*	*S.farnsworthianus*
98	PineFlatRd_brach	serpentine	X	X		*S.brachiatus*	*S.brachiatus*
99	PinyonMtRd_2010	nonserpentine	X	X		*C.hallii*	*C.hallii*
100	Pisgaw_stella	nonserpentine	X	X		*Sl.longirostris*	*Sl.longirostris*
101	PlumCyn_coop	nonserpentine	X	X		*C.cooperi*	*C.cooperi*
102	RanchoDiana	nonserpentine	X			*S.bracteatus*	*S.bracteatus*
103	RichBar	serpentine	X	X	X	*S.tortuosus*	*S.tortuosus*
104	SalineValleyRd	nonserpentine	X	X		*C.crassicaulis*	*C.crassicaulis*
105	ShadowMtnRd_stanpi	nonserpentine	X			*St.pinnata*	*St.pinnata*
106	SilverCyn_cordatus	nonserpentine	X			*S.cordatus*	*S.cordatus*
107	SilverCyn_glaucus	nonserpentine	X			*C.glaucus*	*C.glaucus*
108	Skyway	serpentine	X	X		*S.polygaloides*	*S.polygaloides*
109	SnFelipe_simulans2010	nonserpentine	X	X		*C.simulans*	*C.simulans*
110	SnFelipe_sisymrio	nonserpentine	X	X		*Sy.irio*	*Sy.irio*
111	SnFelipe_thysano	nonserpentine		X		*Thy.curvipes*	*Thy.curvipes*
112	SnGer_batra	serpentine	X	X	X	*S.batrachopus*	*S.batrachopus*
113	SodaLake	nonserpentine		X		*C.anceps*	*C.anceps*
114	StagCove_coop	nonserpentine	X	X		*C.cooperi*	*C.cooperi*
115	StirlingCity	nonserpentine	X			*S.longisiliquus*	*S.longisiliquus*
116	StrawberryLkout_amp	nonserpentine	X			*C.amplexicaulis*	*C.amplexicaulis*
117	StrawberryLkout_bern	nonserpentine	X			*S.bernardinus*	*S.bernardinus*
118	TableMtn_div	nonserpentine	X	X		*S.diversifolius*	*S.diversifolius*
119	TableMtn_tort	nonserpentine	X	X	X	*S.tortuosus*	*S.tortuosus*
120	ThomGorge_drep	serpentine	X			*S.drepanoides*	*S.drepanoides*
121	to_ButtsCyn	nonserpentine	X	X		*S.longisiliquus*	*S.longisiliquus*
122	TuckerMtn	serpentine	X		X	*S.insignis**	*S.glandulosus**
123	TurtleRock	serpentine	X	X	X	*S.breweri*	*S.breweri*
124	WARd_polyg	serpentine	X	X		*S.polygaloides*	*S.polygaloides*
125	WARd_tort	serpentine	X	X	X	*S.tortuosus*	*S.tortuosus*
126	WhisperPines_bbiger	serpentine	X	X		*S.barbiger*	*S.barbiger*
127	Widmer_Rd	nonserpentine		X		*C.heterophyllus*	*C.heterophyllus*
128	Ysabel_het	nonserpentine	X	X		*C.heterophyllus*	*C.heterophyllus*
129	Ysabel_thysano	nonserpentine	X			*Thy.curvipes*	*Thy.curvipes*
	Totals: 129		**116**	**71**	**19**	**46**	**43**

Table S2. Characterization of serpentine (S) and nonserpentine (NS) soils occupied by streptanthoid species, sorted by bareness, chemical and texture attributes and then by p-value within category. Comparisons were performed with Welch's two-sample t-test for samples with unequal variances in R (R Core Team, 2013). Chemistry variables, fine fraction, silt and clay were log-transformed for analyses, and bareness was arcsine square root transformed; means correspond to untransformed values. Significant differences are denoted as follows: *** P<0.001, ** P<0.01, and * P<0.05; in bold, variables that remain significant after Bonferroni correction.

Variable Category	Variable	Units	pValue		Raw NS.Mean	Raw S.Mean	S/NS
Bare	**% Bare**	**%**	**0.00027**	***	**74.656**	**88.547**	**1.186**
Chemistry	**Ca:Mg Ratio**	-	**5.53E-38**	***	**13.577**	**0.402**	**0.030**
	Ni	**ppm**	**1.16E-29**	***	**0.908**	**29.634**	**32.624**
	Mg	**meq/100g**	**2.68E-20**	***	**1.878**	**10.583**	**5.634**
	Ca	**meq/100g**	**1.14E-19**	***	**16.993**	**1.576**	**0.093**
	Co	**ppm**	**5.18E-19**	***	**0.148**	**0.962**	**6.512**
	K	**meq/100g**	**3.09E-18**	***	**0.557**	**0.116**	**0.209**
	Olsen.P	**ppm**	**8.26E-15**	***	**11.975**	**3.462**	**0.289**
	Fe	**ppm**	**1.38E-07**	***	**16.907**	**29.919**	**1.770**
	Na	**meq/100g**	**2.19E-07**	***	**0.080**	**0.031**	**0.384**
	N.Total	%	0.00440	**	0.139	0.067	0.478
	C.Total	%	0.00612	**	2.386	1.111	0.466
	B.SP	mg/L	0.01065	*	0.285	0.165	0.580
	Mn	ppm	0.01798	*	17.657	22.407	1.269
	Cr	ppm	0.05237		0.100	0.132	1.322
	NO3.N	ppm	0.23932		6.742	3.794	0.563
	Cu	ppm	0.24110		1.181	1.410	1.194
	Zn	ppm	0.29128		1.673	0.973	0.582
	pH		0.30408		6.846	6.937	1.013
	CEC	meq/100g	0.41789		19.508	12.305	0.631
	OM	%	0.77925		3.185	2.824	0.887
Texture	**Coarse fraction**	**%**	**1.64E-09**	***	**17.368**	**35.574**	**2.048**
	Fine fraction	**%**	**6.18E-09**	***	**68.004**	**45.661**	**0.671**
	SP	**%**	**0.00042**	***	**38.632**	**44.897**	**1.162**
	Clay	%	0.01203	*	10.610	12.726	1.199
	Silt	%	0.44208		19.066	17.538	0.920
	Sand	%	0.81339		70.329	69.746	0.992

Table S3. Correlations among soils chemical and textural characteristics across 57 populations (34 species) of streptanthoids. Soil chemistry values, fine fraction, silt, and clay were log-transformed as needed to meet assumption of normality, and bareness was arcsine square root transformed.

	Bareness	Frac. COARSE	Frac.FINE	Sand	Silt.Log	Clay.Log	N.Log	C.Log	NO3.N. Log	Olsen.P .Log	K.Log	Na.Log	Ca.Log	Mg.Log	CaMgRa tio.Log	CEC.Log	OM.LOI. Log	pH.Log	B.SP.Log	Zn.Log	Mn.Log	Cu.Log	Fe.Log	Cr.Log	Ni.Log	SP.Log	Co.Log
Bareness	1.000	0.635	-0.722	0.169	-0.089	-0.170	0.043	0.081	0.145	-0.301	-0.588	-0.486	-0.596	0.165	-0.450	-0.474	0.384	-0.405	-0.515	0.130	0.459	0.133	0.573	0.175	0.362	0.272	0.395
Frac.COARSE	0.635	1.000	-0.935	0.151	0.052	-0.133	-0.077	-0.010	0.237	-0.530	-0.614	-0.548	-0.568	0.323	-0.484	-0.360	0.250	-0.296	-0.365	0.153	0.456	0.450	0.507	0.036	0.472	0.169	0.413
Frac.FINE	-0.722	-0.935	1.000	-0.214	-0.015	0.180	0.058	-0.021	-0.277	0.537	0.670	0.592	0.626	-0.295	0.530	0.427	-0.320	0.334	0.462	-0.126	-0.480	-0.282	-0.568	-0.099	-0.468	-0.213	-0.420
Sand	0.169	0.151	-0.214	1.000	-0.875	-0.890	-0.250	-0.210	0.138	0.001	-0.311	-0.557	-0.299	-0.414	0.037	-0.554	-0.259	-0.133	-0.104	0.096	-0.063	-0.477	-0.049	0.088	-0.169	-0.188	-0.189
Silt.Log	-0.089	0.052	-0.015	-0.875	1.000	0.763	0.392	0.412	-0.085	0.021	0.171	0.347	0.191	0.393	-0.094	0.415	0.429	0.019	0.074	0.022	0.164	0.464	0.195	-0.045	0.217	0.300	0.244
Clay.Log	-0.170	-0.133	0.180	-0.890	0.763	1.000	0.222	0.182	-0.041	-0.075	0.232	0.474	0.229	0.596	-0.174	0.607	0.234	0.162	0.074	-0.065	0.151	0.543	0.132	-0.081	0.326	0.185	0.346
N.Log	0.043	-0.077	0.058	-0.250	0.392	0.222	1.000	0.869	0.223	0.484	0.316	0.199	0.250	-0.005	0.174	0.158	0.780	-0.316	-0.026	0.485	0.222	0.237	0.322	-0.208	-0.027	0.633	0.049
C.Log	0.081	-0.010	-0.021	-0.210	0.412	0.182	0.869	1.000	0.113	0.345	0.263	0.117	0.249	-0.037	0.197	0.198	0.760	-0.185	0.054	0.418	0.197	0.183	0.292	-0.192	0.001	0.617	0.092
NO3.N.Log	0.145	0.237	-0.277	0.138	-0.085	-0.041	0.223	0.113	1.000	0.060	0.023	-0.161	-0.057	0.093	-0.065	0.022	0.155	-0.025	0.064	0.260	0.031	0.151	0.033	0.014	0.087	0.171	-0.009
Olsen.P.Log	-0.301	-0.530	0.537	0.001	0.021	-0.075	0.484	0.345	0.060	1.000	0.690	0.341	0.608	-0.502	0.639	0.239	0.025	0.030	0.501	0.184	-0.327	-0.300	-0.369	-0.150	-0.596	-0.074	-0.559
K.Log	-0.588	-0.614	0.670	-0.311	0.171	0.232	0.316	0.263	0.023	0.690	1.000	0.689	0.917	-0.350	0.769	0.648	-0.085	0.337	0.650	-0.029	-0.433	-0.155	-0.635	-0.316	-0.630	-0.154	-0.602
Na.Log	-0.486	-0.548	0.592	-0.557	0.347	0.474	0.199	0.117	-0.161	0.341	0.689	1.000	0.662	-0.071	0.441	0.581	0.024	0.160	0.446	-0.140	-0.359	0.032	-0.392	-0.168	-0.452	-0.012	-0.440
Ca.Log	-0.596	-0.568	0.626	-0.299	0.191	0.229	0.250	0.249	-0.057	0.608	0.917	0.662	1.000	-0.392	0.854	0.715	-0.160	0.436	0.632	-0.097	-0.462	-0.131	-0.680	-0.290	-0.669	-0.175	-0.635
Mg.Log	0.165	0.323	-0.295	-0.414	0.393	0.596	-0.005	-0.037	0.093	-0.502	-0.350	-0.071	-0.392	1.000	-0.794	0.297	0.213	0.167	-0.246	0.039	0.309	0.548	0.465	0.088	0.827	0.373	0.736
CaMgRatio.Lo	-0.450	-0.484	0.530	0.037	-0.094	-0.174	0.174	0.197	-0.065	0.639	0.769	0.441	0.854	-0.794	1.000	0.291	-0.200	0.173	0.517	-0.046	-0.424	-0.297	-0.674	-0.245	-0.865	-0.314	-0.793
CEC.Log	-0.474	-0.360	0.427	-0.554	0.415	0.607	0.158	0.198	0.022	0.239	0.648	0.581	0.715	0.297	0.291	1.000	-0.084	0.694	0.525	-0.167	-0.346	0.169	-0.422	-0.161	-0.083	0.120	-0.134
OM.LOI.Log	0.384	0.250	-0.320	-0.259	0.429	0.234	0.780	0.760	0.155	0.025	-0.085	0.024	-0.160	0.213	-0.200	-0.084	1.000	-0.529	-0.298	0.445	0.539	0.307	0.697	-0.110	0.308	0.795	0.397
pH.Log	-0.405	-0.296	0.334	-0.133	0.019	0.162	-0.316	-0.185	-0.025	0.030	0.337	0.160	0.436	0.167	0.173	0.694	-0.529	1.000	0.472	-0.327	-0.536	-0.173	-0.642	0.050	-0.062	-0.180	-0.170
B.SP.Log	-0.515	-0.365	0.462	-0.104	0.074	0.074	-0.026	0.054	0.064	0.501	0.650	0.446	0.632	-0.246	0.517	0.525	-0.298	0.472	1.000	0.040	-0.336	-0.176	-0.608	-0.035	-0.471	-0.230	-0.467
Zn.Log	0.130	0.153	-0.126	0.096	0.022	-0.065	0.485	0.418	0.260	0.184	-0.029	-0.140	-0.097	0.039	-0.046	-0.167	0.445	-0.327	0.040	1.000	0.431	0.372	0.361	-0.114	0.109	0.342	0.150
Mn.Log	0.459	0.456	-0.480	-0.063	0.164	0.151	0.222	0.197	0.031	-0.327	-0.433	-0.359	-0.462	0.309	-0.424	-0.346	0.539	-0.536	-0.336	0.431	1.000	0.416	0.784	-0.128	0.529	0.278	0.719
Cu.Log	0.133	0.450	-0.282	-0.477	0.464	0.543	0.237	0.183	0.151	-0.300	-0.155	0.032	-0.131	0.548	-0.297	0.169	0.307	-0.173	-0.176	0.372	0.416	1.000	0.402	-0.061	0.484	0.256	0.430
Fe.Log	0.573	0.507	-0.568	-0.049	0.195	0.132	0.322	0.292	0.033	-0.369	-0.635	-0.392	-0.680	0.465	-0.674	-0.422	0.697	-0.642	-0.608	0.361	0.784	0.402	1.000	0.016	0.697	0.558	0.777
Cr.Log	0.175	0.036	-0.099	0.088	-0.045	-0.081	-0.208	-0.192	0.014	-0.150	-0.316	-0.168	-0.290	0.088	-0.245	-0.161	-0.110	0.050	-0.035	-0.114	-0.128	-0.061	0.016	1.000	0.118	0.101	0.034
Ni.Log	0.362	0.472	-0.468	-0.169	0.217	0.326	-0.027	0.001	0.087	-0.596	-0.630	-0.452	-0.669	0.827	-0.865	-0.083	0.308	-0.062	-0.471	0.109	0.529	0.484	0.697	0.118	1.000	0.401	0.933
SP.Log	0.272	0.169	-0.213	-0.188	0.300	0.185	0.633	0.617	0.171	-0.074	-0.154	-0.012	-0.175	0.373	-0.314	0.120	0.795	-0.180	-0.230	0.342	0.278	0.256	0.558	0.101	0.401	1.000	0.396
Co.Log	0.395	0.413	-0.420	-0.189	0.244	0.346	0.049	0.092	-0.009	-0.559	-0.602	-0.440	-0.635	0.736	-0.793	-0.134	0.397	-0.170	-0.467	0.150	0.719	0.430	0.777	0.034	0.933	0.396	1.000

Table S4. Phylogenetic signal (Blomberg's *K*) in serpentine affinity, soil chemical and textural characteristics, and microhabitat bareness of Streptanthoids, calculated over 5,000 randomly selected post-burnin trees from a phylogenetic analyses in BEAST (1). Phylogenetic signal was calculated with functions in the R packages 'picante' ((8); Blomberg's *K* for continuous variables) and 'caper' ((10); Purvis' *D* for serpentine affinity, a discrete binomial trait). Median values for *D*, *K* and p-values are reported, as they represent the most common pattern; mean values are very similar (0.008 greater on average). Calculations were performed on transformed values and on raw untransformed values, to verify that the overall pattern of strong phylogenetic signal in bareness and soil macrotexture is not dependent on variable transformation. Variables included in our phylogenetic analyses consisted of log-transformed chemical soil elements, soil fine fraction, silt, and soil clay, and are denoted with an asterisk (*).

kind	Variable	*D*	P-value	*D* 95% CI
Serpentine affinity	Serpentine Binomial	-2.193	na	(-3.701, -0.582)

Kind	Variable	*K*	P-value	*K* 95% CI	Variable	*K*	P-value	*K* 95% CI
Bareness	% Bare	1.292	0.010	(1.002 , 1.553)	asinsqrt(% Bare)	1.181	0.010	(0.928 , 1.395)
Soil chemistry	Log(Ca: Mg) *	1.151	0.010	(0.921 , 1.382)	Ca:Mg Ratio	0.597	0.069	(0.467 , 0.736)
	Log(Ca) *	0.960	0.010	(0.764 , 1.161)	Ca	0.743	0.010	(0.599 , 0.887)
	Log(Ni) *	0.955	0.010	(0.773 , 1.123)	Ni	0.653	0.188	(0.521 , 0.785)
	Log(K) *	0.949	0.010	(0.757 , 1.141)	K	0.824	0.010	(0.664 , 0.986)
	Log(Mg) *	0.910	0.010	(0.746 , 1.054)	Mg	0.997	0.010	(0.816 , 1.169)
	Log(Olsen.P) *	0.881	0.010	(0.720 , 1.040)	Olsen.P	0.666	0.020	(0.535 , 0.800)
	Log(Co) *	0.829	0.010	(0.661 , 0.990)	Co	0.540	0.505	(0.412 , 0.678)

	Variable	*K*	P-value	*K* 95% CI	Variable	*K*	P-value	*K* 95% CI
Soil Chemistry	Log(Fe) *	0.748	0.010	(0.591 , 0.913)	Fe	0.765	0.010	(0.608 , 0.915)
	Log(CEC) *	0.677	0.030	(0.547 , 0.793)	CEC	0.688	0.040	(0.562 , 0.806)
	Log(pH) *	0.630	0.030	(0.502 , 0.754)	pH	0.639	0.020	(0.510 , 0.766)
	Log(Na) *	0.694	0.050	(0.563 , 0.825)	Na	0.581	0.277	(0.435 , 0.755)
	Log(B) *	0.650	0.050	(0.520 , 0.774)	B	0.577	0.198	(0.451 , 0.717)
	Log(SP) *	0.571	0.119	(0.453 , 0.697)	SP	0.548	0.238	(0.435 , 0.669)
	Log(Zn) *	0.582	0.139	(0.470 , 0.692)	Zn	0.509	0.396	(0.407 , 0.617)
	Log(NO3.N) *	0.632	0.149	(0.506 , 0.740)	NO3.N	0.678	0.079	(0.541 , 0.792)
	Log(C) *	0.583	0.158	(0.459 , 0.712)	C	0.569	0.366	(0.452 , 0.695)
	Log(Mn) *	0.563	0.218	(0.443 , 0.681)	Mn	0.566	0.366	(0.445 , 0.684)
	Log(OM) *	0.578	0.287	(0.465 , 0.692)	OM	0.492	0.713	(0.395 , 0.592)
	Log(Cr) *	0.570	0.327	(0.440 , 0.714)	Cr	0.473	0.644	(0.348 , 0.599)
	Log(N) *	0.512	0.485	(0.404 , 0.626)	N	0.532	0.485	(0.420 , 0.655)
	Log(Cu) *	0.487	0.564	(0.388 , 0.584)	Cu	0.502	0.485	(0.400 , 0.605)
Soil texture	Log(Frac.Fine) *	1.443	0.010	(1.232 , 1.611)	Frac.Fine	1.556	0.010	(1.341 , 1.737)
	Log(Frac.Coarse)	0.941	0.040	(0.759 , 1.117)	Frac.Coarse*	1.117	0.010	(0.940 , 1.263)
	Log(Clay) *	0.771	0.119	(0.651 , 0.882)	Clay	0.612	0.347	(0.495 , 0.726)
	Log(Silt) *	0.581	0.188	(0.459 , 0.700)	Silt	0.562	0.198	(0.442 , 0.681)
	Log(Sand)	0.539	0.455	(0.415 , 0.671)	Sand*	0.572	0.347	(0.449 , 0.692)

Table S5. Relationship of field measured bareness and soil elemental composition, sorted by direction (sign) and proportion of variance explained (adjusted R Square) in 57 populations (34 species) of streptanthoids. In bold are elements that remain significant after a Bonferroni correction to adjust for multiple tests.

Variable	Estimate	pValue	adjR^2
Coarse Fraction	**0.0092**	**2.74E-06**	**0.3899**
log(Fe)	**0.1458**	**3.90E-05**	**0.3126**
log(Mn)	**0.1195**	**0.0015**	**0.1922**
log(Co)	0.0865	0.0072	0.1367
log(OM)	0.1564	0.0093	0.1273
log(Ni)	0.0344	0.0145	0.1110
log(SP)	0.2898	0.0712	0.0522
log(Cr)	0.1686	0.2509	0.0080
Sand	0.0029	0.2660	0.0061
log(Mg)	0.0321	0.2784	0.0046
log(NO3.N)	0.0327	0.3419	-0.0017
log(Cu)	0.0372	0.3825	-0.0051
log(Zn)	0.0322	0.3954	-0.0060
log(C)	0.0297	0.5961	-0.0165
log(N)	0.0191	0.7807	-0.0214
log(Silt)	-0.0393	0.5617	-0.0152
log(Clay)	-0.0788	0.2636	0.0064
log(Olsen.P)	-0.0803	0.0448	0.0692
pH	-0.1357	0.0040	0.1575
log(Ca:Mg Ratio)	**-0.0504**	**0.0019**	**0.1844**
log(CEC)	**-0.1459**	**0.0010**	**0.2063**
log(Na)	**-0.1609**	**0.0007**	**0.2186**
log(B)	**-0.1534**	**0.0003**	**0.2478**
log(K)	**-0.1445**	**2.12E-05**	**0.3311**
log(Ca)	**-0.1055**	**1.54E-05**	**0.3406**
log(Fine Fraction)	**-0.4989**	**5.94E-08**	**0.4872**

Table S6. Phylogenetic independent contrasts (PICs) in nodes with and without inferred soil shifts in the Streptanthoid Complex (clades SC-I, GC, CC), over 1,150 post-burnin trees sampled at random from a 50 million generation BEAST analyses (1). Variables are ordered by significance in PICs difference within category (bareness, chemistry, texture).

Element	mean NO shift	mean Shift	median P-value
% Bare	277.20	168.20	0.1123
Log(CaMgRatio)	31.47	71.29	0.0631
Log(Cobalt)	23.27	43.89	0.1278
Log(Nickel)	53.79	90.71	0.1789
Log(Calcium)	22.92	36.64	0.1878
Log(OlsenP)	15.89	28.33	0.1962
Log(Magnesium)	20.32	37.28	0.2048
Log(Potassium)	15.89	26.50	0.2058
Log(Nitrates)	23.99	39.54	0.2531
Log(Chromium)	5.22	2.07	0.2588
Log(Sodium)	17.82	12.67	0.2989
Log(OrgMatter)	12.48	8.97	0.3232
Log(pH)	1.88	2.60	0.3936
Log(SP)	4.26	3.93	0.4224
Log(Copper)	18.72	18.05	0.4664
Log(Nitrogen)	9.84	11.94	0.4755
Log(Boron)	18.60	14.04	0.5257
Log(Carbon)	11.28	12.05	0.5279
Log(Iron)	17.67	17.86	0.5306
Log(CEC)	15.92	16.58	0.5566
Log(Manganese)	19.85	20.51	0.5609
Log(Zinc)	15.80	18.72	0.5705
CoarseFrac	253.00	278.00	0.4382
Log(Clay)	10.55	14.04	0.4814
Log(FineFrac)	4.59	4.94	0.5043
Log(Silt)	9.51	8.55	0.5519
Sand	269.50	250.10	0.6031

Table S7. Competitive ability measured in a common garden lathhouse experiment and estimated using log Response Ratio (lnRR) to summarize the interactions between a focal Streptanthoid plant and a grass neighbor, is negatively related to field-measured microhabitat bareness. Species-level analyses include seven species (collapsing the Glandulosus Complex), and are based on bareness and lnRR species averages. Three species (*S.glandulosus, S.tortuosus, C.amplexicaulis*) have populations on and off serpentine, which differ in bareness (see Results) and were kept serparate for analyses (thus, n=10). Population-level analyses include only populations for which bare estimates are also available (n=14). Bareness values were asinsqrt transformed. Linear models (LM) were run in JMP Pro v. 10 and R (v.3.03). PGLS models, were run using the function 'pgls' in the R package 'caper' (10).

Unit of analysis	**N**	**Bareness Estimate**	**p-value**	**adj.Rsq**
Species; SG collapsed; LM	10	-1.334	0.039	0.357
Species; SG collapsed; PGLS	10	-1.093	0.087	0.236
Population; LM	14	-1.324	0.004	0.465
Population; PGLS	14	-0.931	0.016	0.341

METHODS IN FULL

1. Characterization of serpentine soils and environments

Soil Chemical Characterization – We analyzed a total of 294 soil samples from 116 populations representing 45 species of *Streptanthus* and close allies (sensu (1); Table S1). Whenever possible, we took 1-3 soil samples per population and sampled replicate populations for each species. Each soil sample was collected from the rhizosphere (first 30 cm of soil) immediately below 1-3 focal plants selected at random within any given population, dried, and stored. To assess soil rockiness we separated each soil sample into three fractions (fine fraction, <1.7 mm; medium fraction, 1.7–4 mm, and; coarse fraction, > 4mm) using standard soil sieves. A portion of the finest fraction was sent for elemental analysis to at the UC Davis Analytical Lab (Davis, CA; http://anlab.ucdavis.edu/) for chemical and textural analyses of the following: total N and C (combustion method); P (Olsen Method); exchangeable K, Na, Ca, Mg (in meq/100g using inductively coupled plasma atomic emission spectrometry, and by DTPA method– both are tightly correlated; we focus on meq/100g); estimated cation exchange capacity (CEC, as the sum of the four exchangeable ions); organic matter (loss on ignition method); pH (saturated paste); Boron (saturated paste); micronutrients (Zn, Cu, Mn, and Fe) and heavy metals (Cr, Co, Ni) using the DTPA (diethylenetriaminepentaacetic acid) extraction method and by nitric acid/hydrogen peroxide closed vessel microwave digestion; saturation percentage (saturated paste); and, particle size analyses (sand, silt and clay, in an aqueous solution using a hydrometer). Details on extraction methods, see http://anlab.ucdavis.edu.

Data on most chemical and textural characteristics of soils were log-transformed to meet assumptions of normality. Conformation to normality was checked using Shapiro's test, and unequal variances were tested using Levene's test in R v. 3.1 (R Core Team, 2014). To compare serpentine and nonserpentine soils we used Welch's t-tests (to account for unequal variances) and generalized linear mixed models (R Core Team, 2014; JMP Pro v.10). We classified soils sampled as serpentine or non-serpentine based on literature, herbarium records, and field observations of the floristic composition of the area. We confirmed our classifications with discriminant function analyses of our soil chemical profiles showing over 99% accuracy in categorizing soils samples.

An important aspect of our soil comparisons is that we do not compare serpentine soils with adjacent nonserpentine soils, which are often highly invaded grasslands, as has been typically done in many ecological studies of serpentine adaptation (2). To understand the evolution of serpentine adaptation in this clade, performance in adjacent grassland soils is not a meaningful comparison, as rarely members of this clade grow in grasslands, but rather grow on rocky or sandy substrates, some of which are serpentine. Instead, to identify exaptations to serpentine in this group, we compare soil composition and habitat attributes only among soils occupied by members of this clade, a unique aspect of this study.

Clade-wide field ecological data collections: Microhabitat Bareness– In a previous study we showed that microhabitat bareness was associated with higher rates of attack by insect herbivores through both descriptive and manipulative experiments (3). Bare environments, by definition, also represent different competitive regimes for plants inhabiting them. In 2011 and 2013 we characterized the microhabitat bareness, at the time of flowering, for 71 populations of streptanthoids representing 37 species (Table S1), by placing 25cm x 25cm quadrats centered on plants naturally occurring in the field and quantifying the percentage of habitat in the quadrat

that was devoid of vegetation cover (including bare soil as well unavailable habitat, such as area occupied by a large rock). Hereafter, we refer to this metric as 'bareness' when describing microhabitats. We repeated these measurements for 5-15 plants per population, depending on population density. Because plants are highly patchily distributed in the landscape, we used a combination of targeted and random sampling to identify focal plants. We first identified areas where plants occurred, then selected a subset of these areas at random, and then randomly selected focal plants within selected patches. When possible, we measured replicate populations at different sites per species. We investigated the potential effect of year in our estimates using sites that were measured in both years. We find that bareness means were not statistically different between years (2011 mean: 79.5; 2013 mean: 75.2; t = 0.587, df = 25.28, p-value = 0.562), and this does not change with transformation (asinsqrt(% Bare: 2011 mean: 1.18; 2013 mean: 1.07; t = 1.089, df = 23.31, p-value = 0.287). We also find that for sites that were measured in both years (n=15), bareness was variable, but correlated between years (r=0.56), even with this limited sample size (r=0.56; Linear Model: adj. R^2: 0.1596, F-statistic: 3.658 on 1 and 13 DF, p-value: 0.08); and removal of one outlier strengthens this relationship considerably (r = 0.6; Linear Model: adj. R^2: 0.3077, F-statistic: 6.778 on 1 and 12 DF, p-value: 0.023),), justifying our use of bareness data collected across years.

We compared the neighborhoods of plants growing in serpentine and in nonserpentine habitats with a Welch's t-test in R v.3.1 (R Core Team, 2014) and JMP Pro v.10, as above. Results with linear models adding species as a random effect yield similar results (not presented). Using the populations for which we had both bareness and soils data (57 populations; Table S1), we analyzed the relationship between bareness and soil elements using univariate linear models in R, and applying a Bonferroni correction to correct for multiple comparisons.

2. Are soil chemical and textural characteristics and microhabitat *bareness* phylogenetically conserved?

We combine metrics of contemporary environments and soils as described above with phylogenetic comparative methods to make inferences about past growing regimes. If there is phylogenetic signal in metrics characterizing contemporary habitats, then present environments might allow us to make inferences about past ones. The approach of using present-day data to infer historical ecological attributes of species has been used to understand biogeographic evolution of many groups, including primroses, dendrobatid frogs, honeysuckles, carnivorous plants, and others (4), as well as to test the adaptive significance of traits (5, 6). While there may be pitfalls in extrapolating from current conditions to past ones, the most parsimonious explanation for patterns with strong phylogenetic signal is that ecological data on current environments carry some consistent aspects of past ones.

To test for phylogenetic conservatism in soil chemistry (e.g., Ca, Mg, Ni, K), texture (e.g., size fraction, particle size), or microhabitat bareness, we used Blomberg's K (7), a standard measure of phylogenetic signal for continuous characters, using the function 'phylosignal' from the package 'picante' v.1.6 (8) in the R statistical framework (R Core Team, 2014). Blomberg's K takes a value of zero when there is a lack of correspondence between a trait's evolution and the phylogeny (no phylogenetic signal); values of K=1 indicate that a given trait evolves under a Brownian motion process along the phylogeny, and; values of K>1 indicate an association between phylogeny and the evolution of a trait stronger than expected under Brownian motion

(strong phylogenetic signal). To integrate over uncertainty in the phylogenetic inference, we repeated our calculations over 5,000 trees of the posterior distribution of a 50 million generation phylogenetic analyses (1) (see also below). For serpentine affinity, a binary trait, we used Purvis' *D* (9), as implemented in the R package 'caper' v.05.2 (10).

Species in the Streptanthoid complex exhibit wide variation in affinity to serpentine, from strict endemism (common) to complete intolerance (rare), with some species having populations growing on and off serpentine (bodenvag species). To account for such within-species variation with respect to serpentine affinity as well as for phylogenetic uncertainty, we generated one dataset for each of 5,000 trees sampled at random from the posterior (selecting one tip per species at random every iteration), and assigned binary serpentine affinity by sampling from a binomial distribution with probability of serpentine affiliation equal to the proportion of records found on serpentine our of the total herbarium records for that species (species records were downloaded from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). Thus, for each of the 5,000 runs, serpentine affinity was resampled for each species based on the proportion of collections found on serpentine. We overlaid collection records onto a GIS layer of serpentine soil using functions in the R package DISMO v. 0.8-17 (11). We also validated our soil affinity assignments with literature, field observations, and expert opinion. We performed all our evolutionary analyses using species averages. Also, due to lack of monophyly in the *Streptanthus glandulosus* complex (1), we collapsed this well supported clade to a single lineage sampling tips at random in each iterations. The species and populations analyzed for each dataset are detailed in Table S1.

3. Are transitions to serpentine accompanied by large shifts in soil chemistry, soil structure or microhabitat bareness?

To explore whether chemical, textural, or microhabitat aspects of serpentine soils occur concomitantly or in a decoupled fashion from transitions in soil use, we used a combination of ancestral state reconstruction and phylogenetic independent contrasts (12) in the context of our detailed soil and environment characterizations.

If serpentine soils used by Streptanthoids differ from nonserpentine soils with respect to chemical, textural, and microhabitat characteristics, we expect that transitions to serpentine soils will be accompanied by adaptations to the attributes that capture the differences between serpentine and non-serpentine substrates, and that we would see large changes in inferred ancestral values of these elements occurring concomitantly with shifts to serpentine. An alternative scenario is that adaptation to tolerate some or all of these elements could precede shifts to serpentine use and serve as potential exaptations to serpentine shifts.

Given that serpentine and nonserpentine environments differ significantly in many soil elements and bareness (see results above), we expect large changes in these attributes occurring at some point in the evolutionary history of Streptanthoids. The question is when these adaptations took place with respect to serpentine transitions. Changes preceding shifts in soil use we interpret as possible exaptations to serpentine shifts.

Using ancestral state reconstruction, we first reconstructed soil use and identified shifts to serpentine and the nodes associated with them. We then calculated phylogenetic independent contrasts (PICs) for the attributes of interest (e.g., Ca:Mg, Ni, %bare) across the Streptanthoid

phylogeny. Because the PICs at a certain node are essentially a weighted average of its descendant nodes' values (taking branch length into account), it is the PICs at the nodes ancestral to the branch/node with reconstructed shifts (i.e., the parent nodes of the inferred soil shifts) that will reflect the magnitude of change associated with soil transitions. Thus, for our analyses, we selected the nodes ancestral to the reconstructed shifts ('SHIFT' nodes), and compared the absolute value of their PICs to the rest of the nodes ('NO-SHIFT' nodes), which do not reflect changes in a given attribute associated with inferred soil shifts. The absolute values of the PICs reflect the magnitude of change but not its direction. A large value in the contrast can thus be interpreted as a large increase or decrease in the value of that character at that node. Similar PIC values in both types of nodes would reflect a lack of association between a trait and a soil shift. Because we also know how the two soil types differ with respect to each of the elements evaluated in PICs (sections 1 and 2), it is possible to make inferences with respect to the direction of the changes observed.

We computed ancestral states with the function 'ace' in the package 'ape' v.3.1-1 (13) which implements a maximum likelihood estimation of ancestral states for binary traits (14), using an equal rates model. We accounted for phylogenetic uncertainty and within-species variation with respect to serpentine affinity by analyzing 5,000 trees sampled at random from the post-burning distribution (1), sampling at random one tip per species per iteration (see above for accounting for variation in serpentine affinity). The PICs were computed with the function 'pic' in the package 'ape' v.3.0-11 (13) in the R framework, which uses the formula: $C_{ij} = (x_i - x_j)/\sqrt{d_{ij}}$, where x_i and x_j are trait values of species i and j, and d_{ij} is the phylogenetic distance between both species. The selection of the parent nodes at which shifts occurred was done with custom scripts in R available upon request.

4. Does bareness predict competitive ability?

Overview. We assessed competitive ability experimentally, growing individuals from field-collected seed from 19 populations representing 9 species spanning the phylogeny and spectrum of serpentine specialization (Table S1). Soils were field-collected from serpentine and nonserpentine sites, and plants were grown with and without a grass neighbor, *Bromus laevipes*. *B.laevipes* is native in California, and naturally occurs at sites with several species of *Streptanthus* s.l., in both serpentine and nonserpentine soils (Jepson Interchange; http://ucjeps.berkeley.edu/interchange/index.html). Plants were grown in ambient outdoor conditions (lath house). For species that frequently occur both on and off serpentine ('bodenvag' species), we used separate serpentine and nonserpentine populations.

Experimental conditions. Soils were collected in late summer/early fall, just prior to the rains in each year, directly under multiple *Streptanthus* plants per site, and kept dry until used. Previous work and our own work in this group have shown that nonserpentine species show very limited survival in serpentine soils (15), so 'nonserpentine' species were only grown in nonserpentine soils, while serpentine tolerant species/populations were assayed on both soil types, and their competitive abilities averaged across conditions, as we are interested in capturing the overall competitive ability of a species (or population) given its origin (serpentine/nonserpentine) across a range of conditions. We used unsieved raw soils to preserve their natural 'rockiness', using a soil mixer to minimize variation in rock content within treatments.

We germinated both our focal streptanthoids and grass seeds in the winter months of November/December in plug-trays with potting soil and allowed them to establish before transplanting them together into 500 mL cone-tainers (Stuewe and Sons, Tangent, Oregon; https://www.stuewe.com/) filled with field soils. Across the experiment, we had an average of 12 replicates per treatment combination (soil x competition), though for one population of *S. diversifolius,* n=3, and one population of *S.tortuosus,* n = 39. We transplanted all plants at a young seedling stage (2-3 true leaves for Streptanthoid seedlings, and ~5 leaves for *B. laevipes*), and grew plants in an outdoors, unheated/unlit lathhouse. During the winter months, when natural rains occur in California, we watered heavily once a day. Once the rains stopped, we misted our experiments twice a day (only once on cooler days). We allowed the plants to grow until the onset of their first flower, when we collected both the focal plant and its grass neighbor for dry biomass analyses.

***Assessing the nature and strength of the interaction with* B. laevipes –** We assessed the intensity and direction of the interaction between *Streptanthus* and *B. laevipes* by comparing the biomass of each of our *Streptanthus* plants grown with a *B. laevipes* neighbor to the average biomass of plants from the same population grown in the same soil but without a neighbor, using the log response ratio (16, 17) of the biomass of plants grown with (B_W) and without (B_{WO}) neighbors, as $lnRR = ln(B_W / B_{WO})$. Positive values of lnRR will reflect facilitation, negative ones, competition, and its magnitude reflects the intensity of the interaction. For the bodenvag species, which have populations on and off serpentine, we kept serpentine and nonserpentine populations as separate data points in the analysis, as soil and bareness qualities are very different across these sites, and populations may be locally adapted to soils (e.g., (2)).

Assessing the relationship between competitive ability and bareness – We explored the relationship between competitive ability measured in the greenhouse experiment (lnRR) and bareness of microhabitat measured in the field using linear models (JMP Pro v.10) and phylogenetic generalized least squares (PGLS; (18)) to account for non-independence of points due to relatedness. PGLS analyses were done using the 'pgls' function in the R package 'Caper' (10) based on the maximum credibility tree in (1), with lambda set to 1 (thus assuming that variation between tips accumulates in proportion to branchlength). To conform to expectations of normality, bareness values were arcsine square root transformed.

We analyzed the relationship between lnRR and bareness using species-level averages from lnRR estimates of 19 populations, which represent 7 species (considering, as above, the *S. glandulosus* complex as a single lineage– 'SG collapsed analyses'). For three of these species (*S. glandulosus, S. tortuosus, C. amplexicaulis*), we have lnRR and bareness estimates from both, serpentine and nonserpentine populations. Thus, our species-level analyses consisted of 10 points. To investigate if the pattern observed could result from more recent or local processes (e.g., local adaptation), we performed an analysis by population ('population-level analyses'), including only those 14 populations for which we have both bareness and competitive ability estimates (as well as relatedness, as these populations were all represented as specific tips in the original phylogenetic analysis–see FigS1 of ref. 1).

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