I. Restoration Goals: Conservation and Biodiversity
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GLOSSARY

active restoration Requiring manipulation by humans for successful colonization and/or establishment of organisms and ecosystem functioning.

functional diversity Having all of the functions required for maintenance of ecosystem processes, but not necessarily all of the species richness.

functional redundancy, functional similarity Having species that may be substituted because their contributions to ecosystem processes are similar or overlapping.

passive restoration Relying on natural successional processes for restoration after the stresses that caused the disturbance have been removed.

reclamation A revegetation or land management goal that includes a lower diversity of species and may include substitutions by introduced species.

reference area An undisturbed or natural area chosen to compare with a restored site to determine the success of restoration.

rehabilitation Creation of an alternative ecosystem following a disturbance, different from the original and having utilitarian rather than conservation values.

restoration The manipulation of organisms and ecological processes to create self-organizing ecosystems that resemble predisturbance structure and functioning and promote conservation of biodiversity.

CONSERVATION OF BIODIVERSITY is the central goal of most restoration efforts and ranges from reintroductions of individual species of rare plants and animals to efforts to reintroduce a high diversity of species. Restoration may be defined as the manipulation of organisms and ecological processes to create self-organizing, sustainable, native ecosystems as integral parts of the landscape, as much as possible as they existed before disruptive human disturbances. In this article, we will examine the possibilities and the limits to restoration of biodiversity.

I. RESTORATION GOALS: CONSERVATION AND BIODIVERSITY

Conservation of biodiversity is the central goal of most restoration efforts and ranges from reintroductions of
individual species of rare plants and animals to efforts to reintroduce a high diversity of species (Jordan et al., 1987, 1988; Bowles and Whelan, 1994; Falk et al., 1996). Restoration may be defined as the manipulation of organisms and ecological processes to create self-organizing, sustainable, native ecosystems as integral parts of the landscape, as much as possible as they existed before disruptive human disturbances. Where propagules of native organisms are remnant, restoration may require reintroducing ecosystem functions such as fire or hydrologic regime to enable natural recolonization and recovery processes. Re-creation of a close replica of a previously existing ecosystem type is increasingly difficult in a world with a growing human population, considering fragmentation and limits to dispersal of organisms; global invasions of exotic species that cause large-scale replacement and even extinction of native species; air, water, and soil eutrophication; and habitat loss by land conversion to urbanization and agriculture. Even nature reserves and parks suffer from visitor overutilization and other impacts, and restoration coupled with more careful management is required to preserve the original flora and fauna.

There are limits to restoration whether biodiversity or functioning of the ecosystem is concerned, but restoring all of the species richness that was originally present on a site is usually more difficult than restoring similar functioning. The reasons are that many rare species are difficult to propagate, their basic biology has often not been studied, they have lost genetic diversity, and their propagules are limited due to habitat loss. They are also less likely to be chosen for many kinds of restoration because they are more expensive to reintroduce and they contribute relatively little as individual species to ecosystem functioning. On the other hand, abundant species are generally better known ecologically, and in some cases, individual abundant species will regulate ecosystem functioning. Restorationists more often focus on reintroducing the abundant plant species or the "matrix" species to imitate succession and recovery of disturbed lands. Reintroducing dominant species enables a recovery of major functions and most of the vegetation vertical and horizontal structure. For instance, John Ewel showed that low-diversity replanted (but not restored) tropical forest in Costa Rica may have similar levels of soil nutrients, organic matter, and nutrient loss, compared to natural forest, but will not have the same conservation value for species preservation.

Additional limits to restoration of diversity are economic, political, and social. Restoration for the intrinsic value of nature, with its complement of biodiversity, often includes participation by laypersons who wish to see nature returned to a state they remember from years ago or that was documented in historical texts or anecdotally. Lesser goals than restoration include reclamation or rehabilitation (National Academy of Sciences, 1974), which have utilitarian values and less emphasis on conservation and biodiversity values. Reclamation may include a less diverse mix of species and exotic substitutions, while rehabilitation is simply to make the land useful again and may produce an alternative ecosystem, such as turning a forest into a pasture.

In this article, we will examine the possibilities and the limits to restoration of biodiversity. Different species have different limits and require different approaches for restoration. We divide the discussion into restoration of plants, animals, and soil microorganisms. This is admittedly an overly simplistic approach, as they all interact. However, points of overlap among the groups are brought out numerous times within each section. The division is logical in that the three groups require different degrees of active or passive restoration, depending on the level of disturbance of a site (Fig. 1). The kinds of disturbances that require restoration are varied. They range from drastic alteration of the ecosystem, such as surface mining or other construction projects that remove the topsoil; to abandonment from agriculture that leaves soil intact but depletes native biodiversity; to alteration of certain ecosystem functions such as fire cycle or hydrologic regime; to extirpation of individual species with no other associated impacts to the physical habitat. Plant introduction and management are central to restoration projects where disturbance has caused vegetation removal or weed invasion. Where plant propagules remain or are readily dispersed, as after abandonment from agriculture in the northeastern United States, passive restoration may suffice. For animals, habitat may be created by manipulating the structure of the plant community, with the hope that the animals will recolonize. This has come to be called the "build it and they will come" hypothesis (see article by Palmer et al. in Restoration Ecology, Vol. 5, 1997). However, recolonization may be restricted by fragmentation, lack of corridors, or lack of propagules, so reintroduction of the animal into restored or intact vegetation may be needed.

For microorganisms, passive restoration is generally the rule in contrast to higher organisms that may be purposefully reintroduced. Very few species of microorganisms that are members of natural ecosystems are
cultured, so they are not even available for restoration purposes. The exceptions are symbions (N-fixing bacteria, mycorrhizae) that are used routinely in agriculture and reforestation, but less often in restoration. All the other taxa that contribute to belowground functioning of native ecosystems are never or rarely cultured, including soil saprotrophic fungi, bacteria, nematodes, and other soil micro- and mesofauna. For all of these groups, we must learn how to manage the soil to promote their recolonization and to understand the distances from which they may be able to recolonize. In addition, there may be 1000's of species of microorganisms even in 1 cm³ of soil. So the argument must be made whether all these species can or should be reintroduced. Many ecologists argue that there is functional redundancy among so many microbial species and that a minimum number of functional groups rather than a minimum number of species are required for restoration of ecosystem functioning.

The goals for restoration may vary for these three groups of organisms. For plants and animals, species diversity concerns are high, but for soil microorganisms, functional diversity is more often expressed as the concern. The limits and possibilities for restoration of diversity vary for the three groups, and the discussion below will expand upon these topics.

II. RESTORING A DIVERSE PLANT COMMUNITY

To improve plant species diversity, the kind of revegetation or vegetation management is determined by the degree of disturbance. These form a gradient of disturbance types and recovery possibilities that require the entire range of active to passive restoration. Heavily disturbed sites such as surface mines need to have all
species reintroduced, whereas slightly disturbed sites may be missing certain species that are not adapted to the new postdisturbance conditions, such as alteration of fire regime. Other sites may require weed control to increase native species diversity. There are no examples of severely disturbed sites that have been restored to their original complement of species. This may be related to the high costs involved, the changed environmental conditions, and the sheer impossibility of artificially reintroducing a large number of species. As richness increases in more productive habitats, the probability of reintroducing even a majority of the species diminishes. One of the best examples of attempts to restore a diversity of species comes from bauxite mining in southwestern Australia, where 80 species or more may be included in the seed mix. However, the adjacent undisturbed jarrah (Eucalyptus marginata) forest may contain more than 200 species. In Wyoming sagebrush-grasslands, mining reclamation regulations are not as strict, and typically only 5–10 native species are planted in an area that may have 50 or more naturally occurring (Fig. 2). The dominant rather than the rare species are typically chosen for revegetation, and the long “tail” of rare species that typifies a dominance-diversity curve for natural areas is missing (Fig. 2). Reclamation and restoration both generally create com-

FIGURE 2  Dominance–diversity curves for reclaimed and natural vegetation in Wyoming sagebrush-grassland. The long tail of inabundant species found in natural vegetation is seldom reestablished in revegetated areas.
munities of a few abundant species but few rare species, whereas undisturbed communities may have the same few abundant species, but in addition will have many rare species.

A. Limits to Restoring a Diverse Plant Community

The reasons for omitting the many species that form the rare species tail in Fig. 2 are many. Seeds or other propagules must be collected locally for the restoration to reflect the local genetic populations, but these are typically not available unless the project is planned well in advance, usually two growing seasons, and the seeds are collected specifically for that project. Collecting native seed is becoming a large industry but it is unusual to have all the species available on the open market at the time they are needed, and even rarer to have the seed collections from local populations (see chapters in Falk et al., 1996).

Loss of genetic diversity and lack of local ecotypes are also a limitation to restoration. Where local extirpations have occurred, the nearest populations may no longer have all the genetic diversity of the original, and restoration in the true sense of restoring genetic as well as species diversity is no longer possible. Locally selected ecotypes have the “home team advantage” of being better adapted to local conditions and also avoid problems of outcrossing and hybrid depression with remnant native adapted to local conditions and also avoid problems of outcrossing and hybrid depression with remnant native individuals (see article by Montalvo et al. in Restoration Ecology, Vol. 5, 1997). Additional discussion of genetic issues is in the section on animal restoration.

One of the appropriate local seeds or propagules have been collected, there is little information on seed dormancy and propagation of most species. The emphasis on conservation biology in the past decade has resulted in increased concern for research on rare species, and information on propagation, microenvironment requirements, reasons for disappearance, interactions with pollinators and other species, and so forth have enabled restorationists to include rare species in revegetation plans. More often, restorationists work with relatively unknown species and must begin research anew for each species, as, for example, the work on restoring the endangered Amsinckia grandiflora (see chapter by Pavlik in Falk et al., 1996). Lack of biological information on species translates into practical economic limitations. Most often, only the species that are best understood with the most available propagules are used.

Once germination and propagation requirements are understood, the plants must go into a field setting that presents a whole new set of problems. Different species germinate at different times and have different growth rates, so some will never emerge from certain seed mixes. The northern Great Plains of the United States are dominated by Bouteloua gracilis in the coal mining regions, but this has proven to be one of the most difficult species to reestablish for mining reclamation. It is a slow-growing, late-germinating, warm-season grass, but when it is seeded as part of a mix of native species, the cool-season grasses germinate first, grow quickly, and dominate. Reclamationists have devised numerous methods to reestablish shortgrass prairie, such as alternating seed drill rows or planting Bouteloua seeds a year earlier. However, the most important consideration for companies that have spent millions of dollars on earth-moving is to stabilize the soil, rather than to establish high levels of diversity that are not required by law in any case. Preventing soil erosion is the first goal, and the mines of this region use a fast-growing native plant mix that reduces the establishment of slow-growing species. The goals of soil stabilization using productive plant species and establishing a diverse mixture are often at odds (Fig. 3).

Reestablishing the full complement of species may require reintroduction in stages, as shown in examples from the tallgrass prairie. When Robert Betz began prairie restoration in the late 1960s at the Fermi Lab prairie in Illinois, he quickly learned that the dominant native grasses could be readily established from seed. He used the grasses to form the matrix of vegetation, followed by later introductions of the less common forbs. These forbs could not colonize naturally into the restored grassland because of the high density of grasses, but could be hand planted. Thus Betz was able to restore 116 plant species to the Fermi Lab prairie, but only by expensive hand labor. Similarly, the Curtis Prairie in Wisconsin, the oldest restored prairie, was initially planted during the 1930s, but plants have been continually introduced since then (see chapter by Cottam in Jordan et al., 1987). Their survival has been monitored, and they now contribute to the most diverse tallgrass prairie anywhere. The Curtis Prairie has over 300 species in 10 acres, more than any remnant natural prairie.

Competition from invasive plant species is another important limit to restoration of diversity. The invasives may be weeds that are part of the successional process, but a more difficult problem than early seral weeds are those invasive plant species that persist and cause vegetation type conversions. In this case, the major restoration activities involve mowing, fire, or selective weed control to remove the offensive species, planting or managing for regrowth of natives, and then continual management to keep the invasives from becoming dom-
FIGURE 3. The relationships among soil fertilizer level, plant species richness, plant productivity, and soil erosion. The trade-off for using fertilizer to promote high initial rates of plant productivity to reduce soil erosion is a loss in diversity.

B. Improving Plant Species Diversity

Restorationists have used many techniques to increase richness of plant communities when the seed and propagule sources are limiting. Taking advantage of the existing seedbank is a primary one, where the seedbank still exists. Mined land reclamation laws in developed nations often require retopsoiling with fresh topsoil, and many studies document the importance of this source. Certain species still need to be supplemented, as in the case of late seral species absent from the seedbank of jarrah forest in southwestern Australia (see chapter by Bell in Allen, 1988). Jarrah seed is never found in the seedbank, and it reproduces vegetatively after fire in natural communities. It must be reintroduced as nursery transplants for revegetation to be successful. While the seedbank is an important source of diversity in many kinds of restorations, it is also notorious for harboring a large complement of early successional and weedy species. Bradshaw and Chadwick...
Dispersal of propagules into the restored site is another way to increase diversity that depends upon landscape structure such as proximity of source populations or existence of corridors. In a study of 2- to 18-year-old revegetated, untopsoiled roadsides in San Diego County, dispersal from adjacent mediterranean shrubland more than doubled the richness from 12 planted species to a maximum of 16 colonizing native species. However, dispersal of native species only occurred when the shrublands were adjacent to the highway, and occurred rarely in urban areas of the highway. Reclaimed surface mines in Wyoming that are surrounded by native sagebrush–grassland have a higher richness of colonizing species than, for instance, a revegetated landfill in Staten Island that is surrounded by subrubia (see articles by Bell and by Ehrenfeld in Restoration Ecology, Vol. 5, 1997). While dispersal is often limited by vectors in terrestrial habitats, aquatic and riparian habitats typically are recolonized rapidly (National Academy of Sciences, 1992). Water is a very effective medium for propagule dispersal, and these habitats are often not even revegetated, unless the soil needs to be stabilized rapidly in riparian edges or the dispersing propagule include unwanted exotic species.

Vegetation may be replanted to attract animals that are seed dispersers or pollinators and thus may create a positive feedback on the future reproduction and diversity of a site. When a limited suite of species is chosen, the selected species become especially critical. Synthetic grasslands that simulated tallgrass prairie had sufficient diversity and especially structure to attract birds and small mammals (Howe and Brown, 1999). Shrub islands were planted on a surface mine in Wyoming to increase the movement of animals and microorganisms onto a site that was otherwise dominated by grasses (Allen, 1988). The feedback of these shrub species and patterns determined both their mortality and recolonization patterns of additional plant species. In Costa Rica, Karen Holl and Daniel Janzen have shown that tree and shrub “islands” within pastures are critical for attracting animals that disperse seeds and then increase the diversity of the plant community.

C. Single-Species Plant Introductions

Individual plant species have been reintroduced where they were extirpated, largely because of laws protecting endangered species. Mitigation laws often require transplantation of a rare species from a site that is about to be destroyed to a safe site. For instance, Howald (see chapter in Falk et al., 1996) documents 40 instances where rare species were transplanted for habitat mitigation purposes in California. Of these, only 9 were considered successful, 7 had limited success, 13 were not successful, and others were unknown or ongoing and too recent to evaluate. The reasons for lack of success were varied but included moving plants to sites where they did not exist previously, having different environmental conditions in the transplant site, or using poor horticultural techniques. Primack (chapter in Falk et al., 1996) planted seeds of 41 species into sites in Massachusetts where they were once known to occur. Of these, only 10 produced seedlings, and only three produced a second generation. In this study, the reasons for failure may have been due to exotic species, changes in natural disturbance regime, and other changes such as anthropogenic nitrogen deposition that causes inappropriately high levels of soil fertility. The relatively few successful transplantations indicate that mitigation transplantation in general is poor policy because the kind of planning and postintroduction management that are required is seldom done in practice. Often little consideration is given to the quality of the habitat into which organisms are being reintroduced. Overall, the reintroduction of one species does little to improve the diversity of a site, but it may be the only option to avoid extinction, provided restorationists and land managers use their best practices.

While many single-species introductions focus on rare species, they may alternatively focus on abundant species. The reintroduction of a keystone species or ecosystem engineer (see Palmer et al. in Restoration Ecology, Vol. 5, 1997) is one way to “jump start” natural successional processes in a community. Shrubs and trees were removed from rangelands for many years in an effort to increase forage production for domestic animals, but this was short-lived and in the long run promoted degradation of the community because the deep-rooted shrubs changed the nutrient and moisture balance of the entire stand. The reintroductions of Pistacia lentiscus in Israel, oak trees in California, or Artemisia tridentata in mined lands in Wyoming enable the shrub or tree island effect to reinitiate, building up soil and biotic resources around the transplanted shrub (Allen, 1988). This could potentially result in further increases in diversity as the shrubs enable recolonization of additional species.

D. Succession on Restored Lands

Restoration depends upon succession to complete the process that was started by revegetation, but succession alone does not always bring us to the goal we wish to
achieve. Revegetated lands are not static and can be expected to undergo change in species density, richness, and relative composition. The degree to which they undergo succession varies, depending upon the amount of colonization, initial species complement, and site conditions. Little change in species composition occurred after bauxite mining in the Australian jarrah forest. The site typified Egler's initial floristics model of succession, where late seral dominants colonize in the earliest stages of succession, because very few species that did not occur in the original seed mix became dominant later on. Sites that were 10 years old appeared structurally different from sites that were 1–2 years old in that woody plants were larger and more evident in the older sites, but most of the same species were present in sites of all age classes. A few surprising species did colonize the older sites, such as a native orchid. In Anthony Bradshaw's experiments on plants colonizing industrial waste heaps in England, most plants that did not establish appeared to be limited by dispersal and establishment, rather than poor substrate. The sites were too distant from propagule sources or had dense stands of initially colonizing species that prevented establishment of a diversity of species. The initial floristics model can also be applied to Wyoming, Pennsylvania, and Czech surface mined lands, where the native grasses that dominated early on allowed little colonization of native trees, shrubs, or forbs after 10–30 years. Even when soil conditions are optimal and sources of propagules for local colonization are available, the initial revegetation treatments will affect long-term successional processes, as shown by recent studies in the journal Restoration Ecology. A 30-year-old planted forest that had been severely disturbed by hydroelectric development in New Zealand showed little change over time when 46 native species were planted. The species composition was chosen to resemble the dominants during secondary succession after fire in natural forest, but had only a fraction of the total diversity. However, an even less diverse stand developed when no vegetation was planted, consisting of a stand of exotic Citrus scoparius and European grasses. A comparison of planted forest stands on bauxite mines in Brazilian tropical forest showed that planting a low-diversity commercial mix resulted in a low-diversity, but high-productivity forest, while seeding and planting mixtures of 70 or more species promoted a diverse, but less productive forest. In all cases, colonization of certain late successional forest species that were not part of the original mix was poor. An interesting contrast comes from the Arctic on the North Slope in Alaska, where more than 100 species of native plants colonized 20 years after planting two native and one exotic grass species over a dozen sites. Thus the productivity and species richness of the initial planted stand will make a large difference in the ability of other species to colonize later. From these examples, and many others in the literature, it is apparent that succession may promote an increase in richness if the planted stand is not so aggressive that it precludes establishment of colonizers. Most often, additional interventions are needed if the desired diversity is to be achieved.

III. RESTORING ANIMAL DIVERSITY

A. An Introduction to Animal Restoration

Like plant restoration, animal restoration involves introducing or encouraging the return of native species to an area or region from which they have been lost. An animal restoration project may involve just a single species, as in the reintroduction of wolves into Yellowstone National Park, or an entire community, as in Augrabies Falls National Park in South Africa, where over 10 species of large mammals have been reintroduced (including black rhinoceros, eland, giraffe, and springbok).

Animal and plant restorations will generally involve the same ecological considerations, and most differences between the two concern a matter of degree and emphasis (Jordan et al., 1988). Save for insects (which represent a challenging form of restoration more in line with promoting microbial diversity), plant restorations generally call for a larger number of species. In terms of ecosystem function, animals have significant roles in restoration as pollinators and herbivores of the plants. Animal roles in ecosystem function also occur when herbivores alter nutrient cycles and where animals may be "ecological engineers" of the physical environment, such as the contributions to soil function from the digging and foraging activities of earthworms or burrowing mammals (Jordan et al., 1987). In general, animals are more mobile than plants and while plants may disperse widely and unexpectedly as seeds and pollen, a single animal may range over scales that are much larger than that of the restoration project and site. Some of John Laundre's radiocollared mountain lions from south central Idaho have appeared as far away as Yellowstone National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in Augrabies Falls National Park, or an entire community, as in August
The ecology of animal restoration draws less heavily from theories of ecological succession and more from the ecology of invasions and the ecology of small population sizes (Major, 1989). Plant restorations, as succession, start with an inoculum of plants that initiate a process of changes in species composition that eventually leads to the desired natural community in terms of structure, function, and appearance. This aspect of succession is absent from most animal restorations except in the case of the mostly passive development of an insect and soil invertebrate community that fits and complements the plant community. With most animal restorations, each species enters the community at a very small population size either as an invader or as a reintroduction. Small and alien describes the starting population. Most random introductions of animals to a community fail. Native animals fail to predators more easily, compete less successfully for resources, often fail to develop or find suitable denning or nesting sites, and sometimes attempt to emigrate from the site. In the absence of preexisting burrows, reintroduced prairie dogs simply roam far and wide in search of colonies. Small animal populations face twin genetic and demographic threats. Small, sexually reproducing populations may suffer inbreeding depression and produce a higher proportion of young with genetic defects. Demographically, small populations may teeter on the edge of extinction. An accidental death, a missed breeding opportunity, or a chance skewing of sex ratios or age distributions may compromise the population irrecoverably.

Animal restoration begins with knowledge of why the species or animal community is currently absent or threatened at the site. Next comes an assessment of whether the site is currently suitable for the animals and an evaluation of what site preparations are necessary to promote success. Then the current status of the animals receives attention to determine the best and likeliest sources of individuals. The animal(s) may be present on site but at low numbers, they may be present near the site or far from the site, or they may only exist as captive populations. Finally, the passive or active restoration of the animals begins with appropriate considerations of how to manage and monitor the project’s success. We will briefly examine each of these steps.

### B. Reasons for the Absence of an Animal or Animal Community from a Site or Region

Habitat fragmentation or changes in land use may reduce or eliminate particular animal species, subsets of species, or entire taxonomic groups of animals from an area. For instance, most animals associate with particular types and structures of vegetation. When altered, by livestock grazing or agriculture for instance, some of the original animals disappear as they cannot find food, nesting, or denning sites or they may be excluded by changing intensities of competition or predation from other animals more suited to the new circumstances. In rivers and lakes, pollution, erosion, and sedimentation drastically change species composition. Everything from invertebrate larvae to fish may die off or be replaced by other species more tolerant of the polluted or modified waterways.

Hunting, poaching, and commercial harvesting may be so intense as to extirpate an animal or group of animals from an area or region. The African gray parrot and South American macaws face threats from those supplying the demand for pets. Accidental mortality in fishing nets threatens many of the world’s populations and species of sea turtle. Overharvest of commercially valuable species has created a litany of crashes such as California sardine, North Sea herring, blue whales, kaluga sturgeon, and southern bluefin tuna. As a valuable source of meat and a denizen of potential rangeland and farmland, the pronghorn antelope of the western half of the United States, like the American bison, faced extirpation by the 1900s.

Exotic species, those species accidentally or intentionally transported by humans into new places, often eliminate native animals via predation, competition, or keystone effects on structure and function of the ecosystem. The introduction of mosquitoes into Hawaii brought bird malaria for which the birds were no more prepared for than the peoples of the Americas were for the introduction of smallpox from Europe. An inoculum of larvae in ship ballast introduced zebra mussels from Europe into the Great Lakes of North America. In the early 1990s, the mussel's spread was spectacular, and with it has come dramatic declines in the abundances of phytoplankton and the fish and invertebrates relying on the phytoplankton. Competition from introduced North American gray squirrels has eliminated the native European red squirrel from much of its former range in England and Wales.

With respect to restoring their wildlife, Australia and Israel provide interesting contrasts. Both have seen their native mammals ravaged. In Israel this has gone on dramatically for millennia whereas it is more recent in Australia. In Israel, overexploitation and habitat modification have been the bane of most animals like lions and crocodiles, both extirpated long ago. Deforestation, reaching its nadir under the Turks just prior to World War I, nearly extirpated the subspecies of European...
The site is cur-
term hopes include first restoring the tallgrass prairie
At Midewin National Grassland south of Chicago, long-
grated, animal restoration may await plant restoration.
If the vegetation of a site has been heavily de-
tation. If conditions are not appropriate,
appropriate combination of food, safety, shelter, and
space for a small population of animals to grow expo-
site assessment evaluates whether the area offers an
in the late 1980s included too small a population (de-
the aquatic and surrounding vegetation and then pas-
sively or actively reintroducing the associated aquatic
vultures, and eagles.
The California condor provides an illustration of a
complex site assessment. Reasons for the decline of
condors that culminated in their removal from the wild
in the late 1980s included too small a population (de-
mographic threats), habitat fragmentation, lack of car-
casses, and lead poisoning from carcasses containing
the site is cur-
red squirrel and jay from Israel's wooded habitats. In
Australia, wildlife habitat is much more available and
overexploitation generally more benign than in the Mid-
sarily and prosper. If conditions are not appropriate,
that might currently or ultimately limit the growth and
the categories of habitat change, overexploitation, or
exclusion by animal species nonnative to the particular
location. Understanding the reason for the absence of
an animal or community of animals is the essential
starting point for animal restoration.

C. Site Assessment and Habitat Restoration
All species have the capacity to grow exponentially
under ideal conditions, but no population can grow
exponentially forever. There are limits to growth, and
population interactions such as competition and predation
from other species can exclude a species from a
community. The goal of site assessment and habitat
restoration is to ensure near ideal conditions for the
single species or the community of animals under resto-
ration. Ideal conditions means ample food, space, shel-
ter, and safety from predation. Limits to growth invites
a consideration of specific factors in the environment
that might currently or ultimately limit the growth and
size of the animal's population. Considerations of com-
petition and predation focus on which current species
at the site, possibly exotic species, might preclude a
successful introduction of the desired species to the site.
Site assessment evaluates whether the area offers an
appropriate combination of food, safety, shelter, and
space for a small population of animals to grow expo-
mentally and prosper. If conditions are not appropriate,
then habitat restoration must precede animal restora-
tion. If the vegetation of a site has been heavily de-
graded, animal restoration may await plant restoration.
At Midewin National Grassland south of Chicago, long-
term hopes include first restoring the tallgrass prairie
and then reintroducing elk and bison. The site is cur-
rently a mix of abandoned munitions facilities, farm
fields, pastures and assorted oldfields, woodland, and
groves. Wetland restorations often require establishing
the aquatic and surrounding vegetation and then pas-
sively or actively reintroducing waterfowl, egrets, or
herons), and fish (sometimes passive or active). Different
species have different needs, and reconstructing those habitats
that fill an animal's needs is central to attracting wildlife
or to introducing wildlife.
The possible reasons for the animals' absence from
a site focuses site assessment. Often several factors com-
bine to explain an animal's absence. When habitat alter-
ation or fragmentation changes and reduces the diver-
sity of animals, the first step is to determine whether
the site has been, or needs to be, revegetated to its
former state. This condition of the site does not have
to be exact with respect to its former state, but rather
it need only include the salient environmental factors
that favor the animal's ecological requirements and apti-
tudes. For instance, many bird species are most respon-
sive to the structure rather than the exact composition
of the vegetation. Hence, bird community restoration
can commence with promoting the appropriate vegeta-
tion structure rather than being particular to its compo-
sition (which may be the goal of a corresponding plant
restoration). Habitat fragmentation offers unique chal-
lenges because the remaining area may simply be too
small to successfully support the desired animal or ani-
mal communities. The site assessment may examine
the need for more space or wildlife easements, the need
for corridors to connect habitat fragments, or the need
to enhance the quality of a habitat fragment beyond its
natural state to permit the successful persistence of
animals in a smaller, more confined space. At Jackson
Hole, Wyoming, a wintering elk population is main-
tained on supplemental hay within a fenced pasture
surrounded by the extensive human developments that
have robbed the elk of most of their wintering habitat.
In spring, the elk return to their natural mountain pas-
tures. In Israel and elsewhere, feeding stations stocked
with animal carcasses or offal have been used to facili-
tate the maintenance and restoration of such animals
as wolves, griffon vultures, and eagles.

The California condor provides an illustration of a
complex site assessment. Reasons for the decline of
condors that culminated in their removal from the wild
in the late 1980s included too small a population (de-
mographic threats), habitat fragmentation, lack of car-
casses, and lead poisoning from carcasses containing
lead shot or bullets. The restoration plan called for captive breeding, gazetting of habitat and habitat corridors, restrictions on development, and for reasons beyond just the condor, the banning of lead shot for hunting. The actual restoration took several approaches to evaluating the complexities of habitat suitability and the ability to introduce a small population of naive animals. First, less rare Andean condors were introduced as a surrogate species. They permitted tests of the reintroduction techniques and indicators of ranging patterns and habitat suitability. The actual reintroductions have used the original site north of Los Angeles but also additional sites, including one near the Grand Canyon. The California release site has more recently had condors but suffers much greater degrees of habitat fragmentation and development. The alternative sites have seen condors less recently, but have the advantage of offering extensive tracts of original and natural habitat.

In response to habitat degradation or fragmentation, habitat restoration may be as simple as adding nest boxes, as in the case of bluebirds at some sites in northern Illinois, or as involved as adding proper soil, microbes, and restoring an entire vegetation community, as in the case of toxic waste sites or former mining operations. Ceasing the use of pesticides or release of pollutants may be all that is necessary to restore a habitat. Peregrine falcons in North America have benefited from the ban on DDT. Portions of fish communities and whole invertebrate communities can recover just from preventing sewage and pollution discharges into waterways. The structure of the environment with respect to shrub cover in arid lands, the mixture of ages and types of trees in forests, and the availability of salt licks and waterholes for wildlife all become considerations for particular habitat restorations. Koala in Australia require particular species of eucalyptus trees as food, whereas gravel beds at particular depths provide spawning grounds for trout of the Great Lakes.

When a species absence is the consequence of overexploitation, success often depends less on the availability of suitable habitat and more on the cessation of hunting, poisoning (including mortality from hazardous chemicals and pollutants), harvesting, or poaching. Wolves were exterminated throughout the western half of the United States through individual hunting and trapping and by explicit eradication programs. Their reintroductions into Yellowstone National Park, Wyoming, and the White Mountains of Arizona involve presumably moderate to high quality habitat. The success of the programs probably depends most on the cessation of poaching, which at present is a minor problem for Yellowstone and a major threat to the Arizona reintroduction. In 1989, it was discovered that stock assessments of cod within the Canadian North Atlantic were wildly optimistic. The stock had crashed. Subsequent quotas followed from the premise that habitat quality remains high and that reduced harvest will be sufficient to promote recovery. In Southeast Asia, edible-nest swiftlets face decline and extirpation. The birds nest in caves, use saliva for nest building, and face true “nest predation.” Humans gather the nests even as the nests may have eggs or nestlings. Even with complete bans on nest harvesting, places like Sarawak, Malaysia, still face intense nest destruction from local people, pirates from countries such as Indonesia, and organized collecting groups. Policing thousands of cave entrances in often remote places throughout the country is impractical. But, until poaching relaxes or ceases, restoration and recovery cannot be achieved. Having reduced poaching of black rhinoceros throughout the 1980s, the Kenyan Wildlife Service has begun the recovery and restoration of current and former populations.

Habitat restoration for overexploited species requires the first step of controlling the harvesting. However, the absence of wildlife from an area may coincide with other changes to the habitat, some which at first may seem subtle. “Nature abhors a vacuum” is a saying recognizing that unused food or opportunities in an environment often become filled by alternative species or by exotics. Habitat restoration may require controlling the abundance of exotic species or those species that compete or prey. Factors contributing to the decline of red squirrels in England include an increase in oaks and a decline in conifers. Both factors assist the exotic gray squirrel in outcompeting the red squirrel. Habitat restoration may require both changes in forest composition and active control measures of gray squirrels. The draining of reservoirs, netting, or poisoning of lakes infested with exotic fish such as carp has preceded several fish restorations in North America.

D. Sources of Animals for Restorations

Small remnant populations, dispersal from other areas, or active reintroductions provide the sources for animal restorations. Ideally, animal restoration should begin while a remnant population still occupies the site. Such a population, while often small, has the advantages of already being established and acclimated to the site. This avoids problems associated with naïve animals unfamiliar with the site. In general, once habitat restoration has assured a quality site, resident populations recover faster than immigrants from other areas, which
animals are relatively cheap and available, the reintroduction population should have the appropriate balance of sexes and age classes and that the animals are prepared for the new environment. When a restoration relies on immigrants, there are the twin concerns of: “Is the site suitable for the establishment of immigrants?” and “Will the immigrants find the site?” When a site such as an oldfield, mine tailings, or forest clearcut is restored, there will usually be successful invasions of insects, soil invertebrates, aquatic invertebrates, mammals, and birds from the environs. For instance, in an oldfield subject to small experimental prairie restorations (Howe and Brown, 1999), there was an invasion of two small mammals (prairie vole and white-footed mouse) and some red-winged blackbirds have shifted their breeding from a nearby pond to the prairie plots. Mourning doves preferentially feed on rather than off of the prairies. Invasions of insects, birds, and mammals ease the restoration effort but sacrifice complete control of the resulting composition of animals. Species that are already well established and abundant in the region of a restoration are the most likely invaders. Rare and remote species are the least likely. Target species may require coaxing in the form of habitat corridors connecting the restoration site with existing populations. Temporary augmentation with food or nesting boxes can encourage reestablishment. In Tsavo West National Park, Kenya, rhinos have been corralled into a sanctuary (ca. 70 km²) that is much smaller than the whole park (ca. 9000 km²). The sanctuary is fenced to keep the rhinos in, patrolled to protect the animals from poaching, and supplied with piped water to maintain permanent water holes.

Animal restoration may require the active reintroduction of animals (Bowles et al., 1994). This is best done by translocating individuals from wild populations, but may require captive breeding. Wild populations provide experienced individuals, whereas captive animals may be particularly naive and unfamiliar with the wild. The reintroduction population should have the appropriate balance of sexes and age classes and sufficient genetic diversity to preclude serious consequences of inbreeding. When the reintroduction is very expensive, it is politically sensitive, or is from a very small source population, great care goes into ensuring that the site offers close to ideal conditions and that the animals are prepared for the new environment. When animals are relatively cheap and available, the reintroductions can be more numerous and there is room for experimentation. Wild asses (onagers) in the Negev Desert of Israel, pronghorn antelope in Arizona, lynx in Switzerland, white rhinoceros in Lake Nakuru of Kenya, and peregrine falcons in various midwestern cities all provide examples of reintroductions from captive or wild source populations. In the case of the Guam rail, this bird had been driven extinct on Guam by the introduction of the brown tree snake. Rather than attempting the impossible task of eradicating the snakes on Guam, the rail has been reintroduced on a neighboring, snake-free island.

IV. PROMOTING MICROBIAL DIVERSITY

A. Microbial Diversity and Functional Redundancy

Compared to plants and animals, microorganisms are highly diverse and offer a special challenge to understanding biodiversity and to assuring successful restoration. Microbes should be the underpinnings of any discussion of biodiversity as they constitute the vast majority of the diversity of any ecosystem at any location, yet are rarely even mentioned in terms of maintaining diversity. Microbes should be a focus, not an afterthought, for restoring disturbed lands. Without animals and most species of plants, ecosystems would stabilize and most ecosystem functions would be performed. Without microbes, the ecosystem would cease to function.

Estimates of microbial diversity range up to $10^9$ prokaryotic taxa per gram of soil, although $10^5$ is generally a more accepted value. In a study of restoration of a Wyoming coal surface mine, 57 different fungal taxa were found out of 135 colonies randomly chosen from approximately 12,500 colony sources (spores, hyphal fragments, bits of organic matter). These taxa were evaluated within a 4-cm² area (using 5 g of soil). Given the numbers, it is not surprising that a large fraction of these organisms remain undescribed. Recent estimates suggest that less than 10% of soil organisms ranging from bacteria to spiders have been described. And, a few efforts that extracted DNA directly from soils have even found new kingdoms of prokaryotes. Despite the difficulty in estimating diversity, every study published has shown a loss in the richness of taxa with severe disturbance. This ranges from soils in the Pumice Plains of Mount St. Helens, which was sterilized, to burned areas in which only the aboveground material and soil...
surface were directly affected. Because of the extremely high microbial diversity, the concept of microbial functional redundancy has been raised. Among those thousands of species, how many need to be restored to maintain ecosystem functions? This is the single largest challenge for studying soil microbes and restoration.

There are three critical issues for evaluating microbial diversity and restoration. The first issue is defining the spatial and temporal distribution of species and functional groups and their relationship to ecosystem processes. The second concern is assessing the richness of organisms within the different functional groups. The third is the system-level capacity for dispersal and natural reestablishment versus the need for artificial introduction of microbial inoculum.

B. Spatial and Temporal Arrangement

Just as important as the richness of organisms are the changes in their spatial and temporal distributions. Unfortunately, few studies have evaluated microbial communities using species increment curves or overlap estimates. Several types of analyses are critical to understanding biodiversity and restoration. These include species \( \times \) area, species \( \times \) time, and dispersion relative to ecosystem processes. Unfortunately, few data sets are available to evaluate microbial recolonization on this basis.

Microbial richness estimates tend to be taken on a per-sample basis. However, plants and animals tend to be analyzed on an area basis. This makes comparative studies difficult but opens an important area of research. Nevertheless, evaluating the spatial array is absolutely critical. Fungi, for example, exist as a network of hyphae (a mycelium) extending from a few millimeters (such as a Trichoderma colony occupying a single fern petiole) to tens of meters in diameter (fairy rings, or the giant Wisconsin Armillaria, for example). For the same Wyoming data set, the species increment rate was the same up to the size of a 400-cm\(^2\) patch of disturbed as well as reference area (Fig. 4). However, in the disturbed site, as one expanded outward, the species increment rate declined whereas it continued to increase in the reference area. In the reference area, new species were added as the habitat changed. In the disturbed area, the habitat was rather uniform across the site (in this case, mixed, respread topsoil on a surface mine). Thus, one conclusion is that microbial activity and composition become more diffuse and repetitive across scales in severely disturbed areas, and overall landscape diversity is lower than in native undisturbed areas.

Frequency of sampling over time is also crucial for describing microbial biodiversity. Many microorganisms are only identified based on sporulating structures. However, these organisms may be present continuously but can only be found periodically. For example, macrofungi are spread widely in the mycelial stage and live for many years. Several continuous years of observations are needed for the right conditions to occur before a sporocarp forms. In many cases, fruiting times may occur over successional time. For example, on Mount St. Helens, establishing the first ectomycorrhiza found on the Pumice Plain took 5 years. We never saw a sporocarp to identify the fungus that formed on the ectomycorrhizal root tips of conifers. Development of techniques for DNA fingerprinting will eventually allow us to identify more of these organisms even when they do not sporulate.

Samples are often taken at the wrong time, leading to erroneous conclusions about microbial diversity. For example, soil animals migrate vertically in response to soil moisture conditions. Soil samples are normally taken from surface soils. Thus, the mesofauna may only be detected when they return to the surface. Usually soil organisms are sampled at the convenience of the investigator, but microbial populations are often event
driven (e.g., precipitation). Thus, frequent or a deterministic sampling regime is needed to detect their presence.

Spatial relationships are just as crucial as temporal ones. Ecosystem processes (e.g., decomposition, mineralization, and immobilization) are not uniform across an undisturbed area. Microbial-regulated processes tend to be highly patchy and organized to optimize production. However, possibly the greatest impact of disturbance on ecosystem dynamics is spatially mixing soils and creating relatively uniform conditions across a site. In fact, this led to an oldfield view of succession that still largely dominates restoration practices, where a relatively uniform aboveground community is planted. However, succession may be a patchwork of starts and stops, with a few initial colonists acting as islands that become the nuclei for future colonists. Succession and microbial composition and activity are tightly coupled to the developing patchwork. In restored or recovering ecosystems, these patch recovery patterns are evident. In many abandoned, disturbed sites, no spatial recovery is detectable.

C. Diversity and Functional Groups

The biodiversity of types of microbes in ecosystems is daunting. However, to a certain degree, maintaining or recovering the functional groups of microbes is the first critical task in restoration efforts. Microbes play every ecosystem role at every site. In fact, microbes alone can, and do, form fully functioning ecosystems without higher plants or larger animals. In the most extreme environments of the Sahara desert and the uplands of the Antarctic Dry Valleys, microbes are the only living organisms, existing on aeolian-deposited or ancient carbon inputs. In many extreme environments, microbes make up the entire ecosystem. These range from the simple endolithic (inside rocks) communities of the Dry Valleys of Antarctica to the thermal pools of New Zealand and Yellowstone geysers. As one proceeds to more favorable environments, more and more types of microbes emerge, subdividing the processes of primary production and decomposition. At all sites, microbes undertake primary production (bacteria, cyanobacteria, algae). The relative contribution of the microbes to the overall proportion of net primary production tends to range from high in more extreme environments (such as deserts and tundra) or situations with dispersed nutrients at low concentrations (open oceans) to low in conditions highly favorable such as tropical rain forests.

In addition to directly fixing C, microbes also catalyze the nutrient cycling processes that transfer elements directly to plants or convert unavailable nutrients into forms that can be taken up and utilized. Thus, they are indirectly linked to carbon fixation by providing limiting resources. Although these organisms are generally modeled as “microbial mass,” they often live syntrophically with plants. Mycorrhizal fungi probably have the largest biomass within this group. These fungi form mutualisms with plants and transfer from soil to plant a range of soil resources, from water to N to P. Importantly, they can also make unavailable soil resources, such as bound P, available, by producing organic acids and phosphatases, and Fe with siderophores. Other prokaryotes fix atmospheric N₂, ranging from free-living forms such as cyanobacteria and Arthrobacter, to symbionts such as Frankia and Rhizobium. Other microbes catalyze almost every other nutrient transformation that is biotically important to the sustainability of ecosystems, from N and S transformations, to Fe state transitions, to immobilization of heavy metals and bioremediation of toxic organics. In the case of mutualistic symbionts, many studies have demonstrated that an increasing diversity of species and genotypes can be critical to establishing and maintaining a diversity of plants.

Microbes are the dominant decomposers. Higher animals only take a small fraction (1–10%) of the NPP; the remainder of the energy goes to microbes. The animals themselves constitute a source of a slightly different C source from plant material, making a new type of C resource. Microbes then utilize almost all of the remaining plant material, thereby releasing the nutrients immobilized in plant tissues. Only a small fraction of C remains, as highly complex plant constituents or recalcitrant microbial compounds. These are critical in that this forms the organic matter essential to recovery of all sites.

1. Free-Living Saprobides

In every study, microbial diversity even of disturbed lands continues to increase with increasing sampling. While the actual slope of species increment curves may be lower than for undisturbed areas, it still remains very high. It is not clear if the reduced diversity of microbes is a factor in these detrimental responses. However, it is clear that if the environmental conditions for free-living microorganisms are present, a high diversity of species and a high density of individual cells will reestablish. Thus, restoration of free-living microbes is largely a matter of management of the soils, rarely by inoculation with bags of “beneficial” microorganisms. To date, there is no evidence that biodiversity per se
of free-living microorganisms limits saprobic microbial activity in restored lands.

Free-living saprobes form the bulk of the microbial diversity in both functional pathways and the diversity of taxa. As we look at the known studies, those processes catalyzed by free-living microbes always occur, sometimes in detrimental levels. For example, Thiobacillus ferrooxidans uses Fe^{2+} in pyrite, which results in the release of sulfuric acid, detrimentally reducing the pH of streams. Immediately following disturbance, there is a rapid mineralization of N, resulting in N leaching and denitrification. Reduction in some of these microbial-catalyzed processes often is an important restoration task.

2. Soil Animals and Food Webs

Microbes consist of prokaryotes and fungi. These are capable of immobilizing nutrients such as N in the presence of excess C. Soil formation is also dependent on mixing of surface organic matter down through the horizon. These activities are undertaken by a food web of enormous complexity. Soil animals generally invade rapidly, either dispersing directly or by moving with soils or other materials. Soil food webs are generally characterized using functional groups as the richness of species is simply too high to characterize in detail. Food web analyses indicate that there are distinct channels (Fig. 5) that can be affected by the soil conditions and the composition of the microbes. Undertaking detailed studies of the role of biodiversity in these food webs is a critical future task. We currently do not know if species changes really matter to the recovery process.

3. Symbionts

Symbiotic microorganisms are much less diverse and clearly play critical roles in the establishment and persistence of vascular plants and plant composition. These roles are basically of two types, pathogens that inhibit plant growth, and mutualists that extract resources and exchange those resources with plants for energy or provide protection in some form, again in exchange for energy.

Plant pathogens are of two basic types for our purposes, specialists and generalists. Specialist pathogens are those that are associated with only a single species or group of host species. They tend to be highly diverse. Generalist pathogens tend to be widely spread across plant groups. Specialist pathogens are known to be devastating in agricultural ecosystems. However, they tend to be much less of a problem in restoration efforts. This probably results from the efforts made to restore a diversity of plants, making it more difficult for a pathogen to find a host and build up adequate inoculum densities. Exceptions exist when there is a high prevalence of a single species coupled with an exotic introduction.

Generalist pathogens may be another matter. These are highly diverse organisms that often live as saprobes except when conditions prove favorable to a parasitic lifestyle. For example, there are a wide variety of fusaria and rhizoctonia fungi found in virtually all soils. These can destroy a wide variety of plants under appropriate conditions. Phytophthora cinnamomi is responsible for loss of plants ranging such as the eucalyptus in the Jarrah forest in Australia. Often, these are almost undetectable except for very short times. In Wyoming, snow mould reduced sagebrush densities up to 60% and reduced growth in the survivors. This “mould” was a complex mix of fungi, not Typhula sp. found in the snow mould diseases of wheat. The disease was opportunistic and only found during El Niño years of high autumn rains and locations of high snowfall accumulation. It was found only one year and only in locations of high snowfall. Plant parasitic nematodes are always found in soils. They are responsible for high levels grazing, but, remarkably, rarely can nematode damage be observed in a restoration project.

Thus, despite the examples where disease was present, there are remarkably few demonstrations where diseases were highly diverse or markedly changed the outcomes of a restoration effort. Even under rather
optimum conditions, such as tropical seasonal forests, we have observed few instances of root or shoot disease and then, it tended to be single root tips or individual leaves, but not widespread across a site. This supports the need to establish a diverse plant community. Clearly, it is generally not desirable to restore pathogens to a restoration site.

Mutualistic symbionts are relatively diverse but that diversity may play unique roles in restoration. Probably the best known are N-fixing prokaryotes. Legumes tend to be important early colonizers as N often limits primary productivity. In croplands, nodulation tends to be highly specific. This led to the all too common practice of using commercial inoculum. However, at sites ranging from glacial outwash in Alaska to Mount St. Helens to a seasonal tropical forest, we have planted or observed invading legumes. In no case were legumes present and functioning nodules absent. We know little about dispersal of rhizobia, but they do appear to be dispersed readily. Further, we now know that host specificity, at least for Rhizobium, appears to be largely associated with plasmids and not a nuclear genomic component. Thus, limitation in nodulation is likely not a function of the presence of rhizobia, but of the conditions of the site.

The effectiveness of the nodulation, however, could be an important question. In well-established hot deserts, Bradyrhizobium was an efficient bacterium stimulating high rates of N fixation. However, it was slow-growing and deep in the soil profile. Rhizobium was fast-growing and found near the surface. It rapidly colonized plants but was not an effective fixer. In pasture soils, different rhizobia are distributed in patches scattered across a site. Thus, while the presence of rhizobia is likely not limiting to restoration, having a diversity of populations capable of acting with a range of plants under a range of conditions may be important.

We know less about Frankia, although there is a wide diversity of associated plants. In bioassays of spread cold-desert soils, we found that the plants failed to become nodulated. However, the soils had high N concentrations, which may have restricted activity. Alternatively, invading species such as Russian Olive has nodules even in areas where it has previously not been found. Unfortunately, beyond just a few observations of groups and N-fixation rates, there are no studies of the diversity of N-fixing species or genotypes in restored areas of these critical groups.

Mycorrhizal fungi have been studied in much greater detail. Their diversity is highly variable. In desert sites, we have found as few as two or three species. Alternatively, in forests, there can be hundreds of species and thousands of genotypes. These fungi are often eliminated by the disturbance event. However, even when they are not completely eliminated, the diversity of species is often radically altered. Moreover, many species depend on a mycelial network that can extend up to many meters across. This spatial structure is always broken up, providing opportunities for new taxa to invade. The resulting pattern is an increase in the intraspecies diversity with more, smaller clones. As these clones expand, some die and disappear while others continue expanding into the open habitats. Thus, intraspecific diversity initially increases as many propagules arrive and then declines as fewer colonies come to predominate.

Recovery of symbionts is a critical limiting step in restoration. There are two limiting steps: first, invasion of propagules, and second, establishment on site. Invasion is by physical or biological vectors. The most notable biological vector is wind. Wind has been shown to move organisms as large as mycorrhizal fungal spores up to 2 km. However, there are important limitations. Spores larger than 70–100 μm in diameter are rarely wind-dispersed. In those cases, animals are the vectors for microbes. Many animals feed on microbial spores. This can occur directly. For example, the diet of many rodents can be predominantly fungal sporocarps. This was the major means for mycorrhizal recolonization on Mount St. Helens following the eruption. Other propagules are transported unintentionally. Ungulates and rabbits feed on forbs and grasses, but in doing so, they tear plants from the soil, bringing fungal hyphae and internal spores and vesicles. Animals such as gophers preferentially feed on the nodules of legumes in addition to mycorrhizal fungi. The microbes are adapted to pass through the guts and are deposited across restored sites. Thus, just as for plants and animals, a key factor in restoration is the proximity of the source areas (Fig. 6).

**D. Microbial Establishment**

Different microbial species have different abilities to reestablish on a disturbed site. Because of their remarkable diversity, we are unable to artificially return even a small fraction of the microbes necessary for successful restoration. Thus, dispersal from surrounding areas is critical. In all of these invasions, two factors emerge as critical: distance and directionality for the appropriate vectors, and a suitable site. Adjacent source areas are important for reinvasion. At Mount St. Helens, for example, disturbed areas within or adjacent to surviving patches were rapidly recolonized. It took several years for sites at a greater distance to recover (Fig. 6). This pattern can be found in many other areas. Both physical and biotic vectors travel along specific pathways. These
Invasion pathways and source areas. Recovery of microbes on Mount St. Helens can serve as a model of reestablishment. There were three critical types of disturbance. In area A, virtually everything was sterilized. Area B was the blast zone, where everything aboveground was eliminated and ash was deposited up to a meter in depth. Area C was the area of high ashfall. Area C recovered rapidly as most organisms survived in protected areas, establishing on the ash within the first year. This included mycorrhizae, nematodes, nitrogen-fixing bacteria, basidiomycetous fungi, mites, and collembole. Some small patches, where pocket gophers survived and emerged, served as islands. Invasion via animal dispersal also occurred from area C (pathway 1). Recovery across the site was well underway within 2–3 years. Area A was largely invaded from vectors moving from area C (pathway 2). This process was quite slow. Windborne microbes took 5–10 years to reestablish. In circumstances where soil microorganisms are limited endomycorrhizal inoculum is available through a few companies.

There are no standards for microbes and restoration. Some protocols require the addition of symbiotic mutualists, but all others assume that microbes recover just fine and will “do their jobs.” In fact, soil microbes probably never “stabilize.” Their short individual life spans, coupled with the ability of some members of each functional group to invade and establish, makes assessment of composition and activity difficult. Inoculation can be an important practice in conditions where little or no inoculum for an entire functional group remains and has little chance for reinvasion. However, restoration requires management of soils, plants, and animals to encourage natural migration, patch structure for concentration of resources, and a complex structure that facilitates spatial and temporal diversity in ecosystem processes. If these conditions are met, it is likely that microbes will be capable of taking care of themselves quite well.

V. CONCLUSIONS

A. Assessing Restoration Success

These examples of restoration of plants, animals, and soil microorganisms all show the difficulties and limitations of restoration of the entire richness of a prior existing community. While dominant plants and animals may be reintroduced, microorganisms are all expected to recolonize naturally. The resultant lower diversity restored communities indicated that if preservation of biodiversity is the goal, then conservation prior to disturbance is the preferred alternative, rather than restoration after disturbance. In focusing on species richness, we have placed little emphasis on ecosystem functioning, even though restoration of functioning is one of the major goals of restoration. Natural ecosystems provide ecosystem services, such as water supply, oxygen, soil stability, natural products, and so forth for free. Reclamation or rehabilitation is usually sufficient to provide these basic services, without the necessity of reintroducing all of the original biodiversity.
Measurements of both structure and functioning are used to assess restoration success. Restoration success is usually assessed by comparing the restoration site to a reference area, a native site with structure and functioning that are predetermined as the restoration goal. Measurements are compared between the reference and restoration sites. Structural measurements, such as the richness, density, and relative composition of species, are easier to measure than functional measures such as decomposition, nutrient cycling, erosion rate, or biological functions such as species reproduction and mortality or food web energy throughput. Yet it is the functional measurements that we need to determine whether the restored land has really stabilized, not simply the relatively easy measurements that require species counts. Measurements of restoration success are often not legally required, so many restoration/reclamation efforts receive no assessment at all. When they are, a species count, density, or percent cover is often all that is required to declare success.

B. Designer Ecosystems

Preservation of certain rare species may require manipulation of the ecosystem to stabilize their populations, possibly to the detriment of associated species. Such actions are already taken in numerous situations. For instance, wetland parks for shore birds have been diked, dredged, and dammed to create aquatic habitat for bird species with different water depth requirements. Pastures in Europe receiving high anthropogenic nitrogen deposition are mowed at critical times of the year to reduce the growth of nitrophilous-dominant plants and promote survival of rare plant species. James MacMahon has termed these "designer ecosystems" because they are highly managed ecosystems that have a specific conservation goal, compared to the ecosystem where the species in question may occur naturally. Biodiversity has become highly manipulated in many areas where human populations are dense and where the remnant landscape is managed to promote as high a diversity of species as possible. Virtually all restored communities are missing species, so in one sense restoration may be considered an unintended experiment to determine the impacts of rare or other missing species on community and ecosystem functioning. This will require more research and monitoring than has been done in the past. One aspect of ecological restoration that has not been emphasized in this article is the general lack of data. Many sites are restored that have never received any kind of monitoring or research, or the data are simply not available. The generalization that restoration will not return the original diversity holds for the limited number of sites that have been studied, but as more data become available, we will understand more about how to manipulate ecosystems to maximize diversity.

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