Community assembly on Californian serpentine soils

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Patches of serpentine soil occur across California, where they are embedded in a matrix of non-serpentine sedimentary-derived soils. In plant ecology, "serpentine" generally refers to soils that are derived from ultramafic rocks and are rich in iron magnesium silicates (Rajakaruna *et al.* 2009). Serpentine soils tend to be poor in essential nutrients like N, P, and K, and have high concentrations of metals like Ni and Co. They are also characterized by low Ca:Mg ratios and low water retention capacity, which impose severe selection pressures (Brady *et al.* 2005; Alexander *et al.* 2007). Plant species that are endemic to these challenging soils comprise up to 10% of the diverse California Floristic Province flora (Kruckeberg 1984). This diversity has inspired many generations of scientists and a considerable body of literature, which can be organized according to the community ecology framework of Vellend (2010).

Selection

The first organizing principle of Vellend (2010) is that of ecological selection, which refers to a deterministic fitness difference between populations of different species. Levine & HilleRisLambers (2009) experimentally showed that there are substantial fitness differences between ten serpentine-adapted annual plant species. Specifically, they showed that the system would be dominated by *Salvia columbariae* within 16 generations if there were no stabilizing niche differences between that reduced the per capita growth rates of large populations. The authors also point out that their study was conducted off of the rocky serpentine patches where a number of their species are dominant, and that species-specific responses to spatial and temporal environmental variation is likely to promote coexistence in this community. This study demonstrates that there are important ecological differences

between serpentine species that can drive their long-term population dynamics.

Ecological selection is also invoked to explain the restricted distribution of serpentine-adapted species. Kruckeberg (1951) showed that both non-serpentine and serpentine-adapted ecotypes of *Gilia capitata* and *Achillea borealis* perform better on non-serpentine soil than on serpentine soil. From this, Kruckeberg concluded that the distribution of serpentine specialists is limited not because serpentine soil provides some special resources, but because serpentine specialists have trade offs that reduced competitive ability in favor of tolerance of harsh conditions. In other words, serpentine specialists have lower ecological fitness on non-serpentine soils than other species and are thus outcompeted in those communities (Kruckeberg 1951; Anacker 2014). Since Kruckeberg's early greenhouse experiments, studies of population dynamics in the field have found general but not ubiquitous support for this hypothesis (Anacker 2014). Moore & Elmendorf (2011) argue that the importance of competition may vary within individual serpentine patches, which can be quite variable in their environments, and call for more subtle experiments to test the role of competition and fitness differences in limiting the distribution of serpentine endemics.

A number of hypotheses seek to explain the physiological basis of the fitness differences driving serpentine population dynamics. Plants adapted to serpentine soils need a mechanism to counteract the suppressive impacts of low soil Ca:Mg ratio (Loew & May 1901; Vlamis & Jenny 1948; Rajakaruna *et al.* 2009; Turner *et al.* 2010). The *selectivity hypothesis* of Kazakou *et al.* (2008) suggests that serpentine plants preferentially absorb calcium ions over the more abundant magnesium ions despite both having a 2^+ ionic charge. O'Dell *et al.* (2006) showed that serpentine plants maintain a higher Ca:Mg ratio in aboveground tissue than non-serpentine plants and the soil in which they were grown, but found that Ca:Mg ratios of root tissue of serpentine and non-serpentine plants tended to be equal to that of the soil. They concluded that serpentine plants selectively translocate Ca^{2+} ions from root to aboveground tissue. This mechanism would give serpentine plants a fitness advantage over non-serpentine plants on serpentine soil, since the former

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can maintain appropriate stoichiometric balances in photosynthetic tissue. The *elemental defense hypothesis* proposes a second mechanism by which serpentine plants gain a fitness advantage. This hypothesis posits that serpentine plants can accumulate large concentrations of the metals abundant in serpentine soils and use those to suppress pathogens (Horger *et al.* 2013). This may give serpentine-adapted plants a strong fitness advantage over poorly-defended non-serpentine plants. Superior herbivory defense may be especially important in serpentine communities, where the reduced stem density increases the apparency of each individual to herbivores (Strauss & Cacho 2013).

Drift

In Vellend (2010)'s framework, drift refers to any random changes in species relative abundance within a community. The importance of drift changes across scales of community assembly processes. At a local scale, drift may play an outsized role as population sizes of all species are generally suppressed. Serpentine patches tend to be small and isolated by large distances relative to dispersal ranges (Harrison *et al.* 2006), so that extirpation risk due to chance events grows for more isolated and smaller hummocks. As invasion of the Californian landscape by European grasses reduces hummock size and increases isolation by encroaching on hummock boundaries, the risk of extinction for native serpentine adapted plants is predicted to increase (Gilbert & Levine 2013). Drift may also play an important role in structuring serpentine communities because the many physiological tradeoffs that the plants need to make can lead to small fitness differences between many of the species. For example, in the 2008 growing season data from Levine & HilleRisLambers (2009), three species (*Plantago*, *Lasthenia*, and *Chaenactis*) all had a low density population growth rate of approx. $r \tilde{} 0.75$. Five other species clustered around $r \tilde{} 0.1$. Therefore, ecological drift may dominate interactions between species within these clusters, while selection can dominate interactions of species in separate clusters.

The role of drift may be diminished when we consider serpentine community assembly from the entire regional species pool. This is because the abiotic stresses of serpentine patches impose a strong environmental filter that likely selects for a narrow subset of species from the regional pool (Weiher *et al.* 2011). In assessing the relative role of neutral processes in structuring multi-trophic pond communities, Chase (2007) showed that communities assembling in ten experimental permanent ponds varied widely, whereas those assembled in droughted mesocosms tended to vary little from one another. This was taken as evidence that the role of neutral processes diminishes in harsh environments. Therefore, the role of neutral ecological processes in shaping serpentine communities may be limited when community assembly is considered at a regional scale.

Speciation

Ecological divergence between ecotypes of a species growing in vastly different environments can result in reproductive isolation to yield distinct species (Schluter 2001). In theory, pleiotropic effects of loci under selection for ecological function can initiate reproductive divergence. After some genetic and functional differentiation develops, reinforcement can maintain reproductive isolation by selection against hybrids (Dieckmann & Doebeli 1999). Such selection against hybrids is especially likely in serpentine systems, as the hybrids are likely poor competitors in the environments available to them (Dobzhansky 1951; Kay *et al.* 2011).

There is ample evidence that such evolutionary processes play out in serpentine plant communities. For example, Wright *et al.* (2006) conducted a reciprocal transplant experiment of serpentine and non-serpentine ecotypes of *Collinsia sparsiflora* and found that plants growing in serpentine had their peak flowering ~2 weeks earlier than those growing in non-serpentine soil. The provenance of seed did not have a significant impact on flowering time; the responses were primarily driven by destination soil. Divergence can occur

even when without significant differences in flowering phenology. For example, Gardner & Macnair (2000) show that the differentially-sized flowers of the serpentine endemic *Mimulus nudatus* and its progenitor *M. guttatus* tend to be pollinated by different bee species that tend to transfer pollen intraspecifically. The authors posit that this pre-zygotic isolation, along with selection against any hybrids that do develop, has driven speciation in this sympatric system. Mismatched flowering phenology has also been documented between serpentine and non-serpentine populations of the serpentine sunflower *Helianthus exilis* (Sambatti & Rice 2007). Even though these phenological mismatches likely represent plastic responses of plants to the environmental conditions on serpentine soil, such differences can contribute to continued reproductive isolation and divergence (Levin 2009). Finally, population genetics on *Arabidopsis lyrata*, which has serpentine-adapted populations in Europe, revealed high F_{ST}, especially in loci associated with ion transporters, further suggesting that serpentine populations can diverge even in the face of gene flow (Turner *et al.* 2010).

A well described case of putative serpentine-driven speciation has been documented in the *Lasthenia californica* complex. Populations of the "A" Race of *L. californica* grow on serpentine patches that have exceptionally high ionic stress due to elevated concentrations of Na and Mg, whereas those of the "C" Race occur on ionically less stressful but drier serpentine patches (Rajakaruna & Bohm 1999). Rajakaruna & Whitton (2004) showed that the races tend to have mismatched flowering phenologies and that pollination success and seed set was substantially lower in crosses between the A and C race than within each race, suggesting a strong prezygotic barrier. Phylogenetic analyses suggest that there is repeated parallel divergence between the A and C races at multiple sites, so that there may be multiple phylogenetically distinct lineages evolving across the *L. californica* range (Rajakaruna *et al.* 2003). Although limited in number, these examples suggest that speciation driven by edaphic specialization may be a common phenomenon in serpentine communities (Brady *et al.* 2005).

Differential selection on serpentine vs. non-serpentine populations is not the only mechanism by which serpentine soils can influence speciation. The fragmented and island-like distribution of serpentine patches can result in genetic and ecological divergence between populations of paleoendemics restricted to distinct serpentine patches (Kay *et al.* 2011). For example, there is substantial genetic differentiation among geographically isolated populations in the *Streptanthus glandulosus* complex (Mayer *et al.* 1994). Geographically distant populations also show substantial levels of postzygotic barriers, suggesting that there may be multiple phylogenetic species within this clade. Populations invading isolated serpentine patches from a single non-serpentine population will, given low gene flow, follow distinct evolutionary lineages, and give rise to new species (Kruckeberg 1986).

Dispersal

See Mishler 2014 in Nature communications- interesting refs about neoendemics' distribution being limited due to limited distribution away from hummocks.

As a first approximation, it is convenient to model serpentine patches in a matrix of non-serpentine soil as isolated islands and study community dynamics under the Macarthur/Wilson island biogoegraphy framework (Macarthur & Wilson 1967; but see Harrison *et al.* 2006 for discussion regarding problems in modeling serpentine patches as islands). Diversity dynamics in island biogeography are driven only by migration from mainland and extinction on islands, and predict that species diversity increases with island size and proximity to mainland. Consistent with these expectations, the diversity of serpentine endemics was higher in regions with greater serpentine area and was lower in subregions with highly isolated patches (Harrison *et al.* 2000). However, it is important to note that these results might be confounded by processes other than dispersal from the non-serpentine matrix onto serpentine patches. For example, regions with larger serpentine areas might have greater endemic species diversity simply because of greater *in*

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situ diversification, as discussed above.

Dispersal also appears to play an important role in driving the spatial structure and maintaining diversity of serpentine communities. Hobbs & Mooney (1985) observed that serpentine patches in northern California were had a great deal of spatial heterogeneity, as there were dramatic shifts in species dominance. This patchy distribution appears to be driven in part by an interaction between plant dispersal and patchy disturbances caused by the fossorial western pocket gopher *Thomomys bottae*. These gophers continue to burrow into late summer, when they cover up the dispersed seed of *Lasthenia*, *Plantago*, and other forbs with up to 10cm of soil. Most grasses continue to disperse seed later into the summer after the soil disturbance- thus, their seeds remain closer to the surface and are more likely to germinate and establish in the spring. In other words, Hobbs & Mooney (1985) suggest that dispersal phenology drives the clumped distribution of bunchgrasses on serpentine, which reflect burrowing patterns of gophers in previous years.

Conclusion

Serpentine plant communities are an outsized component of the diversity of the California Floristic Province: serpentine endemics comprise ~10% of the taxa though serpentine soil only occurs on ~1% of the landscape. The harsh environmental conditions on serpentine patches strongly select for genotypes capable of maintaining an appropriate aboveground Ca:Mg ratio despite a mismatch in soil chemistry. Plants capable of coping with all of these stresses generally converge onto a "serpentine syndrome" of traits and are likely to have fairly similar ecologies, as a result of which their relative abundances are likely to drift. Selection against hybrid genotypes and temporal separation in peak flowering, along with limited dispersal between isolated hummocks, likely drives speciation. Limited dispersal within and between patches is thought to drive spatial heterogeneity and allow for the persistence of poor competitors that disperse later in the season.

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