PART THREE

Synthesis

What Have We Learned from Serpentine in Evolution, Ecology, and Other Sciences?

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We conclude this book by briefly reviewing some of the most provocative conclusions from the foregoing chapters. We hope these examples, though not exhaustive, illustrate the wealth of general scientific understanding that has come from studying serpentine ecosystems. If this book provides inspiration for future collaborations between disparate workers—earth and life scientists, evolutionary biologists and gene-free ecologists, naturalists and theoreticians, basic scientists and those who aim to save the world—then serpentine will have served as a good model system for the excitement and synergy that comes from crossing sharp boundaries.

HOW DID GEOLOGISTS DEDUCE THE PROCESS OF SEAFLOOR SPREADING?

Prior to the plate tectonics revolution, geologists believed that ocean basins were old and unchanging, but we now know the ocean crust is the youngest and most dynamic part of the Earth's crust. New ocean crust forms at seafloor spreading centers, and most of it later disappears via subduction, or the disappearance of one crustal plate beneath another. The nature of seafloor spreading was one of the key unanswered questions as evidence mounted for plate tectonics in the 1950s and 1960s. As Chapter 1 describes in historical detail, the decisive step in resolving this

question came from the reinterpretation of ophiolites, terrestrial assemblages of rock that include large amounts of ultramafic rock (serpentinite, peridotite), as well as lesser amounts of gabbro, diorite, basalt, and chert. Beginning in the mid-1960s, these long-observed assemblages came to be understood as segments of oceanic crust and underlying mantle stranded on continents during subduction. Examination of ophiolites led to the development of models for oceanic crust formation that have since been tested and refined through deep-ocean studies and other means. Ophiolites provide a window in time, because oceanic crust not stranded on land seldom lasts more than 200 million years.

Although ophiolites are the major form in which serpentine (ultramafic rock) occurs on land, serpentine also occurs in other interesting settings described in Chapter 1: mélanges scraped off during subduction, exposed mantle from beneath continental crusts, and the somewhat mysterious stratiform complexes that may represent an early era in Earth surface history. We also know that ultramafic rocks and minerals compose the Earth's entire mantle and nearly all of its ocean crust. The fact that we think of their chemistry as strange is the result of our dwelling on the abnormally light, silica-rich rocks of the comparatively thin continental crust.

WHAT LIFE IS FOUND IN THE "DEEP BIOSPHERE" OF EARTH AND PERHAPS OTHER PLANETS?

Extremophile biology is the study of the microbes (Bacteria and Archaea) inhabiting hot springs, deep sea vents, mine effluents, and other environments of extreme temperature, pressure, pH, and/or chemical composition. They include the deep biosphere, subsurface zones such as rock and sediment interiors, where chemosynthesis supports a substantial fraction of Earth's biomass. Studies of the deep biosphere's geochemical, metabolic, genetic, and evolutionary processes are important sources of evidence concerning the origin of life on Earth and its potential for existence on other planets.

The serpentinizing subsurface is the "large-volume reaction zone in the planetary interior" where mantle meets water (Chapter 2). Temperatures are amenable to microbial life, and serpentinization produces reducing solutions enriched in Ca^{2+} and OH^- and possibly in dissolved hydrocarbons from abiotic sources. Microbes evidently make use of hydrogen oxidation coupled to methanogenesis and/or the reduction of sulfate, nitrate, and iron or other metals, as deduced through the identification of functional DNA sequences from these fluids. Challenges to life include high pH, scarce carbon, and fluctuations in chemistry and temperature. The microbiology of the serpentinizing subsurface has been explored at the recently discovered Lost City deep sea hydrothermal fields, the Mariana Trench, and several terrestrial serpentinite settings (Chapter 2).

Other planets, including Mars, are known to support the ingredients for serpentinization, so the study of the serpentinizing subsurface is closely linked to the generation of predictions for extraterrestrial life. Studies at Lost City have also led to speculation about the origin of life on Earth, as well as to evidence for lateral gene transfer as an evolutionary mechanism of possible importance.

DO ISLAND-LIKE TERRESTRIAL HABITATS GIVE RISE TO EVOLUTIONARY RADIATIONS?

Some of the most spectacular examples of rapid evolution and morphological change come from lineages that colonized oceanic islands and diversified to fill empty niche space. Serpentine outcrops are so island-like in appearance that it is tempting to look for similar phenomena. However, these outcrops are only truly insular from the perspective of the endemic species, which are usually a minority of the flora. When a new endemic lineage arrives on serpentine, rather than encountering unused resources, it may face substantial competition from the nonendemic (tolerator) flora. Thus, it is perhaps not surprising that transitions to serpentine endemism are not associated with increased rates of evolutionary diversification (Chapter 3).

Although it has been suggested that geographic isolation among separate serpentine outcrops could contribute to speciation, there are few examples, with the exception of the *Streptanthus glandulosus* complex (Chapters 3–5). This may be due in part to the shortage of biosystematic studies on the comparatively small number of genera that contain numerous closely related serpentine endemics (in California, candidates would include *Streptanthus*, *Hesperolinon*, *Allium*, and *Calochortus*; Chapter 3). It is also possible that the lack of examples is a real phenomenon reflecting the highly limited abilities of endemics to disperse among outcrops.

HOW EASILY CAN NATURAL SELECTION LEAD TO SPECIATION?

Early evolutionary biologists, most notably Darwin, assumed that the origin of new species was a direct outcome of natural selection, arising readily from adaptation to novel environments. Later theorists realized that even when divergent selection is strong, however, modest levels of gene flow can undermine the evolution of reproductive isolation and thus prevent such ecological speciation (Chapter 4). Geographic isolation has therefore come to be widely regarded as a key ingredient in most cases of speciation. The question remains: to what extent and under what conditions can divergent selection lead to speciation in the presence of gene flow? Strong selective gradients at edaphic boundaries, as well as the abundance of serpentine-endemic species that may have evolved from serpentine-intolerant

ancestors, have made serpentine a classic model system for this central unanswered question (Chapter 4).

Recent studies on the genera *Leptosiphon* and *Layia* appear to illustrate, respectively, the early and the final (speciation) stages of divergence across serpentine–nonserpentine boundaries. Other serpentine studies have illustrated some of the prerequisite mechanisms: strong fitness trade-offs between soil genotypes, which reduce the effective gene flow between soils, and divergent selection on flowering times, which contributes directly to reproductive isolation (Chapter 4). Although serpentine studies have not fully resolved the major questions about speciation in the face of gene flow, they provide some of the most compelling potential examples and research opportunities.

A quicker route from adaptation to reproductive isolation is the classic idea of catastrophic selection, in which adaptation to a new environment such as serpentine entails a major genomic reorganization that confers immediate intersterility between an ancestor (in this case, a serpentine-intolerant species) and a descendant (in this case, a serpentine endemic). Though this has been proposed in the past for serpentine *Clarkia* species, there is little current evidence to support it (Chapter 4).

Ecological speciation is not the only mode of origin for serpentine endemics, because they arise as often from serpentine-tolerant as serpentine-intolerant taxa (Chapter 3). The evolution of endemics from serpentine-tolerant (bodenvag) ancestors—in other words, speciation associated with the loss of ability to grow off of serpentine—has not been widely studied but is presumably at least as strongly related to change in climate and the competitive environment as to any genetic change in the lineage. In the *S. glandulosus* complex, several endemics appear to have arisen through the breakup of a widespread bodenvag ancestor during a period of environmental change (Chapters 3–5). In Sweden, *Arenaria norvegica* became confined to serpentine in southern regions after forests expanded during postglacial climatic warming, but it remained a soil generalist north of the latitudinal treeline (Chapter 17).

DOES EVOLUTION REPEAT ITSELF?

Because they are found throughout the world and are globally consistent in their chemistry, serpentine environments provide a much repeated natural experiment in plant adaptation. Global comparisons demonstrate that tolerance to serpentine has evolved many times in unrelated plant families and genera (Chapter 3). Pathways to serpentine tolerance vary among families and species, involving different mixtures of low intrinsic growth rate, high allocation to roots, early flowering time, and selective uptake, exclusion, or internal translocation of Ca, Mg, and metals (Chapter 5).

Local adaptation and ecotypic differentiation are nearly ubiquitous in species that grow both on and off serpentine (Chapters 5, 7), and serpentine tolerance has sometimes evolved repeatedly within such species, as shown by closer relatedness between serpentine and nonserpentine ecotypes within the same region than between serpentine ecotypes in different regions (Chapter 5). The tools of genomics and proteomics, applied to serpentine and nonserpentine ecotypes, are just beginning to reveal some of the specific genes and metabolic mechanisms underlying serpentine tolerance (Chapters 6, 7).

Preadaptation to environmental challenges such as serpentine is also common, as evidenced by high prevalence of tolerance within a taxonomic group; tolerance to metal-rich environments is unusually common in Brassicaceae and Euphorbiaceae, for example. Mechanisms underlying preadaptation to serpentine are just beginning to be understood. It may be easier for grasses than other vascular plants to adapt to serpentine because the structure of their cell walls requires less calcium (Chapter 5).

WHY IS THE WORLD GREEN?

This classic ecological question refers to the observation that most plant biomass is not consumed by herbivores in most ecosystems, and one equally classic answer has been that plants are under strong pressure to evolve chemical and physical defenses making them tough, spiny, toxic, and/or indigestible. Plant antiherbivore defenses inspired some of the earliest developments in coevolutionary theory and continue to be its premier subjects. Some theory predicts that higher levels of defense are favored in harsh and unproductive ecosystems, because the relative fitness costs of herbivory are greater where resources are scarce. The resulting diminished food quality for herbivores could reinforce a lesser flow of energy and a simplified food web structure in unproductive environments. Soil-specific selection for antiherbivore defenses could also contribute to the fitness trade-offs that promote the evolution of edaphic specialization, as could other soil-specific selective pressures related to mycorrhizae, pollinators, and pathogens. Plant–animal and plant–microbe studies on serpentine have been surprisingly few, but existing studies have tended to support these predictions, as well as demonstrate that plants may be more visible and vulnerable in open environments, and that plants may coopt soil elements such as Ni as defenses (Chapter 8).

HOW DO SPECIES RANGES EVOLVE?

Invasion biologists have long studied the dynamics of species range boundaries, including the potential role of rapid evolution, and climate change has brought renewed interest to these questions (Chapter 9). One long-standing theory predicts

that species ranges are limited by the fact that gene flow emanating outward from core populations in benign environments inhibits the potential for local adaptation in marginal, stressful environments. This model has been relatively little tested, but biological invasions in serpentine mosaic environments provide nearly ideal settings. In invasive *Aegilops triuncialis* (barbed goatgrass), dense core populations are found in serpentine grasslands, and sparser marginal areas occur where grassland soils give way to shallow rocky soils. Although conditions in the core and the margin created strong differences in selection, overall performance was found to be equal in the margin and the core; also, because plant density inhibited dispersal, migration was not higher from core to edge than the reverse. Studies of *Aegilops* also demonstrated some novel mechanisms promoting invasion success, including adaptive transgenerational plasticity, in which goatgrass growing on serpentine produces offspring with shortened flowering time and lower photosynthetic rates that are beneficial to fitness on serpentine. Finally, research on serpentine and nonserpentine populations of *Erodium cicutarium* examined how dispersal evolves in a mosaic environment; on serpentine, there is greater localized variation in fitness, which selects for lower dispersal (Chapter 8).

IS COMPETITION WEAKER IN UNPRODUCTIVE ENVIRONMENTS?

Ecologists disagree over whether and how the strength of plant interactions changes along gradients related to productivity. One viewpoint holds that in harsh and unproductive environments, competition decreases and may even give way to facilitation; another holds that competition must be at least as important in unproductive environments as in richer ones, although it may shift from primarily above-ground (light) to below-ground (nutrients) as productivity decreases. According to the second viewpoint, if unproductive environments demonstrate either higher diversity or lower resistance to the addition of new species than richer ones, it must be because spatial heterogeneity in resources is greater, rather than because competition is weaker (Chapters 10, 11).

Serpentine studies support the notion that competition is weaker in less productive environments, both within serpentine along gradients of soil depth and chemistry and between serpentine and nonserpentine environments (Chapters 10–12). Experimental neighbor removal had weaker effects on the success of target species at the harsher end of a natural productivity gradient (Chapter 10). Within harsh serpentine sites, numbers of exotic species were positively correlated with numbers of native species even at a very local scale, in contrast to the competition-based negative correlation found on richer sites (Chapter 11). Also, overall species richness was lower at harsh sites, contradicting the idea that higher spatial heterogeneity at the harsh sites could explain the coexistence of natives and

exotics. Finally, a review of the available evidence suggests that disturbance plays a significantly weaker role in maintaining diversity in serpentine than nonserpentine environments, as would be expected if competition played a lesser role in limiting diversity in these environments (Chapter 12).

Exactly why plant competition appears to be weaker on serpentine remains unresolved. It seems unlikely that nutrient scarcity alone could reduce the intensity of competition. It may be that water and nutrients, which tend to be the limiting resources in unproductive environments, are less easily monopolized by one or a few species than light, which tends to be the limiting resource in more fertile environments. Plant functional traits (see below) and seasonality may also play roles in reducing the potential for competitive dominance on unproductive soils.

IS DISTURBANCE LESS IMPORTANT IN UNPRODUCTIVE ENVIRONMENTS?

Ecologists tend to assign disturbance—defined as the removal of above-ground biomass—a central role in structuring natural communities. At a local scale, disturbance temporarily shifts dominance to fast-dispersing and fast-growing (weedy) species; it may reduce local diversity, especially if it is excessively frequent or intense. At a regional scale, disturbance is likely to increase diversity, especially if it is heterogeneous in its frequency, intensity, and location. Because the primary ecological effect of disturbance is to reduce competition, its effects on communities should vary along environmental gradients that influence competitive intensity. Multiple theories therefore predict that disturbance should play a lesser role in maintaining diversity in unproductive environments. This prediction is generally borne out by studies showing lesser effects of fire, grazing, or soil disturbance on the diversity of plant communities on serpentine compared with nonserpentine soils (Chapter 12).

Lower disturbance dependency in unproductive ecosystems has both ecological and evolutionary facets. Ecologically, an individual species may respond less to a given fire on serpentine, where the vegetation is already more sparse and open, than on nonserpentine, where the same fire results in a larger pulse of available resources. Evolutionarily, species are less likely to show specialized adaptations for postfire regeneration in serpentine communities, where space and light are less limiting, than in nonserpentine communities. In addition, the lower biomass of unproductive communities may result in lower natural frequencies and intensities of fire and grazing, and thus to a lesser degree of adaptation to these disturbances (Chapter 12).

Recovery from natural or human disturbances may be exceptionally slow in environments such as serpentine (Chapters 12, 18). This suggests that management of nutrient-poor habitats may need to take account of a lower natural disturbance

regime and a greater sensitivity to excessive disturbance, such as the increased frequency of fire caused by climate change (Chapter 17). Although it is possible to restore or revegetate environments such as serpentine once they are heavily altered, this requires striking a balance between amending sites enough to allow native species to establish and not amending them so much that exotic species take over (Chapter 18).

Low-nutrient systems may be dramatically altered by anthropogenic nutrient deposition, especially in conjunction with invasions by exotic species with functional traits conducive to fast growth (Chapters 12, 16–18). Mowing, grazing, and burning may be necessary to maintain and restore native vegetation in these circumstances (Chapter 18).

HOW DO PLANT FUNCTIONAL TRAITS MEDIATE THE OUTCOMES OF ECOLOGICAL PROCESSES?

Plants in unproductive environments show a consistent syndrome of traits, including slow intrinsic rate of growth, high relative allocation to below-ground structures, and slow rates of leaf turnover. Underlying all studies that compare ecological processes along productivity gradients is a fundamental question: are differences in response, such as the differences in competitive strength or disturbance outcomes between serpentine and nonserpentine soils, the result of the properties of the environments themselves, or of the traits of species inhabiting those environments? This question is sometimes overlooked, as when reviews of competition strength along productivity gradients fail to distinguish between studies that vary soil fertility but strictly control the identities of competitors versus studies that use competitor removal within naturally variable communities (Chapter 10).

Growing evidence supports the idea that plant functional traits play a key role in determining the ecological properties of soil fertility gradients (Chapters 10, 12, 16–18). For example, the best predictor of the strength of competition across a natural fertility gradient was a multivariate measure of plant community composition (Chapter 10). Target species benefited the most from competitor removal at sites dominated by tall annual grasses and forbs characteristic of fertile soils, and least at sites dominated by short-statured serpentine endemics; soil fertility itself was a weaker predictor of competitive strength. Likewise, the slower recovery of biomass following fire in serpentine than nonserpentine chaparral is partly the result of the lower frequency of postfire resprouting by shrubs, and the lesser postfire increase in diversity is related to the lack of obligately fire-stimulated germination in herbs, both of which reflect an evolutionary history of lower fire frequency. Conversely, the greater enhancement of native species diversity by grazing in serpentine (compared to nonserpentine) grasslands is caused by a greater prevalence

of short-statured native annual forbs, the functional group that benefits most by the reduction in biomass of tall exotic annual grasses caused by grazing.

Plant traits are a critical issue in studies of the functional effects of biodiversity and the consequences of its loss (Chapter 16). Serpentine grassland studies have been valuable in demonstrating that community biomass is enhanced more by the diversity of functional types, for example, N-fixers, early- and late-season annuals, and perennials, than by the diversity of species per se (Chapter 16). However, an unexpected and potentially general finding from serpentine studies is negative selection, in which the species that competitively dominate mixtures are ones that have relatively low biomass when grown in monocultures. This effect, which in hindsight might be expected in a low-nutrient environment, tends to limit the degree to which functional diversity enhances productivity.

Global change effects may also depend on plant functional traits. One experimental study concluded that low-nutrient environments are relatively invulnerable to changes in temperature and precipitation because plant growth responses are so strongly limited by the slow-growing, stress-tolerating trait syndrome; some serpentine studies support this conclusion and others contradict it, and evidence remains scarce (Chapter 17). The low biomass and slow-growing plant traits found in low-nutrient environments also reduce the degree to which these environments sequester carbon and exert other biotic feedbacks on global atmospheric change (Chapter 16).

DO DIFFERENT LIMITING FACTORS HAVE SIMILAR ECOLOGICAL CONSEQUENCES?

In generalizing from serpentine to other low-productivity environments, it is important to consider differences in limiting factors. Scarcities of resources for which plants compete, such as nutrients and water, are unlikely to have the same ecological effects as salinity, unfavorable temperatures, cation (e.g., magnesium) excess, or other limiting conditions for which plants do not compete. The serpentine syndrome involves multiple limiting factors, including nutrient and water scarcity and cation excess, and the same may be true of some other special edaphic environments, such as limestone, dolomite, alkali sinks, and acid heaths. In other unproductive environments, such as granitic, sandstone, and shale barrens, the main limiting factor is poor water retention in shallow, rocky soils, and in others, such as deserts and alpine zones, plant growth is limited by climate (e.g., the length of the snow-free season or the rainy season). It would be interesting to investigate the extent to which the common features of all these environments—slow growth and its associated plant traits—do or do not lead to ecological similarities, such as the reduced roles for competition, disturbance, and herbivory observed in studies of serpentine.

HOW ARE ECOLOGICAL PROCESSES AFFECTED BY LANDSCAPE HETEROGENEITY?

Landscape ecology investigates how ecological processes are affected by the spatial complexity of landscapes. Examples include edge effects, source-sink dynamics, and matrix effects, in all of which the flow of organisms through landscapes affects population abundances and community structure. Serpentine-containing landscapes show striking heterogeneity along gradients from shallow and rocky to deeper and finer soils, between adjacent communities such as serpentine chaparral and serpentine grassland, and along the boundaries between serpentine and other soils (Chapters 10–12). This heterogeneity has been shown to contribute to the coexistence of potentially competing native and exotic species, and hence to landscape-scale diversity (Chapter 11). The influx of species from surrounding nonserpentine habitats appears to elevate diversity at the edges of serpentine outcrops (Chapter 14). There have been surprisingly few studies yet that have actually measured or manipulated the flow of organisms in serpentine mosaic landscapes and attempted to determine the ecological consequences of such movement (but see Chapter 8).

HOW ARE INTERACTIONS AND DIVERSITY AFFECTED BY THE SPATIAL ISOLATION OF HABITATS?

Island biogeography theory and, more recently, metapopulation and metacommunity theory examine the ecological consequences of spatially isolated habitats (Chapter 14). Small and isolated habitats are generally expected to support transient populations and low diversity, but species may survive in a well-connected regional network of small habitat patches. "Fugitive" species may coexist with their predators, competitors, or diseases by being able to disperse faster through such a regional patch network. Serpentine outcrops, with their discrete, island-like distributions and their specialized floras often rich in rare species, are an attractive setting for testing these ideas.

One question that has been of great interest to conservation biologists is whether plants on isolated habitat patches suffer reduced reproductive success as a result of pollinator limitation (Chapter 13). Several studies in serpentine environments have found evidence that plant fitness is sensitive to spatial isolation, but the patterns are less straightforward than expected. Pollinators may be too mobile or too unspecialized to produce the predicted effects of isolation on visitation rates. Plants in resource-poor environments such as serpentine may also show low degrees of pollinator specialization, high levels of self-compatibility or clonal reproduction, and highly persistent seedbanks or below-ground structures, all of which tend to buffer populations against pollinator scarcity.

Another question is how overall species diversity is affected by habitat configuration (Chapter 14). In a comparison of small serpentine outcrops to sites within very large outcrops, small outcrops had lower local (alpha) diversity and higher among-site (beta) diversity of serpentine specialist plants, much as expected. Small outcrops also had higher local diversities of generalist species, suggestive of edge effects. However, when plant diversity was studied across a much larger array of serpentine outcrops chosen more representatively, few effects of spatial habitat structure were detected. It appears that serpentine might provide opportunities for testing some aspects of spatial ecological theory, but that the theory may have more limited value for understanding plant diversity on serpentine—an interesting comment on the model system concept.

WHAT ARE APPROPRIATE CONSERVATION STRATEGIES FOR SPATIALLY COMPLEX LANDSCAPES?

The design of reserve networks has become a cornerstone of modern conservation biology. Goals include the protection of rare species and communities, the representation of all species and communities, and the provision of corridors for movement across landscapes (Chapter 15), which is especially important in light of climate change (Chapter 17). Serpentine landscapes, with their widely dispersed rare species and communities, illustrate the value of new analytical tools for reconciling these potentially conflicting conservation goals (Chapter 15). Because they have narrow geographic ranges and are confined to small outcrops, serpentine-endemic plants may be exceptionally vulnerable to extinction under climate change, and serpentine may prove to be a good model system for experimenting with more active approaches, such as managed relocation (Chapter 17).

One recently proposed solution to climate change involves mining massive amounts of serpentine for carbon sequestration (Chapters 1, 17). This will certainly create a need for the large-scale revegetation of devastated landscapes on harsh soils (Chapter 18). We conclude in the sincere hope that a solution gentler to some of the Earth's most botanically fascinating ecosystems can be found.