Multiple origins of serpentine-soil endemism explained by preexisting tolerance of open habitats

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Plant specialization on soils derived from unusual parent materials is an important contributor to regional biodiversity. These stressful substrates include serpentine, gabbro, and other ultramafic rocks rich in heavy metals. The effect of substrate on plant diversity is illustrated by serpentine soils in California: they comprise less than 1% of the surface of the state (1), but serpentine endemics (species restricted to serpentine soils) make up about 10% of the flora (2). How such "edaphic endemics" (plants restricted to stressful soils) evolve is a long-standing question that remains largely unresolved. For example, plant tolerance of serpentine soils may often involve tradeoffs in competitive ability, and restriction to serpentine soil may reflect poor competitive ability on less stressful soils rather than obligate association (3–5), although possible counter-examples exist (6). A common feature of plant communities on stressful soils is the wide spacing of plants and openness of the habitat. Openness may itself be stressful for a variety of reasons (detailed below) (7–9). In PNAS, Cacho and Strauss (10) use a novel comparative experimental approach to explicitly assess the role of openness vs. soil chemistry as factors in the evolution of plant tolerance of, and endemism to, serpentine soils.

Plants that tolerate and are endemic to stressful ultramafic soils have become a well-developed system for the study of adaptation, speciation, endemism, competition, and community ecology (2, 6, 11). Classic studies have shown the probable role of elemental imbalances (e.g., high concentrations of heavy metals, including Ni, Co, Cu, Cr, Pb; low Ca:Mg ratios; and low concentrations of macronutrients), although there is no consensus on the main causes of stress and species exclusion (2, 6). There may indeed be a diversity of causal factors, as might be expected from the diversity of plant lineages in which serpentine tolerance and endemism have evolved, each with different genetic and physiological starting points. Regardless of the physiological causes, there are well-defined serpentine floras and vegetation types recognized in North America, including Cuba; Europe, including Britain; South Africa; and Oceania, among other regions. The floras are characterized by very high endemism, and the vegetation is usually sparser and often more xeromorphic (appearing drought adapted) than nearby vegetation on "normal" soils (Figs. 1 A and B).

The openness of the habitat may itself be a source of stress contributing to endemism. Several authors have found that the balance between competition (for light, water, and/or nutrients) and facilitation between neighboring plants in a landscape depends on the level of stress: in a benign landscape competition dominates, but in a stressful environment, facilitation dominates (8, 9). As the habitat gets more open, especially in hot, dry climates (e.g., summer in regions with Mediterranean climates), the paucity of neighbors means greater exposure to the drying effects of wind and high direct-radiation loads, as well as the stress of high leaf temperatures and potential UV damage. Recent research has also shown that plants in sparsely vegetated sites are also more apparent to herbivores (e.g., more susceptible to attack by herbivorous insects), and such plants may have had to evolve expensive counter adaptations (e.g., increased chemical defenses and/or more cryptic foliage) (7).

A series of studies from a remote corner of northeast Alaska illustrates a possible biological connection between edaphic endemism and open habitats. Studies in the region have noted the narrow distribution of possible relict plant species, disjunct from nearest relatives by hundreds of kilometers (12–14). Some of these endemics appeared, at first, to

be restricted to greenstone (an ultramafic mineral) outcrops (12). Later observations (13, 14) and experiments (14) showed that all putative greenstone endemics were found also on a variety of other parent materials. The taxa are indeed rare and disjunct but endemic to south-facing slopes so steep and dry that they are largely open habitats with sparse vegetation. Thus, plants adapted to the stress of dry, open habitats can have similar ecological behavior as edaphic endemics. This could lead one to ask if adaptation to open habitats might sometimes be the first step toward tolerance of ultramafic soils.

Cacho and Strauss (10) address this and related questions by looking at the evolution of tolerance to open habitats and to various elements associated with serpentine soils in relation to soil shifts across the phylogeny of a group of wild mustards (*Streptanthus* and relatives; "streptanthoid mustards") in which serpentine endemism has evolved four to five times (15). They use a powerful, but rarely realized, approach in evolutionary ecological research: that of integrating comprehensive sets of measurements and/or experiments into a molecular phylogeny (16) to gain insights into the evolutionary history of soil specialization.

Intriguingly, Cacho and Strauss (10) find evidence that tolerance to open habitats appears to have evolved before tolerance of serpentine soils (Fig. 1C) and hence was a preaptation (preadaptation). Cecchi et al. (17) also concluded recently that preaptations (e.g., for drought tolerance) have been critical in the origins of serpentine tolerance, but had no direct evidence to support their hypothesis. Cacho and Strauss (10) also provide evidence that tolerance of stressful soil elements evolved in streptanthoid mustards coincident with, or after, switches to serpentine soils, rather than before switches to serpentine, as expected. In addition, in a novel, common
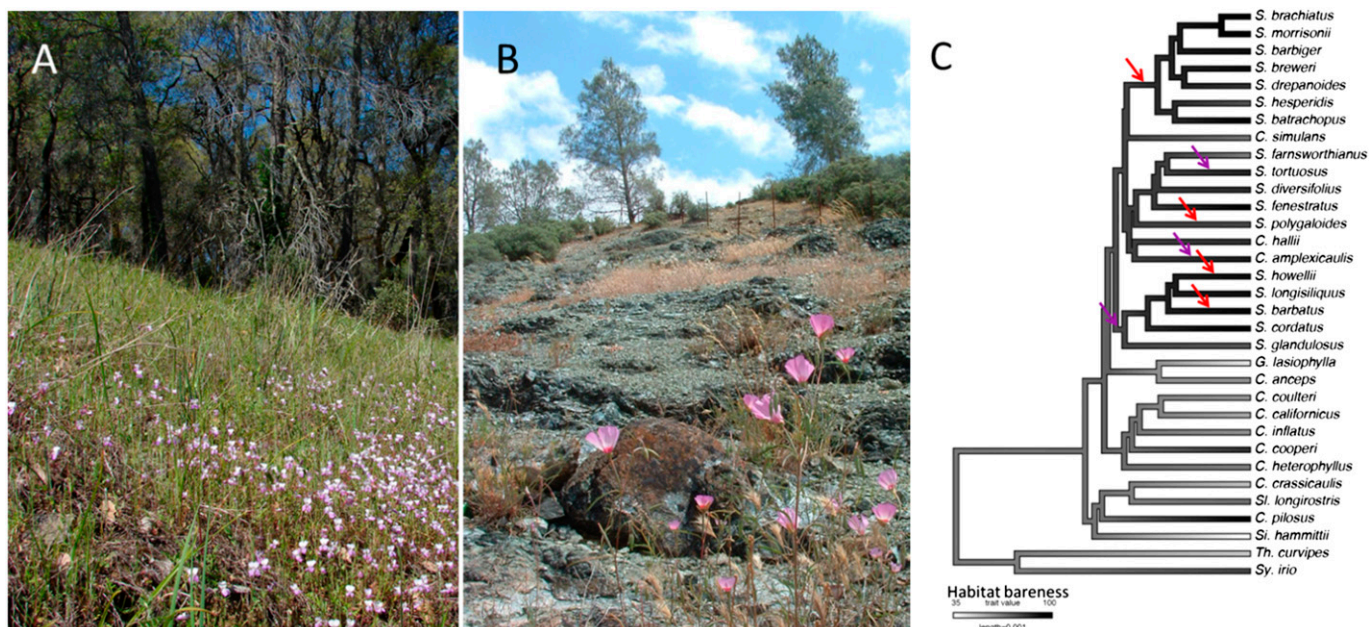
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Fig. 1. Evolution of serpentine-soil endemism from occupation of normal soils is apparently contingent on prior adaptations to occurring in open habitats. (*A*) Dense vegetation characteristic of normal soils in Napa County, CA. Pink flowers are *Collinsia sparsiflora* Fisch. and C.A. Mey, a species with normal and serpentine ecotypes. (*B*) Open, sparse vegetation on a serpentine outcrop in nearby Lake County, CA. Pink flowers in foreground are *Clarkia gracilis* subsp. *tracyi* (Jeps.) Abdel-Hameed and R. Snow, a subspecies largely restricted to serpentine soils. (*C*) Maximum-credibility tree of the streptanthoid mustards, showing inferred evolution of open-habitat adaptations (maximum-likelihood ancestor-state reconstruction; shading on branches, with darker indicating occurrence in more open habitats; reprinted with permission from ref. 10. Arrows indicate inferred origins of serpentine endemism (>87% of records from serpentine soils; red) and serpentine tolerance (>11%, <87% of records from serpentine soils; violet), evolving from occupation of normal soils (branches to left of the violet or red arrows; data from ref. 10). Soil-type optimization on branches used ordered parsimony, where serpentine tolerance is assumed to be a precursor of serpentine endemism. (To simplify the diagram, inferred coincident origins of tolerance and endemism are not shown.)

environment competition experiment, the authors show that plants from more open habitats have lower competitive abilities. Importantly, this relationship is similar whether the plants are from bare habitats in serpentine-soil landscapes or from bare habitats in normal soil landscapes.

The multiple origins of serpentine tolerance in the streptanthoid mustards raise a long-standing question in evolutionary biology: how do new ecological adaptations originate and why do parallelisms occur? The answer in both cases may be that critical preexisting features that enable an ecological shift are already in place. A recent study by Christin et al. (18) found evidence for multiple parallel origins of C4 photosynthesis in grasses and that these shifts were contingent on appropriate preexisting leaf anatomy (exaptation). The parallels to the present study (10) are striking. Thus, there seems to be growing support for the idea that major adaptive transitions in evolution often, or even usually, occur through the prior establishment by chance of one or more preaptations (19–21). Once these preaptations are in place, it becomes much more likely that multiple independent parallel shifts (parallelisms) will occur, hence explaining the commonness of parallel evolution as is often observed in adaptive traits (15, 18, 21). Additional detailed phylogenetic comparative studies, such as this one (10), may show evolution by exaptation (preaptations acquiring new functions) to be the dominant theme wherever parallel evolution is observed in groups of related species.

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