Chapter 16

SYNTHESIS AND FUTURE DIRECTIONS: WHAT HAVE HARSH ENVIRONMENTS TAUGHT US ABOUT ECOLOGY, EVOLUTION, CONSERVATION, AND RESTORATION?

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INTRODUCTION

Harsh environments, due to their extreme conditions and unique biota, have piqued human interest over the centuries. Botanists interested in the study of plant diversity are especially drawn to harsh environments because they are frequently characterized by unique plant communities with relatively high proportions of rare and endemic species. Such plant communities, which are often restricted to fragmented islands of habitat, offer exceptional opportunities for exploring biogeographical and ecological theory (Harrison, 2011), including aspects of plant-plant (Davies, 2011; Moore & Elmendorf, 2011) and cross-kingdom (Strauss & Boyd, 2011; Wolf & Thorp, 2011) interactions. Plants found in harsh environments also provide model organisms for the study of adaptation and evolution (O'Dell & Rajakaruna, 2011; Ostevik et al., 2012). Adaptation is a central focus in Darwin's theory of evolution by natural selection, and harsh environments provide prime settings in which to examine the factors and mechanisms driving adaptive evolution (Levin, 2001; Via, 2009). Some of the earliest evidence of rapid evolution in plants has come from studies of plants growing in

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extreme habitats such as metal-rich mine tailings (Chapters 11, 14; Antonovics et al., 1971; Bradshaw, 1991; O'Dell & Rajakaruna, 2011) and serpentine outcrops (Chapters 6, 11; Kay et al., 2011). Plants found in harsh environments provide unique challenges for conservation (Chapter 14; Thorne et al., 2011) and restoration (Chapters 14, 15; O'Dell & Claassen, 2011) and are especially prone to stressors associated with climate change (Chapters 7, 13; Damschen et al., 2011; 2012). Plants of harsh environments also serve as model organisms for investigating the genetic and physiological bases for tolerance of abiotic stress (Chapters 4-6, 9, 11; Jenks & Hasegawa, 2013; Kantar et al., 2011; Szabados et al., 2011), with important applications in agriculture, restoration, and conservation (Chapters 9, 14, 15). In this chapter, we summarize what harsh environments have taught us about the diversity, ecology, evolution, conservation, and restoration of plants, lichens, and microbes found in harsh environments. Finally, we highlight areas of research needed to expand our understanding of the role that harsh environments may play in generating and maintaining plant and other biotic diversity.

HARSH ENVIRONMENTS AS MODEL SETTINGS FOR STUDIES ON BIODIVERSITY

Alpine summits (Nagy & Grabherr, 2009), polar regions (Thomas et al., 2008), arid deserts (Ward, 2009), remote oceanic islands (Stuessy & Ono, 2007), saline flats (Flowers & Colmer, 2008), acidic bogs (Rydin & Jeglum, 2009), rock outcrops (Anderson et al., 1999), and even wastelands created by human activities such as mining (Walker, 2011), all provide extreme habitats for plants and other biota adapted to harsh abiotic factors. Such habitats are characterized by extremes in temperature, light, water availability, and chemical and physical soil attributes. Adaptation to such environments often leads to population differentiation and subsequent speciation (Kay et al., 2011; O'Dell & Rajakaruna, 2011), thereby generating biodiversity. Harsh environments also often provide a refuge for species which may be at a competitive disadvantage in more benign habitats (Anacker, 2014; Moore & Elmendorf, 2011). Whether through adaptive evolution or exaptation (*i.e.,* ecological filtering), harsh environments often contain a unique assemblage of plants and other biota able to thrive under conditions inhospitable for most other organisms (*i.e.,* extremophiles; Bell, 2012; Pikuta et al., 2007).

Much attention has been focused on microbes as model organisms for the study of the diversity and ecology (Chapters 1, 2; Margesin & Miteva, 2011; Seckbach, 2007; Takai, et al., 2005), physiology and genetics (Chapters 1, 2; Gerday & Glansdorff, 2007), and evolution (Chapters 1, 2; Rampelotto, 2013) of extremophiles. The study of extremophile biology and ecology has shed light not only on other organisms found in extreme environments on Earth, but also has implications for the study of astrobiology (Chapter 1; Cardace & Hoehler, 2011; McCollom & Seewald, 2013). The roles that microorganisms (Chapters 1, 2), as well as terricolous and saxicolous lichens (Chapter 3), play in the ecology of both below- and above-ground habitats via their influence on biogeochemical processes— including weathering, pedogenesis, nutrient cycling, and nutrient acquisition by plants—has also received much attention (Casamayor et al., 2013; Kirchman, 2012; Southworth et al., 2013).

The intimate and inseparable relationship between plants and their substrates results from the need for plants to obtain water and nutrients from the substrate upon which they grow. Thus, it is no surprise that the chemical and physical attributes of the substrate control many aspects of plant diversity, ecology, and evolution. Plants closely associated with harsh substrates have been described as indicators of the minerals and elements found within the substrate, and close observation of such substrate-plant relations has led to biogeochemical prospecting worldwide (Brooks, 1983; Martin & Coughtrey, 1982). Studies of the diversity, physiology, genetics, ecology, and evolution of plants found on extreme substrates have generated much interest in recent years (Jenks & Hasegawa, 2013), particularly the study of plants found on serpentine (Chapters 2, 3, 6, 10, 11, 13-15; Alexander et al., 2007; Brady et al., 2005; Brooks, 1987; Harrison & Rajakaruna, 2011; Roberts & Proctor, 1992), gypsum (Chapters 2, 5, 14; Escudero et al., 2014), dolomite (Chapters 5, 14; Pignatti & Pignatti, 2013), gabbro (Chapter 14; Wilson et al., 2010), metal-rich mine tailings (Chapters 2, 3, 6, 10, 11, 14, 15), and saline soils (Chapters 2, 4, 11, 14). Plants associated with unique geomorphologic features such as mountains (Chapter 7; Clausen, 1951; Körner, 2003; Nagy & Grabherr, 2009) and deserts (Ward, 2009) have also been the subject of much study due to their unique assemblages of plant species possessing adaptations to climatic extremes and other abiotic and biotic stressors. Such plants have also served as models for elucidating mechanisms of convergent evolution, showing how similar functional and phenotypic diversity can be maintained among phylogenetically distinct lineages in response to similar selective pressures (McGhee, 2011; Reich et al., 1997).

Harsh environments have played an important role in generating biodiversity both at the species and community levels, as well as in maintaining biodiversity at varying spatial scales (Yost et al., 2012). Inventories of this biodiversity are still incomplete and continued inventory efforts are needed, particularly given that the current wave of human-mediated extinctions is expected to crest as the sixth major extinction event that has occurred during life's 3+ billion-year history on our planet (Pievani, 2014).

HARSH ENVIRONMENTS AS MODEL SETTINGS FOR STUDIES ON ECOLOGY

American plant ecologist Frank Egler is reputed to have said: "Ecosystems are not only more complex than we think; they are more complex than we can think." Ecological studies are difficult to implement and interpret due to their multivariate nature; multiple factors interact in complex ways making it difficult to determine how specific environmental factors impact organisms. Harsh environments have characteristics that, because they are extreme, amplify their influences on organisms, thereby making it easier to identify their effects. Thus, studies of harsh environments allow us to better understand the importance of specific ecological factors in generating and maintaining taxonomic and functional diversity (Harrison & Rajakaruna, 2011). For example, in California (USA) shrublands dominate in dry areas, but in more benign areas, shrublands are restricted to environments typified by harsh soils (Chapter 8). Competition is a major factor influencing this distribution, limiting shrublands to more stressful habitats under more productive settings. Similarly, serpentine endemism appears to peak under high precipitation (*i.e.*, high productivity) in California (Fernandez-

Going et al., 2013) as well as globally (Anacker, 2011), suggesting that higher competition resulting from greater regional productivity could restrict stress tolerant species to harsh habitats. Recent studies have shown that at the community level, there is greater species, functional, and phylogenetic turnover across serpentine and non-serpentine soil boundaries in California's mesic northwest than in the arid south (Anacker & Harrison, 2012; Fernandez-Going et al., 2013). Recent tests (*e.g.,* Serrano et al., 2014) of this concept (*i.e.*, the Inclusive Niche Hypothesis; Colwell & Fuentes, 1975) have demonstrated the interplay between competition and stress tolerance in determining the distribution of stress-tolerant species. The patchy nature of some harsh environments has allowed the application of island biogeography theory and, more recently, metapopulation and metacommunity theories (Harrison, 2011) and has provided insights into life history traits that may be selected for (or against) in patchy, often harsh, habitats (*e.g.,* Shenk, 2013; Spasojevic et al., 2014).

Adaptation to harsh environments may also involve ecological partners. For example, chapters in this book highlight how specific characteristics of fungi allow them to tolerate harsh conditions, both as the mycobiont in lichens (Chapters 3, 7) and as partners in mycorrhizal interactions (Chapters 2, 5, 7), as well as how their stress tolerance can influence such mutualistic associations. Rodriguez et al. (2008) documented "habitat-adapted symbiosis" in which certain fungal endophytes conferred particular types of stress tolerance (either heat or salt tolerance) on *Leymus mollis* (Poaceae) plants from specific habitats (geothermal or coastal). For example, Rodriguez et al. (2008) found that the fungal endophytes that provided salt tolerance to the coastal grass population conferred salt tolerance on tomato and rice when the endophytes colonized tissues of those hosts. Other symbioses are often not addressed, but likely can be of great importance. As an example, note the possible role of pollinators (*e.g*., bumblebees) in limiting the northern range extent of legumes (Chapter 7). Antagonists may also play an important role in the distribution of organisms, and stresses conferred from harsh environments may affect the impacts of such antagonists as well. As demonstrated by metal hyperaccumulator plants (Chapter 10), tolerance of a stress (in this case heavy metal stress) can lead to plant adaptations that result in uptake of elevated levels of metals or other generally toxic compounds, which may deter or confer resistance to herbivores or pathogens. Stresses found in harsh environments may magnify the importance of organismal interactions such as mutualism or exploitation, providing opportunities to study the ecological and evolutionary importance of these interactions (Chapter 7; Strauss & Boyd, 2011).

Harsh environments are model settings for closely examining cross-adaptation, which is when a trait that evolved for one function becomes useful as an adaptation for another, and exaptation, which is when non-adaptive traits become adaptive when placed in an alternative context (Barve & Wagner, 2013). Traits that confer tolerance of one type of stress may confer tolerance of other stresses, which may allow species to occupy habitats which would otherwise be inhospitable (Chapters 4, 9, 11). New modeling tools have improved our ability to study exaptation. For example, Barve and Wagner (2013) analyzed bacterial metabolic networks and determined that particular pathways have latent potential as evolutionary innovations (in their study, an evolutionary innovation was defined as a bacterium's potential ability to utilize a particular carbon source for its metabolic reactions). They found that a bacterium able to utilize glucose as a sole carbon source for all its metabolic reactions also may be able to utilize 44 other sole carbon sources. Thus, ability to utilize glucose provided opportunities for a bacterium to utilize other carbon sources for which its metabolism was not

adapted. Similar techniques may be applicable to other areas of biology that involve complex networks (*e.g.,* genetic networks or food webs) to reveal potential pathways that are not currently utilized. This approach may reveal the potential for organisms to respond to new environmental stresses: for example, once we have a more complete understanding of how gene networks determine tolerance to particular types of stress (Chapter 9), we may be able to show how the ability to tolerate one stress can pre-adapt an organism to a different stress. Because harsh environments impose strong selection pressures on organisms, they may be good initial subjects for this approach.

One of the major challenges in studying the effects of environmental stress is defining physiological stress and measuring its level in an organism. For example, salinity tolerance is a continuous variable rather than a binary one, and so it is more useful to have a measure that reflects the degree of tolerance to a particular stress rather than reducing tolerance to a binary condition which is either present or absent (Chapter 4). This approach may help to fine-tune our understanding of the effects of stress on plants and other organisms. Connecting specific genes to traits that confer stress tolerance is now possible using model organisms about which we have a profound genetic knowledge (Chapters 9, 11). Ecologists can use these model organisms by comparing the performance of genetic lines with specific genes "turned on" or "off." This single-gene approach is made more complex because stress tolerance often results from multi-gene adaptations (*e.g.*, Agarwal et al., 2013); however, our increasing ability to study genetic networks and to process large datasets will help to deepen our understanding of the genetic basis of adaptation to harsh environments.

An increased understanding of the genetics, physiology, and ecology of harsh environments has many applications in agriculture, conservation, and restoration. The success of both agricultural production and restoration efforts are limited by environmental stresses; alleviating the effects of environmental stress could allow increased success in both of these endeavors. Knowing how stress limits organisms or affects organismal interactions may allow us to manipulate biological systems to favor outcomes we consider to be desirable.

HARSH ENVIRONMENTS AS MODEL SETTINGS FOR STUDIES ON EVOLUTION

Harsh environments provide model settings in which to explore evolutionary questions, as has been highlighted by several chapters in this book. Here we summarize how studies of plants, fungi, and lichens found in harsh environments have contributed to our understanding of broader evolutionary themes which are central to understanding how diversity is generated and maintained. Whether accommodation of harsh environments comes about by ecotypic differentiation or by phenotypic plasticity has long interested ecologists. Turesson (1922) and Clausen et al. (1940) represent two classic works on evolutionary ecology, describing how experimental methods such as common garden and reciprocal transplant studies can be used to examine the roles of phenotypic plasticity and local adaptation in habitat specialization (Wright & Stanton, 2011). These studies, combined with genetic studies, have shown that species found in harsh environments either have genotypes that confer broad tolerance to wide-ranging environmental conditions (Baker, 1965; Parker et al., 2003; Richards et al., 2006) or have genotypes that confer adaptation to specific biotic or abiotic stressors

characteristic of the environment in which they occur (Bieger et al., 2014; Leimu & Fischer, 2008; Yost et al., 2012). Although there is much evidence for ecotypic differentiation and species-level endemism among plants found in harsh environments (Chapters 4-6, 9, 11; O'Dell & Rajakaruna, 2011), such specialization is not as common among mycorrhizal fungi (Chapters 2, 7; but see Chapter 5), lichens (Chapters 3, 7; Rajakaruna et al., 2012), or bryophytes (Chapter 12, Briscoe et al., 2009) found in similar environments.

Plants found in extreme environments have often been used to explore the mechanisms that drive the evolution of habitat specialization (Harris & Rajakaruna, 2009). Such studies have revealed that habitat specialists tend to arise via two mechanisms (Chapter 8): neoendemics, arising from nearby, non-specialized relatives via rapid and local speciation (Anacker & Strauss, 2014; Kay et al., 2011; O'Dell & Rajakaruna, 2011), or paleoendemics, resulting from gradual speciation via biotype depletion (Kruckeberg, 1957; Mayer & Baseda, 2010; Mayer et al., 1994). Whether there is directionality in the evolution of habitat specialization (*i.e.,* endemism) has been another avenue of interest that has been addressed by plants growing in extreme environments. The increasing availability of molecular phylogenies has provided us with unparalleled tools to ask questions about the evolutionary dynamics of habitat specialization (Chapters 4, 5; Anacker, 2011). Phylogenetic analyses of serpentine-tolerant plants (*e.g.,* Anacker, 2011; Anacker et al., 2011), halophytes (Chapter 4), and gypsophiles (Chapter 5) have demonstrated that tolerance to serpentine, saline, and gypsum soils, respectively, has been gained numerous times within various groups of angiosperms and has even been lost (although rarely) in some groups. These studies suggest that traits conferring stress tolerance are evolutionarily labile. Differences in the evolutionary dynamics of edaphic tolerance among different lineages may result from the association of stress tolerance traits with other ecophysiological strategies related to environmental stress, with stress tolerance more easily gained in those lineages with certain enabling traits as starting points (Chapters 4, 11); such enabling traits may enhance the capacity of those lineages to evolve other ecophysiological strategies for stress tolerance (see Chapter 4 for a discussion of trait associations for salt tolerance). Research by Anacker et al. (2011) shows that among 23 genera found in California, the direction of serpentine endemism is mostly from non-tolerant and tolerant species to endemic species, with a few reversals from the tolerant or endemic state to the non-tolerant state. Their work suggests that the evolution of edaphic endemism, and possibly other forms of habitat specialization, may represent an evolutionary dead-end. Recent work on *Knautia arvensis* (Caprifoliaceae) suggests that this may not always be the case, as serpentine endemic cytotypes and genotypes are often able to influence surrounding populations by repeated episodes of introgression and polyploidization (Kolář et al., 2012). Similarly, in *Streptanthus* (Brassicaceae), clades with endemism are often quite diverse, with endemism having evolved numerous times (and having been lost at least once). This suggests that endemism is not always an evolutionary dead-end and that endemic species have the potential to radiate further, even within the same habitat (Ivalú Cacho et al., 2014).

Plants found in harsh environments provide ideal models for exploring the parallel (*i.e.,* independent) evolution of traits responsible for adaptation and reproductive isolation (Levin, 2001), as well as parallel speciation (Ostevik et al., 2012; Rajakaruna & Whitton, 2004). Parallel (or repeated) evolution provides strong evidence for the role of ecology as a driver of divergence (Nosil, 2012). Levin (2001) suggests that repeated evolution of traits may not be unusual in taxa that have undergone ecological radiation, particularly in those taxa adapted to

environments posing strong divergent selection (*e.g.*, harsh environments). Contrary to these findings, Ostevik et al. (2012) note that there are few studies which show the repeated evolution of traits conferring adaptation and reproductive isolation, citing only 23 potential cases of parallel ecological speciation in plants. However, of the 23 cases they cite, 13 are from plants adapted to harsh edaphic (Brattler et al., 2006a; b; Mayer & Baseda, 2010; Nyberg Berglund et al., 2004; Rajakaruna et al., 2003; Westerbergh & Saura, 1992) or other extreme ecological settings (*e.g.,* dunes, alpine environments, etc.). This suggests that plants found in harsh environments are ideal models for examining the potential for repeated evolution of ecologically driven traits.

The potential evolutionary costs associated with endemism to harsh environments have been another area of recent research. Habitat specialists often appear to be less competitive (Anacker, 2014; Kay et al., 2011) and more susceptible to herbivory when found in "normal" habitats (Kay et al., 2011; Lau et al. 2008; Strauss & Boyd, 2011). To our knowledge, the evolutionary costs of habitat specialization relative to broad tolerance have not been compared using pairs of sister taxa found in such environments. Such information would help to address why some species become endemic to a particular habitat while others maintain genotypes that are able to tolerate wide-ranging habitat conditions.

In this modern era of genomics, we have many tools with which to explore the genetic basis of adaptation to harsh environments (Chapters 4-6, 9, 11; Brattler et al., 2006a; b; Turner et al., 2010; von Wettberg & Wright, 2011), including differences in the nature of adaptation to disparate habitats with similar abiotic stressors (*e.g.*, arid and saline habitats contributing to water stress, saline and serpentine soils contributing to ionic stress, or desert and alpine environments contributing to light and heat stress). The tools at our disposal can reveal the genetic architecture of adaptive traits which confer reproductive isolation (*i.e.,* speciation genes; Chapter 11; Nosil & Schluter, 2011), revealing new insights into the mechanisms by which natural selection can bring about reproductive isolation and speciation. As noted in Chapters 7 and 9, however, our model systems are not representative of all organisms or life history strategies, and we need to continue to add new model systems to allow comparative approaches to explore adaptive genetics.

Two evolutionary principles emerge from the chapters in this volume. One is that traits of organisms can "pre-adapt" them for particular stressors and may promote the evolution of new species or ecotypes in response to local environmental conditions (Chapters 2, 4-6, 9, 11). The other is that investigations of the genetic architecture of adaptation to stressors usually reveal multiple evolutionary origins (Chapters 4, 10). Several chapters (Chapters 4, 5, 9, 10) highlight the usefulness of phylogenetic approaches in explaining the timing and number of adaptive events related to particular stresses. As our phylogenetic understanding continues to be further resolved, these tools will give us improved information about how and when lineages have gained ability to tolerate these stresses. This, in turn, can push our understanding of adaptation deeper into evolutionary time and connect the origins of adaptive traits to other major events (*e.g.*, climatic, tectonic, or astronomic events) that have influenced Earth's biotic and abiotic history.

Whereas much attention has been paid to adaptation and evolution of vascular plants under harsh environmental conditions, it is critical that we continue to expand our knowledge of the diversity and evolution of under-studied groups such as cryptogams (Chapters 3, 12), microbes (Chapters 1, 2; Porter et al., 2011; Springer, 2009), and invertebrates (Chapters 7, 10; Wolf & Thorp, 2011) found in harsh environments, including the roles these organisms

may play in the evolution of stress tolerance (Chapter 2) and habitat specialization (Chapters 5, 7) in plants.

HARSH ENVIRONMENTS AS MODEL SETTINGS FOR STUDIES ON CONSERVATION AND RESTORATION

Harsh environments, characterized by extremes in chemical and physical factors, often harbor unique ecotypes, species, and communities (Chapters 2-5, 7, 10, 13, 14). Identifying and cataloging such unique biological elements are first steps toward their conservation (Jacobi et al., 2011; Wulff et al., 2013). Although harsh environments may be difficult for exotic species to colonize, exotics, when established, can create conservation problems in these habitats. Vallano et al. (2012) demonstrated that anthropogenic nitrogen deposition may promote invasion by exotics by increasing the fertility of serpentine soils, and thereby shifting competitive relationships to favor non-native species, particularly non-native annual grasses which have greater nitrogen use efficiency relative to many serpentine-adapted species. Similarly, nitrogen deposition has had drastic effects on native plant diversity in other harsh habitats, especially arid deserts in California (Schneider & Allen, 2012) and nutrient-poor bogs in New England, USA (Gotelli & Ellison, 2002). In addition to invasion by *non-adapted* exotics, sites with harsh soils such as serpentine (Chapter 6), gypsum (Chapter 5), metal-rich mine tailings (Chapter 14), and saline soils (Chapter 4) may be vulnerable to invasion by exotic species which are adapted to similar substrates in other regions of the world. Because they are adapted to extreme substrates within their native range, such species may be better able to colonize extreme habitats elsewhere relative to other non-adapted exotics. As such, adapted exotics may pose a greater threat to extreme habitats. This has caused much concern regarding the use of non-native species adapted to extreme geologies for the purposes of habitat restoration (Chapter 14; Gall & Rajakaruna, 2013; Ma et al., 2013), as well as for phytoremediation and phytomining operations (Chapter 15).

On a broader scale, extreme habitats also pose unique challenges for the management of protected areas (Chapter 14; Gordon et al., 2002; Thorne et al., 2011), including in the development of networks of protected land (*i.e.*, conservation networks) to effectively preserve biodiversity. Conservation networks are critical for protecting species that are restricted to habitat islands such as those formed by serpentine (Chapter 6), gypsum (Chapter 5), and limestone-derived soils (Clements et al., 2006), as well as to protect species found in other spatially isolated or fragmented habitats (Harrison, 2011) such as alpine summits (Chapter 7; Gordon et al., 2002). Although the importance of conservation networks is well known, the development and management of conservation networks requires tremendous coordination among stakeholders and acquisition of lands owned by a range of public and private parties, which may be a limiting factor in their development.

Climate change is a major challenge to the conservation of global biodiversity (*e.g.,* Bellard et al., 2012). The impacts of climate change on biodiversity may be disproportionately detrimental for species with geographically restricted or patchy distributions, such as species restricted to harsh environments (Chapter 13). As the climate changes, habitat for these species may migrate, be significantly altered, or disappear altogether. For example, low islands are vulnerable to sea level rise (Wetzel et al., 2013), and

polar regions are particularly susceptible to rising temperatures (Chapter 7; Gormezano & Rockwell, 2013). In alpine settings, upward movement of climate zones may drastically impact species, and in some cases, climate change may cause upper elevation zones to disappear entirely (Chapter 7; Beever et al., 2011). Dispersal ability may be a challenge for species restricted to extreme habitats if climate change causes such habitats to shift to areas where a species cannot disperse, or to areas where it cannot disperse rapidly enough (Chapters 7, 13). Damschen et al. (2012) used species distribution models to examine the risk of extinction for plant species endemic to serpentine outcrops and determined that many factors, including a species' dispersal ability and the geographic distribution of the suitable habitat, can affect this outcome (also see Chapter 7). In addition to affecting habitat distribution, climate change may also affect species interactions, particularly plant-pollinator mutualisms in fragmented habitats (Wolf & Thorp, 2011). Changes in the phenology of plant-pollinator mutualisms may lead to reduced fecundity and a gradual decline in populations. Studies of harsh environments have revealed the potential for rapid evolutionary change in plants on the order of decades to centuries (O'Dell & Rajakaruna, 2011); however, it is unclear how this potential for rapid evolutionary change may affect plant response to climate change. There is some evidence that plant communities on extreme soils change little in response to changes in climate; however, it is not clear how generalized this condition may be (Chapter 13).

Much research has been focused on ecologically appropriate restoration methods for extreme habitats (Chapter 14). Much of our understanding comes from the restoration of saline wetland habitats (*e.g.,* Zedler, 2000), which has resulted from the Clean Water Act and similar wetland protection laws in the United States and elsewhere, as well as from the reclamation of former mines and quarries (*e.g.,* Williams & Schuman, 1987), which has resulted from the Surface Mining Control and Reclamation Act and similar laws in the United States and elsewhere. Restoration efforts have focused on both single-species and ecosystem approaches as well as passive and resource-intensive approaches (Chapter 14). Methods range from low-tech to highly-engineered, including modification of soil physical and chemical properties, restoration of hydrologic regimes, slope engineering, landscape re-contouring, erosion control, and extensive planting (Chapter 14). Long-term monitoring studies and increased reporting of restoration outcomes are expanding our understanding of the restoration of these extreme habitats; however, data remain difficult to access, and disparate monitoring parameters and methods, as well as high variability in site characteristics and land use history, make it challenging to compare results and identify trends among restoration sites. The development of monitoring networks and international standards will make it easier to compare results among restoration sites and will make the data more useful.

Studies on the restoration of extreme habitats have highlighted the need to understand the nature of adaptation or habitat restriction to inform restoration methods (Chapters 11, 13, 14). We are only beginning to understand the role of mycorrhizae in plant establishment and survival in extreme environments, with some evidence that mycorrhizae may confer stress tolerance to their plant partners (Chapters 2, 5, 7). An improved understanding of mycorrhizal interactions in extreme environments is likely to improve the outcome of restoration efforts. Similarly, we have limited knowledge of plant-soil feedback loops and the potential responses of extremophiles to long-term changes in soil chemistry resulting from nitrogen deposition or other anthropogenic pollution (Chapters 13-15), making it difficult to identify appropriate restoration measures. More basic research on habitat function and plant response in extreme

environments is needed to develop better restoration approaches, particularly low-cost and environmentally-friendly approaches.

The limited availability of habitat and the patchy distribution of species restricted to extreme environments make them particularly vulnerable to anthropogenic impacts and highlights the importance of conserving such habitats (Chapters 13, 14). Reducing impacts of climate change and increasing the resiliency of plant communities restricted to extreme environments should be a focus of conservation efforts. Conservation networks will be a critical component in strategies to protect these patchily distributed habitats and to buffer them from the effects of climate change. A number of geobotanical preserves and other similar conservation efforts have been established globally (Rajakaruna & Boyd, 2008); however, more work is needed to improve the public's understanding of these botanically rich habitats and the need for their conservation.

The resource needs of our expanding human population continue to increase human impacts on all areas of the planet, including harsh environments that may have experienced little prior impact. Basic inventories of species are still needed in many harsh environments; this is illustrated in several chapters (*e.g.,* Chapters 2, 3, 5, 10) in which important gaps in our knowledge are discussed. Climate change poses a major challenge to life across the globe and increases the importance of conservation efforts that take climate change into account (Chapters 7, 13; Cowie, 2013). Unfortunately, we need improved tools for predicting the effects of climate change on biodiversity; Bellard et al. (2012) summarize the drawbacks of current techniques but conclude that most modeling approaches predict major negative effects on global biodiversity. An improved understanding of the mechanisms by which environmental stresses affect the distribution of species may aid in producing better climate change models and better management approaches for threatened species or communities (Chapter 7, 13-15). Harsh environments are often more easily damaged by human activities and are a unique restoration challenge due to the prevalence of abiotic stresses inherent to the site. As we obtain more complete species and population inventories of harsh environments and gain experience with restoration techniques, we will be better able to restore damaged areas and recover all or part of their former species composition and ecological function.

CONCLUSION

Harsh environments are important biological resources and represent some of the most promising frontiers in the study of ecology and evolution. They are important depositories for a significant portion of life's diversity, they illustrate how organisms respond to environmental challenges, and they provide resources important to both human society and other life on Earth. We can also learn much about basic biological, ecological, and evolutionary principles—including natural selection, adaptation, and coevolution—from studies that focus on plant and other life found in harsh habitats. This knowledge can be employed in numerous biotechnological applications beneficial to human society (*e.g.,* Chapters 11, 15; Agarwal et al., 2013; Peleg et al., 2011). This book builds on the current interest in plants and other organisms found in harsh environments (*e.g.,* Aroca, 2012; Horikoshi & Grant, 1998; Liebezeit et al., 2000; Lubzens et al., 2010; Lüttge et al., 2011) and

shows the importance of harsh environments to current and future research in all aspects of plant biology, ecology and evolution, and the conservation and restoration sciences.

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