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Ilkka Hanski: The legacy of a multifaceted ecologist

Testing spatial ecological theory on Californian serpentine outcrops: a review

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Outcrops of serpentine bedrock bear as close a resemblance to islands as any terrestrial habitat, with floras often highly distinct from those of the surrounding matrix. In 30 years of research in California, I found that the sizes and spatial distribution of serpentine outcrops may influence extinction and colonization, alpha and beta diversity, reproductive success and genetics, and other facets of plant (and animal) ecology in ways consistent with spatial ecological theory. Such 'spatial effects' were detected primarily at scales of 10^2–10^3 meters separating habitat patches, whereas habitat quality and climate effects predominated at smaller and larger extents, respectively. Most regions containing sets of small outcrops (< 10 ha) also contain large ones (> 10^2 ha), making the detection of spatial effects dependent on careful site selection. This review highlights the interplay between testing theory and understanding the most important processes shaping biodiversity in a particular study system.

Introduction

Spatial ecology addresses the effects of large-scale habitat structure, such as the area and isolation of habitat patches, on population and community processes. Ever since its origins in the influential model of island diversity by MacArthur and Wilson (1967), spatial ecology has enjoyed a well-developed mathematical basis (e.g., Hanski 1999, Holyoak *et al*. 2005) and strong linkages to conservation biology (e.g., Hansson *et al*. 1995, McCullough 1996, Collinge 2009). Although spatial ecological theory has become highly diverse, a consistent central principle is that the dispersal of organisms across landscapes and among distantly separated habitat patches can influence population persistence, outcomes of species interactions, and community diversity. Isolation and small patch size are generally seen in a negative light; extinction is more frequent and diversity is lower on small islands far from mainlands (MacArthur and Wilson 1967), and species may be unable to persist in landscapes that fall below thresholds of patch area and isolation (Hanski 1999). When competitive or predatory interactions are strong, however, intermediate levels of patch isolation may promote greater population persistence and community diversity than would be supported by a highly connected landscape (Holyoak *et al*. 2005).

Empirical tests of the influence of habitat structure on ecological processes are challenging because processes at large spatial scales usually take place over long time scales, and both of these factors tend to limit the possibilities for either experimental manipulation or direct observation. Many of the successful tests of spatial theory have taken place in laboratory microcosms, outdoor mesocosms such as grasslands mown into patches of different sizes, and in a few cases, experimentally fragmented forests (*see* reviews in Holyoak *et al*. 2005, Collinge 2009). Some of the most influential and important insights have come from observational and lightly manipulative analyses of natural systems, with by far the most outstanding family of examples being the work by Ilkka Hanski and colleagues on the butterfly *Melitaea cinxia*, its host plants, and its parasitoids in the Åland Islands (*see* recent review in Ojanen *et al*. 2013, and references therein). However, over the last several decades of rapid development of spatial ecological theory, questions have arisen about how extensively it applies to large-scale natural systems (e.g., Eriksson 1996, Harrison & Taylor 1997, Fahrig 2002, Freckleton & Watkinson 2002, Baguette 2004).

For the past 30 years, my collaborators and I as well as a handful of colleagues elsewhere have used the distinctive biotas of outcrops of serpentine soil as a model system in which to test diverse facets of spatial ecological theory. In this review, I ask the converse questions "What have we learned from studies of serpentine biotas about spatial ecological theory?" and "How has spatial ecological theory helped us understand serpentine biotas?" By necessity, most of the studies reviewed here concern the serpentine flora, although a few animal studies are covered too, and the majority of cases come from my own work in California. In addition to studies focusing on serpentine outcrop area and isolation, this review covers several studies of spatially isolated small wetland ("seep") habitats within serpentine outcrops, and the one study I am aware of that measured the dispersal of organisms among serpentine outcrops and the effects of the surrounding 'matrix' habitat on such dispersal. More briefly, I will also mention a few other issues that might be considered to fall within spatial ecology, including the spatial patterning of communities within continuous habitats, changes in species interactions along environmental gradients, the nature of spatial niches, spatial relationships of native and exotic species, and evolutionary processes across sharp habitat boundaries.

Study system

The term "serpentine" as used informally by ecologists refers to ultramafic (Mg- and Fe-rich) rocks, principally serpentinite and peridotite, and the soils derived from them. Most exposures of these rocks are derived from oceanic crust, and occur in present or former subduction zones where parts of downgoing oceanic plates have stuck to the edges of continents, giving the outcrops a characteristic belt-like and patchy distribution within mountainous regions. Serpentine is a harsh environment for plants because of its low levels of Ca relative to Mg, low levels of primary nutrients, and, in some cases, elevated levels of metals (Ni, Co, and Cr) and/or coarse rocky texture giving rise to low water availability. Throughout the world, vegetation on serpentine is shorter and sparser than the vegetation of most other soils. Distinctive floras occur on serpentine, both because it excludes many plant species from the surrounding communities, and because it often supports substrate specialists ("serpentine endemics"). (For reviews of serpentine ecology, *see* Brooks 1987, Kruckeberg 1984, 2006, Alexander *et al*. 2006, Harrison & Rajakaruna 2011). Many serpentine endemics have narrow geographic distributions and are considered sensitive or rare taxa (Safford *et al*. 2005).

Serpentine floras and faunas have been studied most extensively in California, where roughly 5700 km^2 of serpentine support an estimated 246 endemics, making this one of the temperate zone's richest serpentine floras (Safford *et al*. 2005). The serpentine flora of California evolved *in situ* and is found nowhere else (Raven & Axelrod 1978), making it a clearly defined group of habitat specialists. Evolutionists have long studied California's serpentine endemic flora as an example of the linkage between adaptation and speciation (Stebbins 1942, Stebbins & Major 1965, Raven & Axelrod 1978). The floristics, distribution and evolutionary ecology of this flora are well known (Whittaker 1954, Kruck-

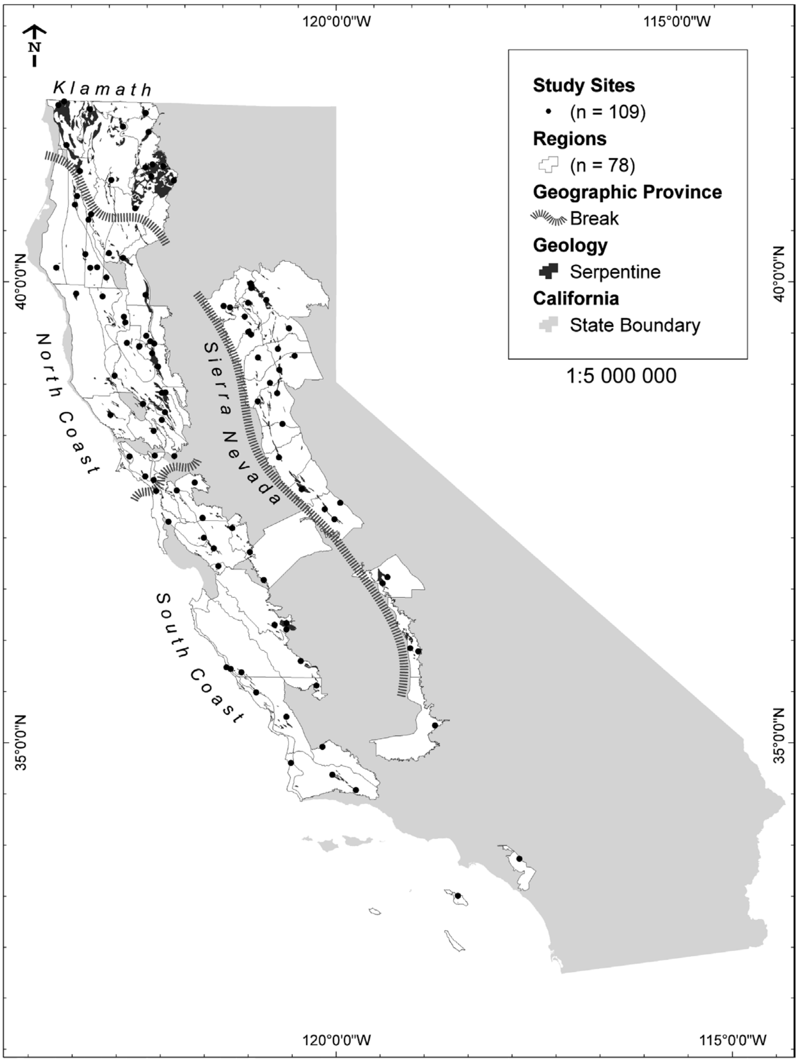

Fig. 1. Serpentine outcrops in California, and regions used to study spatial effects on plant community diversity at a large scale. Serpentine distribution is taken from a statewide map, and regional boundaries are generated from two floristic databases. The Sierra Nevada geographic province is separated from the North and South Coast provinces by the Great Central Valley, and the two southernmost sites are included in the South Coast province; *see* Harrison *et al.* (2006).

eberg 1984, 2006, Safford *et al.* 2005) and considerable botanical, geological and other large-scale data are available. Serpentine in California is found in four broad, geologically-defined provinces: the Klamath-Siskiyou Mountains, the North Coast Range, the South Coast Range, and the Sierra Nevada (Fig. 1). Serpentine vegetation ranges from conifer woodlands in the north, through shrublands in much of the state, to grasslands in the south. As in many other parts of the world, California's serpentine flora has been far less affected by agriculture, logging, and other forms of land conversion than the floras of more productive soils, although there are heavy localized impacts from urbanization, mining, and off-highway vehicle use. Surprisingly large areas of relatively intact, late-successional forest and shrubland can be found on serpentine. Grasslands on serpentine have been subject to more extensive habitat conversion, but where they persist, they support communities far richer in native species than the grasslands on other soils.

Population persistence

Metapopulation theory has become the dominant framework for understanding the dynamics of populations in naturally discontinuous or human-fragmented landscapes (Hanski 1999, Holyoak *et al*. 2005, Collinge 2009). Species are viewed as “populations of populations” existing on networks of habitat patches. Each patch can either be occupied or unoccupied by the species, and moves between these two states according to continuous rates of colonization (C) and extinction (E). A species never persists for long at the local (patch) scale, where constant turnover occurs; it can only persist at the regional (metapopulation) scale as long as C exceeds E, which would be the case, for example, if patches are not too far from one another, or are connected by habitat corridors, or the species is expanding its range. Moreover, even if C does exceed E, a very small metapopulation (too few patches) can still go extinct by chance. The overall view is that individual populations are transient, but that species can survive regionally in sufficiently large and well-connected universes of patches. The potential applications of this model to conservation biology, wildlife management, and restoration ecology have become the subjects of an extensive literature (e.g., McCullough 1996, Hanski 1999, Collinge 2009).

One of the first tests of metapopulation theory in a natural system concerned the Bay checkerspot butterfly (*Euphydryas editha bayensis*) in the San Francisco Bay Area, California, USA. Larvae of this butterfly feed on annual plantain (*Plantago erecta*), and the extensive patches of this plant which they require are found almost exclusively on serpentine outcrops, although the plant is not a strict serpentine specialist. Classic work by Paul Ehrlich and colleagues (Ehrlich 1961, 1965, Singer & Ehrlich 1979) had shown that adjacent populations of the Bay checkerspot fluctuated and went extinct independently, an observation that contributed to the early development of metapopulation ideas. By the late 1980s, many Bay checkerspot populations had gone extinct because of urbanization and its side effects, except in the relatively rural southern end of its range, where a population of roughly 10^6 butterflies inhabited a large serpentine outcrop called Coyote Ridge, and a handful of smaller populations were also known.

In metapopulation studies it is necessary to measure the habitat suitability, degree of isolation, and occupied or unoccupied status of all habitat patches within a landscape. Thanks to the detailed geologic maps for the region, I was able to locate around 60 serpentine outcrops in a 50 × 30 km area and search them for the Bay checkerspot and its host plants (annual plantain, *Plantago erecta*; owl’s clover, *Castilleja densiflora*) and nectar plants (goldfields, *Lasthenia californica*). In addition to the Coyote Ridge population, I observed 9 other populations of 10^1–10^2 butterflies, and 17 serpentine outcrops on which host and nectar plants were present but butterflies were absent. I then built statistical models that accurately predicted butterfly presence–absence from two independent factors: habitat suitability (a combination of outcrop area, topography, and host and nectar plant abundance) and isolation (distance of each outcrop from the large Coyote Ridge population). Only patches within 4.5 km of Coyote Ridge had butterfly populations, even though many suitable outcrops existed at greater distances (Harrison *et al*. 1988).

This observational analysis, combined with simulation modeling, showed that the large Coyote Ridge population functioned as a stable ‘mainland’ to an archipelago of smaller, transient ‘island’ populations (Harrison *et al*. 1988). Dispersal experiments and other evidence indicated that the checkerspot was an ineffective navigator and colonist, and that irregular topography in the ‘matrix’ between outcrops further inhibited dispersal (Harrison 1989). The butterfly did not depend for its persistence on the extinction-colonization balance portrayed in the classic metapopulation model, but only on the continued existence of the mainland, Coyote Ridge. In turn, several factors contributed to the size and stability of the Coyote Ridge population: a very large serpentine outcrop, a grazing regime that benefitted the host and nectar plants, and finely dissected topography that buffered the butterfly population through cooler and warmer years (Weiss *et al*. 1988).

Not completely deterred by this experience, I subsequently tested metapopulation theory by resurveying around 140 populations of 5 rare plants in a serpentine landscape that had been surveyed 17 years earlier for a mining company’s environmental impact study (Harrison *et al*. 2001). These plants were summer-flowering habitat specialists found in widely scattered small wetlands, or seeps, on serpentine in the otherwise summer-dry environment. Numbers of populations remained roughly constant between the two time periods (1980–1981 *versus* 1997–1999), although around 40% population turnover had occurred. As expected under metapopulation theory, less-isolated seeps were more likely to have become colonized, and populations in more-isolated seeps were more likely to have gone extinct. However, molecular analysis later showed that in one of the species (serpentine sunflower, *Helianthus exilis*), levels of genetic variation were too high in the seemingly recolonized populations to be consistent with a recent colonization event, and were more consistent with reappearance from a dormant seedbank (J. B. M. Sambatti *et al.* unpubl. data). The role of seedbanks in preventing local extinction is a widespread finding in plant metapopulation studies (Erikkson 1996, Freckleton & Watkinson 2002).

In hindsight, it seems understandable that these species may not have fit the classic metapopulation model well. Their patchy serpentine habitat is fixed in ecological time, rather than being a transient resource such as gopher mounds in a meadow or treefall gaps in a forest, giving them no clear evolutionary mandate for effective long-distance dispersal. The greatest natural threat faced by plants and insects in this habitat is multiple years of drought, a stress that affects large regions synchronously. There is therefore little chance for these organisms to attain higher fitness through dispersing among habitat patches; both the sedentary behavior of the butterfly, and the long-term seed dormancy of the plants, make good evolutionary sense. For these and other reasons, some authors have concluded that even though many organisms occupy patchy habitats, there are few examples of metapopulations in which regional persistence depends on a delicate balance between local extinction and colonization (Eriksson 1996, Harrison & Taylor 1997, Freckleton & Watkinson 2002, Baguette 2004).

Species interactions

Theory suggests that patchy environments may help to stabilize antagonistic interactions, such as those between predators and prey, diseases and hosts, or competing species (Holyoak *et al.* 2005). Isolated patches can serve as temporary refuges for the host, prey or inferior competitor, where they survive until the disease, predator, or superior competitor catches up. This body of spatial theory has been tested in a number of experimental systems, but seldom in any large-scale natural habitat such as serpentine. Good candidates might be the serpentine-endemic wild flaxes, *Hesperolinon* spp., and their rust fungus *Melampsora lini* (Springer 2007), because of their strong antagonistic interaction in the patchy serpentine environment. With regard to mutualistic interactions, such as pollination or mycorrhizal associations, the main prediction theory makes about patchy habitats is that colonization and persistence in isolated habitats become even more challenging because both taxa have to be present. For example, many studies have examined whether plants suffer reduced reproductive success as a result of lower pollinator visitation in fragmented habitats (reviewed in Harrison & Bruna 1999). Two specific examples are briefly summarized here.

Serpentine morning glory (*Calystegia collina* ssp. *collina*) is a widespread serpentine endemic in northern California, growing in dense clonal patches. Its insect pollinators include both specialists and generalists. Plants on small (< 5 ha) outcrops produced substantially less seed than plants on large (> 300 ha) outcrops, even though they received no fewer visits by pollinators and did not have lower heterozygosity or genotypic diversity indicative of inbreeding depression. Pollen transplant experiments showed that plants were self-incompatible, and that on small outcrops, their isolation from conspecifics caused them to receive too little non-self pollen (Wolf *et al.* 2000a, 200b, Wolf & Harrison 2001). Serpentine sunflowers (*Helianthus exilis*) did not suffer reduced pollinator visitation as a result of spatial isolation either among serpentine outcrops or among seeps within outcrops. However, rates of seed predation by a tephritid fly were lower for *H. exilis* in more isolated seeps. The absence of *H. exilis* from the smallest serpentine outcrops (< 1 ha) could be explained by the absence of suitable habitat at those sites (Wolf *et al.* 1999). These studies supported the idea that living in small and isolated patches affects species interactions and plant reproductive success, but only for some species, and not necessarily via the mechanisms that ecologists have traditionally thought about.

Community diversity

Diversity of communities in patchy habitats might be expected to reflect the processes of local extinction and recolonization. Small and isolated habitat patches are expected to have lower local diversity (fewer species per patch) than larger or less isolated ones, as a result of higher extinction and lower colonization rates (MacArthur & Wilson 1967). But an entire ensemble of patches might have a greater regional diversity (aggregate number of species) than an undivided habitat of equal area, because of the potential for competing species to coexist in a subdivided environment (Holyoak *et al*. 2005). Higher regional diversity in spite of lower local diversity would mean that patchy habitats have higher "β-diversity", or differentiation among sites in species composition, than undivided ones.

As a historical footnote, the importance of considering spatial scale in studies of community diversity was first recognized by Whittaker (1960) in a comparison of serpentine and non-serpentine communities along topographic gradients of microclimate (not among discrete habitat patches) in the Siskiyou Mountains, USA. Whittaker proposed the terms "α-diversity" for the number of species at a local site, "β-diversity" for the differentiation in species composition among sites along a topographic gradient but still within a "community" as he defined it (i.e., the assembly of species found within a given elevational band on a given soil), and "γ-diversity" for the number of species in the entire community. In his original definition, (average) $\alpha \times \beta = \gamma$. Modifications of this system have been widely used by ecologists ever since (Jost 2007).

To test the influence of spatial subdivision on patterns of diversity, I compared local (α), regional (γ), and among-site (β) plant species diversity on 24 small serpentine outcrops (< 3 ha) and 24 sampling sites with exactly the same spacing within 4 large (> 500 ha) serpentine outcrops (Fig. 2). As expected, for serpentine-restricted (endemic) species, average local diversity was lower but among-site diversity was higher in the 24 patchy sites than the 24 continuous ones. Regional diversity was identical in the two sets of sites, and there were no particular species restricted to either the patchy sites or the continuous ones. It appeared that the patchiness of small serpentine outcrops did not alter overall endemic diversity, but redistributed it from the local scale to the among-site scale. For the species not restricted to serpentine, diversity was higher at both the local and the regional scale in the patchy sites than the continuous ones, consistent with edge effects. This was particularly true for exotic species, which were much more numerous on the small outcrops than the large ones (Harrison 1997, 1999). Later work suggested that the edges of small serpentine outcrops, surrounded by exotic-rich nonserpentine habitats, may be ideal settings for the evolution of serpentine tolerance in exotics such as the grasses *Avena fatua* and *Bromus hordeaceus* (Harrison *et al*. 2001).

For the plant communities of serpentine seeps, Freestone and Inouye (2006) used randomization tests to show that among-site differentiation (β-diversity) was significantly higher than expected due to chance alone, both among separate seeps within the same serpentine outcrop, and among seeps on separate outcrops. However, the community differentiation among seeps within the same outcrop could be explained by environmental variation such as soil chemistry differences, while the differentiation of communities among seeps on separate outcrops could only be explained statistically by geographic distance. They concluded that at the scale of seeps on separate serpentine outcrops, although not at smaller scales, the spatial isolation of seeps limits plant dispersal and thereby affects the composition of plant communities.

Based on the above studies, there seemed a clear potential for spatial structure to play a role in shaping the overall distribution of plant diversity on serpentine outcrops across California. To test this proposition, my colleagues and I measured regional plant diversity in 78 serpentine-containing regions (81–5306 km^2), and local diversity at 109 sites (1000 m^2 plots) nested

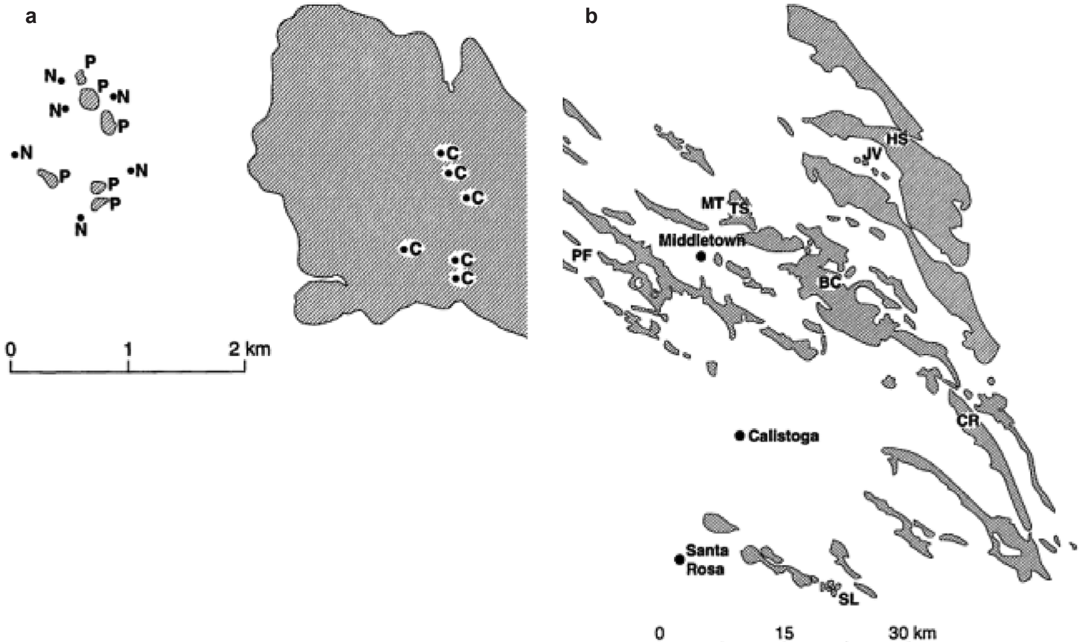

Fig. 2. Serpentine outcrops used to study spatial effects on plant community diversity at an intermediate scale. (**a**) One cluster of patchy serpentine sampling sites and one paired cluster of continuous serpentine sampling sites with the identical spacing (P = patchy, C = continuous, N = nonserpentine sampling sites). (**b**) Distribution of eight of these sampling clusters across the study region (two-letter acronyms = sampling clusters). *See* Harrison (1997, 1999).

within those regions (Harrison *et al*. 2006) spanning the California Floristic Province. We expected that the diversity of serpentine endemic plants would be lower at local sites on smaller and more isolated serpentine outcrops, yet potentially higher in regions with more spatially complex serpentine (e.g., regions with greater numbers of separate outcrops for a given total area of serpentine). These expectations were not met. In a multivariate model considering > 70 regional and local variables, the only significant spatial influence was that endemic diversity at the regional scale was higher in regions with a greater total area of serpentine. Endemic diversity at the regional scale was also highest in regions with abundant rainfall, and in which the serpentine has been exposed longest in geologic time. Endemic diversity at the local scale was highest at sites with rocky soils within endemic-rich regions (Harrison *et al*. 2006).

By far the strongest predictor of endemic diversity, total species diversity, and community composition on serpentine was mean annual precipitation (or its correlate, the remotely-sensed index of plant productivity known as NDVI or normalized difference vegetation index; Grace *et al*. 2007). Later we found that the positive relationship of plant diversity to large-scale, climatically-driven productivity was driven entirely by the positive response of species of northerly (mesic) biogeographic origin, suggesting a mechanism based on evolutionarily conserved physiological tolerances (Harrison & Grace 2007). Benign climates with abundant precipitation promote the functional divergence and physiognomic distinctiveness of plant communities on serpentine and nonserpentine soils (Fernandez-Going *et al*. 2013).

It might appear contradictory that the spatial structure of serpentine habitats affected plant diversity within an individual region but not across the entire realm of Californian serpentine. Once again a possible resolution seems obvious in hindsight. In models of single species, Fahrig (2002) showed that the spatial structure of habitats may only be important under a narrow range of conditions: for example, when the species is neither too poor or too good a disperser relative to distances among patches, and when the habitat is neither too scarce or too common (e.g., when it comprises 15%–20% of the landscape). Conversely, she found that when dispersal is high or habitat is more common than 20% of the landscape, species persist regardless of spatial structure, and when dispersal is low or habitat is scarcer than 15% of the landscape, species become extinct regardless of spatial structure. Her result implies that it may be possible to find significant spatial effects by looking for them in settings where they are likeliest to be important, such as the small *vs*. large outcrop comparison described above, yet not to find them in a more heterogeneous set of locations that are intended to be representative of the study system as a whole, as in the statewide study described above.

Serpentine "islands" in evolutionary time

The island-like nature of serpentine might be important because of its evolutionary as well as its ecological consequences (Kruckeberg 1991, Ackerly 2003). Plant evolution on serpentine is a vast topic that is mostly beyond the scope of this review. However, it is relevant here to ask whether the occurrence of serpentine as many separate outcrops has been an important factor in patterns of adaptation and/or speciation. Analogously to the well-known evolutionary radiations on oceanic islands, the colonization of serpentine might be associated with increased diversification, and closely related and ecologically similar species might be found on separate outcrops, suggesting a role for spatial structure in stimulating allopatric speciation. Little evidence for such patterns on serpentine has been found so far, however. In most lineages, transitions to serpentine are associated with diminished or unchanged rates of speciation (Anacker *et al*. 2011). Once again, climate is by far the most important factor promoting diversity; serpentine endemics tend to originate from serpentine-intolerant ancestors in benign, mesic climates (Anacker & Harrison 2012a), and benign climates also promote the survival of ancient lineages that contribute to high phylogenetic community diversity (Anacker & Harrison 2012b).

Climate change and distributional shifts

Another long-term consequence of an island-like distribution might be a higher rate of extinction under a changing climate. Warming and drying trends in recent millenia have been associated with latitudinal range shifts of hundreds of kilometers (Raven & Axelrod 1978) and elevational range shifts of hundreds of meters (e.g., Briles *et al*. 2005). If climatic changes do not greatly affect the degree to which species are restricted to serpentine — which is admittedly questionable — it is hard to imagine how serpentine endemics can have survived while confined to small outcrops with little elevational or latitudinal room to migrate. One possibility is that extinction has sorted the serpentine flora and eliminated those species that inhabited marginal climates or lacked climate-resistant traits. In California, "triply rare" species — restricted to serpentine, locally sparse, and having small geographic ranges — tend to be found in wetter climates and regions with larger areas of serpentine, suggesting a possible enhanced role for past extinctions in shaping the present-day distribution of the serpentine flora (Harrison & Inouye 2002, Harrison *et al*. 2008).

In addition, growing evidence suggests that plants restricted to serpentine are relatively resistant to climate change because of their tendency to exhibit suites of stress-tolerant functional traits such as low specific leaf area (Damschen *et al*. 2012, Harrison *et al*. 2014, Eskelinen & Harrison 2015). In contrast, there is no tendency for serpentine floras to show a higher prevalence of traits promoting effective long-distance dispersal, either when comparing serpentine to nonserpentine, or when comparing communities on small patchy serpentine outcrops to those on larger and more continuous outcrops (Spasojevic *et al*. 2014).

Other spatial issues

Besides the patchy distribution of serpentine outcrops, another attractive feature of serpentine for spatial (and other) ecological studies is the interestingly heterogeneous patterning of plant community composition often seen in serpentine grassland floras. Models of the self-organization of spatial pattern in systems with competition and disturbance were applied to serpentine habitats at Stanford's Jasper Ridge Biological Preserve (e.g., Wu & Levin 1994), although later studies found the observed patterns to be driven to a large extent by the underlying (literally) variation in soil depth (Lobo *et al*. 2008). Spatial heterogeneity caused by soil depth provided a theory-based mechanism for the widely observed tendency of native and exotic species to be negatively correlated at small scales but positively correlated at larger scales (Davies *et al*. 2005, 2007). Spatial productivity gradients resembling classic "catenas", from shallow, rocky serpentine soils on hilltops through deeper and finer-textured alluvial serpentine bottomland soils, have proven useful for testing how the strength of competition is related to resource availability (Elmendorf & Moore 2007) as well as for testing alternative theories about spatial niches (Harrison *et al*. 2010).

Conclusions

What have we learned from studies of serpentine about spatial ecological theory? The serpentine environment includes many small and isolated outcrops, and studies in California suggest that these may be valuable settings for studying issues related to small population size, reduced colonization and gene flow, altered rates of interaction among species, and lower community diversity. The studies reviewed here have confirmed some straightforward predictions (e.g., lower endemic plant diversity on small outcrops) and contradicted others in interesting ways (e.g., lower pollen quality, rather than lower pollinator visitation or inbreeding depression, reduces plant reproductive success on small outcrops). Given the current emphasis on the consequences of biodiversity for ecosystem function, serpentine might next provide a good setting to test for effects of habitat area and isolation on functional attributes of plant communities.

How has spatial ecological theory helped us understand serpentine biotas? The answer to this is less clear, in part because a considerable amount of the serpentine in California consists of outcrops that are not terribly small. Of the total of 5761 km^2, approximately 44%, 82%, and 99.5% is found in outcrops of greater than 100, 10, and 1 km^2, respectively (using Jennings 1977). It is difficult to find regions within which there are numerous small outcrops within a few km of one another but no large ones, the circumstances that would give rise to the maximum significance for processes that depend on dispersal among small outcrops. Nearly all of the serpentine endemic plant diversity in a given region may be found on the larger exposures of serpentine within that region, giving the processes that occur within "mainlands" an overriding effect compared with processes that occur among "islands". Serpentine endemic diversity is highest in regions with more serpentine and wetter climates, and the high diversity in California as a whole probably largely reflects the occurrence of serpentine across a wide range of climates and source floras, rather than spatial effects *per se*.

Where large-scale climatic events such as droughts are the major causes of local extinctions of populations, natural selection is likely to favor adaptations to "escape in time" rather than in space. Strategies for escape in time include seed banks, belowground storage organs, selfing, and pollinator redundancy. These have the side effect of reducing the sensitivity of population persistence to habitat area and isolation, as others have also concluded (Eriksson 1996, Freckleton & Watkinson 2002). Serpentine endemics that occur only on one or a few small outcrops (e.g., *Clarkia franciscana* in the San Francisco Presidio, *Calochortus tiburonensis* and *Streptanthus niger* on the Tiburon peninsula) illustrate the ability of some plants to persist for a very long time in spite of small population size and total isolation.

Williamson (1989) once said that island biogeography theory was "true but trivial", meaning that he believed only transient species undergo population turnover on islands in ecological time, while resident species diversity is higher on larger islands because of habitat heterogeneity rather than because of extinction and colonization dynamics. While this is a harsh critique, it seems possible that something similar could be said of spatial ecological theory as applied to serpentine systems: predictions may be successfully tested, and interesting insights may be gained about limitations of and potential improvements to theory, but paradoxically, the theory does not explain the lion's share of the patterns in the ecology of serpentine systems.

A good model system in the conventional sense is one that varies only in the aspect of interest, and has particular attributes that make the aspect of interest likely to be important. In the case of spatial theory, this might mean a patchy habitat of uniform quality, varying only in patch area and isolation, occupied by organisms with moderate dispersal abilities and no dormancy, and subject to random and independent local disturbances. This kind of model system enables us to ask whether a particular theory or idea *can* work, but not whether it actually *does* help explain and predict phenomena in complex natural systems. Serpentine has been a good system for better recognizing the difference between those two goals.

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