Nothing Succeeds Like Succession: Ecology and the Human Lot

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The administration of the University is sympathetic with these aims and shares, through the Scholarly Publications Committee, the costs of publishing and distributing these lectures.

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James A. MacMahon was selected by the committee to deliver the Annual Faculty Honor Lecture in the Natural Sciences. On behalf of the members of the Association, we are happy to present Professor MacMahon's paper.

Committee on Faculty Honor Lecture
Nothing Succeeds Like Succession:

Ecology and the Human Lot

by

James A. MacMahon

67th Faculty Honor Lecture
Utah State University
Logan, Utah
Nothing Succeeds Like Succession:
Ecology and the Human Lot

by
James A. MacMahon*

Prologue

An Honor Lecture provides a rare opportunity for me as a scientist. First, I have the chance to share, and in a sense to justify, my chosen and cherished discipline, ecology, before an eclectic audience. Second, I have a reason to consider my profession in a broader perspective than I normally do, given the pressures of day-to-day teaching, of grantsmanship, and of acting the role of stern taskmaster to my graduate students. I relish the opportunity to dabble, with an ecological perspective, in history, in philosophy, and in other areas.

First, I will discuss my discipline in the context of science as a whole. These comments will then act as a background for a discussion of my current research about the ecological process of succession. Following this "primer," I will attempt to address the human implications of my work by considering the general nature of disturbance, the initiating force of succession, and the types of man-made or anthropogenic disturbances. Finally, I will offer some suggestions about reconstructing ecosystems following anthropogenic disturbances. Ultimately, I hope my pursuits, which often seem to others to be the esoteric dalliances of a "nature freak," will emerge as part of a highly focused perspective.

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Ecology as a Science

Ecology is the study of the relationships between organisms and their environment. In the usual sense, ecologists imply that the word *environment* includes all entities outside an organism. This word not only encompasses abiotic factors, such as radiation or rainfall, but also includes biotic interactions, both those occurring between individuals of the same species and those involving unrelated species. This perspective makes ecology a less circumscribed science than any other. By definition any environmental factor or any organism is fair game for the ecologist. In a sense, the universe is the ecologist’s object of study, although most ecologists demand at least the presence of one organism before they initiate an inquiry.

For all of the things that ecology can be, there are a few things that it is not. Ecology is not a system of beliefs or values, nor a code of behavior, nor a methodology for recycling human litter. It is true that some non-scientific neophytes who term themselves ecologists believe that all of these things are part of their realm, and while it is also true that these attitudes may characterize individual professional ecologists and their personal beliefs, these attitudes or values do not characterize ecology per se. Data, experimentation, deduction, and induction are the canon as well as the methodology of all science, including ecology.

Unfortunately, ecology is quite young as a self-conscious body of knowledge and ecologists are thus often constrained to an alpha level of inquiry; we describe what we know empirically and attempt to generalize from a few data points to universal principles. Such generalization can only be verified by additional study. Nonetheless, it is sometimes a useful exercise to see how far a particular generalization can be carried without it being falsified by empiricism.

It is my intention, here, to wander between what I know to be true empirically and what I believe to be true because some general principle seems to be emerging. I will discuss a series of ideas that should formally be referred to as concepts, although many of my colleagues would call them theories. Concepts, as opposed to theories, are not falsifiable. Both theories and concepts are necessary for a scientist, but only theories are a part of science because they are independent of our personal beliefs, interests, or tastes. Concepts express a scientist’s world view. Ideally, concepts may eventually lead to the generation of
a theory where, based on the value of an independent variable, a specific prediction about a dependent variable can be made with some bounds of statistical probability.

Unfortunately, even when I believe that my concepts have been turned into theories, I am damned by the metaphysical curse plaguing most scientists. Despite our sometimes vociferous objections to the contrary, all scientific research is guided by numerous metaphysical maxims (Bunge 1974). Let me be more clear. Metaphysical philosophy, to me, includes consideration of first principles particularly those related to ontology (the philosophy of the nature of existence) and cosmology (the philosophy of the origin and structure of the universe). The maxims that underpin science, as adopted from Bunge (1974), are as follows:

1) There is an external world.
2) The world is composed of things.
3) Forms are properties of things.
4) Things associate into systems.
5) Every system, except the universe as a whole, interacts with other systems in certain respects and is isolated from further systems in other regards.
6) Everything changes.
7) Nothing comes from nothingness nor goes to nothingness.
8) Every thing satisfies laws.
9) There are several kinds of law (e.g., causal and probabilistic laws).
10) There are several levels of organization (e.g., chemical, biological, social).

It is perfectly clear to me that all of my thoughts and actions as a scientist presuppose all these maxims. Thus, the reader must be warned that this is the case when interpreting either my concepts or my theories.

My musings here will be confined to one aspect of ecology, a general process termed succession. My approach will be highly anthropocentric and my emphasis will be iconoclastic in the sense that I will
attempt to challenge some of the "conventional wisdom" of my
discipline. My presentation may seem teleological or even anthropo-
morphic because of its style. The reader must trust that my work and
mind are not.

A Succession Primer

Succession is the biological recovery of a particular area following
a disturbance. The succession concept also includes the origin of a
biological community on new geological substrates, e.g., volcanoes,
newly formed mountains, or lakes that have begun to "fill in." It
doesn't take a scientist to tell us that after a forest fire, herbs and
shrubs invade a previously forested site and that eventually trees may
make a comeback, or that if a field is fallow for long enough, "wild"
plants and animals will dominate a once neatly maintained farm. In
fact, the observation of succession has been traced to Theophrastus
(300 B.C.) and even though the term was not coined until 1825, older
writings abound with excellent empirical descriptions of succession for
a variety of ecosystems.

The concept of succession as a universal process received its
greatest impetus from the writings of North American scientists,
especially those of Henry Chandler Cowles (1869-1939) and Frederic
E. Clements (1870-1945) concerning plants and Victor E. Shelford
(1877-1968) concerning animals.

It was Clements (1916 and 1928) who went furthest to propose
mechanisms for the successional phenomenon. His argument, in
essence, was that a site which underwent development to a "climax
formation" involved the "initiation" of that site and a series of subse-
quent processes, for which he coined specific terms.

The development of a climax formation consists of several
essential processes or functions. Every sere must be initiated, and
its life-forms and species selected. It must progress from one stage
to another, and finally must terminate in the highest stage pos-
sible under the climatic conditions present. Thus, succession is
readily analyzed into initiation, selection, continuation, and
termination. A complete analysis, however, resolves these into the
basic processes of which all but the first are functions of vege-
tation, namely, (1) nudation, (2) migration, (3) ecesis, (4) competi-
tion, (5) reaction, (6) stabilization. These may be successive or interacting. They are successive in initial stages, and they interact in a most complex fashion in all later ones. In addition, there are certain cardinal points to be considered in every case. Such are the direction of movement, the stages involved, the vegetation forms or materials, the climax, and the structural units which result.

Clements's six basic processes have been largely ignored by contemporary ecologists. The history of the concept of succession the last 50 years has regularly included papers that start out by damning Clements and then turn to the exposition of a new and seminal approach to succession that clarifies all scientific points under contention. Actually, the vast majority of these post-Clements workers have reinvented the wheel; a careful reading of Clements's words would have obviated the need for their various contributions. This is not the forum to produce a litany of examples of this type. Someone interested in such a listing might consult Robert McIntosh's (1980) very personal interpretive-recounting of the history of the succession concept.

Let us assume that by giving a modern interpretation to Clements's processes, we might understand, at least superficially, how succession generally occurs. His initiation phase simply infers that either a disturbance occurs that alters an existing biotic system and thus starts the process of succession (secondary succession) or that some virgin geomorphic substrate (i.e., one that has not been previously altered by the succession of a biota) is available to colonizing organisms which will take part in changing the raw geological substrate into soil (primary succession). The difference between primary and secondary succession forms a continuum of possibilities such that any polar example is easy to distinguish, but that vast middle ground is more difficult to pinpoint. I see no real reason for distinguishing between the two, and for this discussion I will simply refer to "succession" without a modifier. I will address examples that involve what most workers would term secondary succession. This is the usual case whenever man is the initiator of perturbation.

The exact nature of the disturbing agent is an important part of succession in that the disturbance sets the scene for all the changes that follow. Thus, the denuding agent characterizes the first process, nudation, and that process as it affects a specific plot of ground deter-
mines the beginning characteristics of succession. The character of nuddation may have strong subsequent influences as well.

The initial biota of a disturbed plot of ground may originate from many sources, all of which can be subsumed into two categories—residuals and migrants. Residuals are those propagules of organisms that reside on a plot of ground after a denuding force has altered that plot. Residuals may be brought to the site by such denuding agents as wind or flood. However, the most common situation is that the original site still retains propagules of some organisms, usually below the ground surface. Pieces of plants or animals capable of asexual growth or reproduction, entire individuals, spores, seeds, etc., all might be residuals.

Migrants, those individuals or propagules that move to a particular site following a disturbance, represent both chance migration of species and some highly directed movements. Species vary in their vagility or capacity to move, and thus some species are preadapted to move. For many species with small propagules, prevailing wind may carry organisms in very definite directions from very specific source areas. Several other species' characteristics facilitate migration, among them large population size, specialized structures that may aid in "hitching a ride" on more vagile organisms, and a broad range of tolerances for environmental situations. Not surprisingly then, the first organisms, e.g., plants, to appear on a denuded site are residuals mixed in with "weedy" species. In this case, the word weed implies that plants are common, widespread, small-seeded, prodigiously reproducing species. Following several types of disturbances, western rangelands are often covered by Russian thistle (Salsola iberica), a non-native weed. This plant was apparently introduced into North Dakota in 1873-74 in flaxseed shipped from Russia. It can produce 30,000-200,000 seeds per plant. The round-shaped plants break at ground level and are blown around by the wind, dispersing their seeds and giving the plant its other common name, tumbleweed. This species has been so successful in the West that 70% of alfalfa seed samples and 28% of small-grain samples examined by the Wyoming Seed Laboratory contained Russian thistle seeds (Alley and Lee 1979). Thus many soils have seed reserves that can immediately respond to disturbance. Our own experience with mined lands near Kemmerer, Wyoming, is that research plots, regardless of their experimental
treatments, were covered by Russian thistle the first year after the site was fallowed.

It is important to emphasize that many native plants which “pop up” on disturbed lands have similarly impressive powers of weediness. I chose a non-native species as an example only because it is well known to western residents. Indeed, native species like fireweed (Epilobium angustifolium) are abundant after many disturbances, especially fires, in forested areas of the West. Fireweed was the first and by far the most abundant colonizer on Mt. St. Helens in the summer following the May 18, 1980, blast. The rapid colonization of the volcano by fireweed may be due to its vegetative reproductive capacities rather than to its seeding habits (Keating et al. 1982).

Clements pointed out that it did not matter whether or not propagules remained on a plot as residuals or were early migrants; they would ultimately have no role in succession if they did not become established. Establishment is his process of ecesis, which together with migration he termed invasion—a general process requiring successful completion of both of its two components.

Ecesis implies that the species can, and does, undergo all its life processes through reproduction. For example, a residual plant seed must germinate, grow, and reproduce before it completes ecesis. For some early successional species, particularly some residuals, nudation is mandatory for their establishment. Such is the case for many fire-adapted species where they may require post-fire seedbed characteristics to grow or they may require fire to break seed dormancies. In some species the adults cannot sexually reproduce without fire, e.g., wire grass (Aristida stricta) in the southeastern United States and knob-cone pine (Pinus attenuata) in southern California.

Once species are established, their successful reproduction increases populations to levels where individuals of one species or of different species are sufficiently abundant so that they interact. Clements, with his plant-oriented viewpoint, thought that competition for available resources was the universal outcome of population increases. A contemporary interpretation would be that any of a number of biotic interactions might occur that could affect the fate of the members of the developing ecosystem. These interactions could include positive interactions, such as the development of mutualisms or proto-cooperation, as well as negative ones, such as parasitism and predator-prey interactions.
In the case of competition, the species mix on the plot might be altered by the competitive exclusion of one species by another, or a simple change in relative dominance of species might occur without the total loss of one species. Regardless of what happens, the plants and animals, in their specific proportions, may alter the environment. Obviously, soil organic matter usually increases as succession progresses. In addition, various species may add specific chemicals to the soil, e.g., via the biological fixation of nitrogen, or they may change the concentration of molecules throughout the soil profile. Animals change soil texture by burrowing or by trampling. Plants change the soil surface temperature via the shade that they create and this in turn alters the vapor pressure deficit within their canopy. With all of these changes, the ground is no longer similar to the barren, recently denuded areas. The sum of these plot changes is included in the reaction process; that is, the plot itself reacts to the biota and becomes an essentially different plot. As this happens, migrants, which at first found the plots to be hostile environmentally and could not establish, may now encounter a benign environment where ecesis is possible. Migrant establishment may lead to further plot changes, which forms yet a different complex of animal and plant species and thus migration, ecesis, and reaction continue until the species complex and the environment reach an approximate equilibrium where there appears to be very little compositional or physiognomic (life form) change over time. This is stabilization, or the attainment of climax.

I have argued that this equilibrium is more apparent than real (MacMahon 1980, 1981) and that what really happens is that the long-lived perennial plants, once established, dominate our vision for their lives—hundreds or even thousands of years. This “aspect” dominance eclipses the day-to-day, year-to-year changes that constantly occur as the majority of an ecosystem’s components are continually reacting to the vagaries of their biotic and abiotic environment. Thus, the concept of climax, or a truly equilibrium ecosystem, is appealing to us because of visual perception, but it is of little reality in the functioning of an ecosystem. It is imperative that our management strategies be based on the reality of constant change and not on the facade of stability.

To summarize, succession may be compared to a form of sequential biological editing. A perturbation occurs, certain species or
chemicals are deleted from a site, and the site is thus radically altered. The remaining entities, plus a "rain" of new ones are further edited by their capacity to establish. As growth and reproduction occur, another editing process takes place whereby biotic interactions change the membership list of the plots—both for biotic and abiotic plot constituents. And so the editing continues—sometimes drastic, sometimes so minor that it is not easily detected and the story line appears unchanged—climax is reached. Figure 1 depicts a common successional sequence in northern Utah, where following fire or logging, subalpine meadows establish which are invaded by aspens which are in turn replaced by subalpine firs and ultimately these are replaced by the long-lived Engelmann spruce.

Figure 1. A stylized successional sequence beginning, following fire, as meadows, which are subsequently invaded by quaking aspen (Populus tremuloides), then by the relatively short-lived subalpine fir (Abies lasiocarpa), and ultimately by the long-lived Engelmann spruce (Picea engelmannii). This sequence depicts events documented for the subalpine of northern Utah.

From MacMahon and Anderson 1982. Used with permission.
The Nature of Disturbance

Since succession is so intimately tied to perturbation processes, a further discussion, first of disturbance in general and then of anthropogenic disturbance, is in order. Disturbances are generally viewed as catastrophic events originating with the physical environment. Peter White (1979) points out two problems with this viewpoint. First, not every disturbance is catastrophic. Indeed there is a gamut of disturbance intensities ranging from those that are so subtle that they cannot be easily measured (e.g., the falling of a single tree) to those that totally lay bare a landscape, even removing the soil (e.g., a major volcanic event). A second problem is that certain ecosystems are disturbed by factors that are initiated or, at the very least, promoted by the organisms themselves. When this is the case, the disturbance regime may actually be required to maintain the integrity of that ecosystem. In the West, several types of pine forests, including long-persistent lodgepole pine stands, function in this manner. The lodgepole stands are maintained by a complex of interactions, which includes beetles introducing fungi, which kill some trees creating fuel for fires, which enhance regeneration of the lodgepole stands, and so on in a cycle.

The important point is that disturbances are very individualistic events. To determine their potential influences on succession, the following factors must be considered:

1) The type of disturbance—effects of fire are different from those of overgrazing.

2) The intensity of the disturbance—fires of different intensities may have different effects on the seedbed.

3) The areal extent—small areas have high periphery/area ratios, and events related to the edge can alter the whole area rapidly; in large areas the peripheral influence may have to “creep” as a moving front across the larger landscape.

4) The timing of the event—the same event during different seasons can have significantly different effects.

5) The frequency of disturbance—this parameter is particularly important compared to recovery time of an ecosystem.

6) The nature of the area disturbed—this includes consideration of vegetation, climate, geographic position, etc.
Note that none of the above distinguishes between anthropogenic disturbances and natural ones or between those with abiotic versus biotic influences. Each event has its own characteristics some of which it shares more closely with unrelated events, than it does with other disturbances of the same kind. For example, defoliation of a tree by insects or by a human activity may have more in common—in the context of an ecosystem—than defoliation of two trees by different insects. One insect may girdle a branch resulting in leaf fall while another may transmit a leaf pathogen causing similar leaf fall. The difference might be that the girdler also kills branches resulting in the accumulation of decomposition-resistant woody litter, while the defoliating pathogen, vectored by the insect, causes simple leaf fall and its concomitant labile litter.

Disturbances that occur in North American vegetation include: fire, windstorm, ice storm, ice push on shores, cryogenic soil movement, wide temperature fluctuations, precipitation variability, alluvial processes, coastal processes, dune movement, inundation by salt water, landslides, volcanic influences, karst processes, and last but not least, various biotic processes (White 1979). Interestingly, while this list is meant to represent natural disturbances, many of these categories occur in response to man as an affecting agent, e.g., fire, dune movement, karst processes, landslides, biotic, and others.

Some disturbances are really cyclical, and man often uses the predictability of the disturbance for his own purposes. A case in point is the deposition of organic matter by the annual flooding of flood plains. Many agricultural areas in countries around the world were developed in response to this yearly "fertilization" as an aid to the production of crops. Even places where the interval is longer there may be cyclic perturbation. Thus, we often speak of the 50- or 100-year floods that are not as predictable as yearly floods but that may have a similar capacity for fertilizing flood plains.

These last examples hint that all disturbances are not "bad." Indeed, it is clear from a variety of data that humans do better, in terms of personal health, in areas that are characterized by changeable and moderately extreme weather, i.e., zones of high climatically related disturbance. This phenomenon is so striking that medical geographers often correlate maps of climatic variables with maps of health, yields, income, and other measures of human well
being. I want to emphasize two points in this regard. First, maps of climatic variables (e.g., rainfall or mean temperature) when taken individually do not show strong correlations to human health as clearly as do those which use composite indices (Auliciems 1972). Second, this human-climate correlation is not related in any way to the longstanding controversy concerning environmental determinism—the environmentalism of older geographers (Oliver 1973).

Man-Induced Disturbances

In this human-oriented discussion, let us consider potential disturbances caused by man, particularly by European settlers as they occupied the conterminous United States. In the process, we can evaluate the nature, intensity, extent, and timing influences of their various actions as they relate to ecosystem change. This consideration should set the stage for a discussion of “remedies.”

Figure 2 is borrowed from the chapter of a book that discusses the history of Australasian vegetation (Adamson and Fox 1982). The interesting feature is that these authors identify a series of human interventions that matches the United States experience very closely. I will use this outline to discuss what European man’s arrival represents, in terms of disturbance analysis, for the United States.

Displacement of Natives. When Europeans arrived on the North American continent it is often thought, but wrongly, that they stepped into the “forest primeval.” This fiction has occurred not only in the minds of novelists, but also in the minds of contemporary ecologists. In fact, Indians of eastern North America had cleared sites around villages, leveled wooded areas for raising crops, and set fires, generally of modest extent, twice a year. The fires were predictable and cyclic. Fires were purposely set to drive game, increase visibility, facilitate travel, increase the supply of grass seed and berries, etc. (Day 1953). The actual total impact of burning activities cannot be determined (Russell 1983). However, it is clear that these landscape perturbations in conjunction with the differential planting of desirable plant species caused a man-modified landscape in some areas.

These observations are for the period between 1600 and 1800, where the observations are on solid ground. The impact of Indians
Changes in vegetation are:

(D) the direct result of the particular human activity
(F) due to changes in fire regime
(S) due to changes in soil properties
(H) due to changes in hydrology at or remote from the site

Figure 2. European impacts on vegetation. Changes in vegetation are brought about directly or indirectly by a wide variety of activities of European man.

From Adamson and Fox 1982. Used with permission.
before 1600 is more speculative, but some data and inferences do exist. In Ohio, Indians, mainly hunter-gatherers, occupied the area for some 9,000 years before the settlers arrived. The later inhabitants (1000 B.C.-700 A.D.), including the Adena who introduced agriculture to Ohio, and the more recent Hopewell, were gradually moving away from the hunter-gatherer lifestyle and were thus clearing the landscape for agriculture (Potter 1968). The Adenas raised pumpkins and squash, sunflowers and wild seed plants. They did not have Indian corn or maize; the Hopewell raised both. Both groups were mound builders and chose village sites along river terraces or relatively flat outwash and till plains. All these areas were characterized by good natural drainage and soils where parent materials were high in calcium, e.g., limestone or dolomite. Thus, the early influences were probably limited to watercourses and riparian or flood plain situations. Nonetheless, there is a long history of human land use, though it seems probable that the more destructive Indian influences were commenced during the last 1200 years.

In the arid Southwest, the time scale of human land use is similar. Hunter-gatherers are known from about 12,000 B.P.; corn first appeared about 5,000 B.P. and well-developed secondary agricultural peoples existed by 800 A.D. In Arizona, by 800 A.D., the Hohokams had developed a complex irrigation system which was similar to the current Salt River Project and which clearly altered the desert landscape along watercourses (Martin and Plog 1973).

Utah parallels the other two examples. From 10,000 or more years ago until 400 A.D., Utah was occupied by a hunter-gatherer group. This culture, the Desert Archaic, produced complex tools and wandered, not at random, but in response to seasonal cycles in the abundance of plants and animals. The Fremont peoples, a farming group, occupied the area between 400 and 1200 A.D. They had permanent home sites, planted corn, squash, and beans, and made pottery. At some sites their farming activities were extensive. Despite their horticultural activities, they continued to harvest wild plants. Fremonters were followed about 1300 A.D. by Shoshoni-speakers (Paiute, Gosiute, and Ute), who met the European settlers. This last group reverted to the gatherer lifestyle, thus dissipating their influence on the landscape (Jennings 1978).

Thus, when the settlers arrived at various points in the United States the land had been modified, often drastically, for periods of up
to 12,000 years, but with an increasing disturbance regime through time. The landscape may have evolved in response to the cyclic predictable disturbances of Indians. The colonizing Europeans imposed a less predictable series of perturbations on the landscape and they increased the intensity and extent of disturbance. Additionally, settlers with European habits and tools initiated new kinds of disturbances. As the Indians were displaced, the whole scenario of disturbance changed and nearly every disturbance parameter was altered. Species of plants probably had their ecosystem importance and geographic distribution altered by human activities over this whole period. It is possible that selection of plants by man during this time even altered the gene pools of both desirable and undesirable species.

Farming and Grazing. In many ways the settlers mimicked the Indians, at least in the East. Indians girdled trees to kill them and later burned the land. Pioneers did the same, only they cut the trees more deeply so that they fell during windstorms into a tangled mass to be burned later. The more effective and extensive killing techniques produced more intense and widespread fires than those of the Indians. Chains and horses were used to remove the stumps which Indians left. Wetlands were drained and sometimes burned.

Areas on hills, slopes, or lands which were otherwise not suited to farming were used to gather fuelwood. In addition, cattle, horses, and hogs were allowed to graze freely on the woodlands. These grazing activities can inhibit deciduous tree reproduction via consumption of all seedlings and seeds, while conifers are less affected [see for example the effects of boars in the Great Smoky Mountains National Park (Bratton 1974)].

Non-native plant seeds, both crop and weed species, were introduced in abundance. Escape of such plant species or even domesticated animals for that matter has had numerous consequences. The effects of wild burros and wild horses in the West and boars in the Southeast are too well known to repeat. Suffice it to say that animals can eat some plant species to local extinction, while in other cases they act as dispersal vectors for plants with protective seed coats.

The northeastern deciduous forest was the main site of early European settlement. The soils of these forests develop by the process of podzolization and are characteristically low in fertility. Nonetheless,
settlers were slow to move westward to the high calcium, rich soils of the mid-continent. In part this was due to the lack of trees. Settlers were imprinted by the forest physiognomy and thus the great prairie areas were foreign to their experience (Weaver 1954). Whatever the reason, their persistence and agricultural habits decimated the eastern deciduous forest.

Even when the settlers moved westward, they built homes among the scarce trees. Of course, a longing for trees was not the only drawback to prairie settlement. Wet areas were associated with fever and ague. Dry areas required wells. And the impenetrable sods defied the settlers' attempts to rapidly establish farmlands. The development of the steel plow (John Deere 1837-40) provided the first satisfactory means of turning sod. In addition, the developing railroads opened access to better markets and brought in fuel and building materials which did not exist in the monotonous sea of grass. As the prairie was opened, the loss of topsoil to erosion and the change in species composition in response to grazing rapidly changed a vegetation type which may have been closer to "primeval" than some of the forests or even the deserts.

In Utah the agricultural activities of the settlers may have altered the landscape as much as anywhere in the United States, even given that Utah contains so much "wilderness" area. The reasons for the degree of this change are numerous. First, the settlers in Utah were Mormons, a persecuted people who were escaping to establish their own exclusive area which would be self-sustaining. Agriculturally, this required irrigation because of the climate. Settlement sites had to have dependable land for cultivation, irrigation water, native forage for livestock, and nearby range. All early settlements in Utah and at Franklin, Idaho, met these requirements by being established at the base of the mountains, on the valley plain, but usually on an alluvial fan at the mouth of a watercourse (Stewart 1941). It is difficult now to believe that these areas were all lush grasslands. Edwin Bryan, entering the Salt Lake Valley by way of Weber Canyon on July 30, 1846, found fresh green grass in many areas. He makes no mention of sagebrush, which he does mention in other portions of his journey. July 22, 1847, two days before the Mormons entered Salt Lake Valley, Brigham Young received a letter from his three scouts, Orson Pratt, Willard Richards, and George A. Smith. Commenting on Salt Lake
Valley they say, "Timber can hardly be said to be scarce in this region for there is rarely enough to be named and sage is as rare as timber, so that if you want to raise sage and greasewood here you had better bring the seeds with you from the mountains. In many places the grass, rushes, etc., are ten feet high but no more. Feed abundant and of the best quality." (Cottam 1961). Similar expanses of grass were described for Utah Valley (Wakefield 1936), Rush and Tooele Valleys (Christensen and Hutchinson 1965), and Cache Valley (Tanner 1940). Changes in Utah vegetation from as far back as 1868 have been recorded in an extremely interesting series of photographs (Rogers 1982).

Even before the Mormon pioneers settled Utah many changes had occurred. Until at least 1824, bison were abundant in some areas of Utah. By 1843 when Fremont traveled down the Bear River the bison were virtually gone and by 1847 the Mormons found only bones. This was due in part to Indians and to the establishment of trading posts where the coin of the realm was skins (Tanner 1940).

**Forestry.** In our sense, rather than forest husbandry per se, the pioneers' forestry was really lumbering. The species composition of forests was drastically altered. Undesirable species increased in abundance while desirable species became less common. Our quantitative records of forest composition before intensive settlement are derived mainly from the habit of pioneer surveyors, including George Washington (Spurr 1951), of establishing witness trees at the corners of section boundaries. Usually, this tree and two others (whose bearing and distance from the "witness tree" were noted) were measured, identified, and recorded. Contemporary ecologists can reconstruct the pre-settlement vegetation from these data. It is clear that species like beech and sugar maple were less abundant before the pioneers. Beech could not be used for much; large trees usually had developed heart-rot and small trees were too soft-wooded. Maple, on the other hand, was desirable, but as a living tree to produce sugar rather than as lumber. Trash trees, such as black walnut, could only be used for fence rails or to stoke the fires of a metals industry which required vast acreages of some species. Understory species were not spared, e.g., ironwood (*Ostrya*) was used to make rail-splitting wedges. Many species of trees were felled and shipped to England. The forest changes were extensive, interestingly selective, and they occurred recently.
enough in the past that interpretation of what appear to be, by today's standards, mature forests may be quite different from those of Indian times and only distantly related to a real “native” forest—whatever that was (Gordon 1969).

As agriculture moved westward to the plains, forested areas of the East were allowed to regenerate, but often not to their former composition. As much as 90% of the land surface in some areas, e.g., Massachusetts, which had been felled at one time or another in the past— but at different times—is now forested and thus represents a mosaic of site histories which is difficult to reconstruct and interpret.

A major difference between Indians and settlers was that ultimately settlers wanted to prevent forest fires. Certain fire-dominated systems, e.g., Ponderosa pine forests, were adapted to frequent low-intensity fires. Fire prevention increased the disturbance interval causing large fuel buildups such that when a fire did occur it was more intense and damaging to the trees than the fires to which they were adapted (Cooper 1960).

Thus, in addition to denuding some forest areas forever, the colonizers altered most aspects of the natural forest disturbance regime, at least in some areas.

Urbanization. Urban development clearly alters the landscape, most obviously by removing native plants and animals. Less obvious is the fact that our occupation of urban areas changes the climate (Table 1) and introduces non-native plants and animals as ornamentals or for food production, thus creating new ecosystems. These ecosystems, in addition to their novel species composition, contain new geometric patterns of vegetation both vertically and horizontally, and they are founded on altered energy inputs. An example of the biotic alterations is that of birds in a mature residential area in southwestern Ohio compared to the surrounding beech-maple forests. Urban areas had fewer bird species but more biomass and greater density than forests. This led to an increase in dominance by a few species. Particularly obvious was the loss of insect-foraging species, which gleaned leaves or drilled bark, in favor of ground gleaners. This was related to the change in vegetative cover, losing the middle layers of vegetation and causing discontinuities in the upper layers (Beissinger and Osborne 1982).
TABLE 1. Differences between urban and rural abiotic factors expressed as the amount by which urban differs from rural.*

<table>
<thead>
<tr>
<th>Factor</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>0.5-1.5 °C higher depending on time of year</td>
</tr>
<tr>
<td>Relative Humidity</td>
<td>2-8% higher depending on time of year</td>
</tr>
<tr>
<td>Dust Particles</td>
<td>10 times greater</td>
</tr>
<tr>
<td>Clouds</td>
<td>5-10% more</td>
</tr>
<tr>
<td>Fog</td>
<td>30-100% more depending on time of year</td>
</tr>
<tr>
<td>Radiation</td>
<td></td>
</tr>
<tr>
<td>Total Insolation</td>
<td>15-20% less</td>
</tr>
<tr>
<td>Ultraviolet</td>
<td>5-30% less depending on time of year</td>
</tr>
<tr>
<td>Windspeed</td>
<td></td>
</tr>
<tr>
<td>Annual Mean and Gusts</td>
<td>10-30% lower</td>
</tr>
<tr>
<td>Precipitation</td>
<td>5-10% more</td>
</tr>
</tbody>
</table>

*From Landsberg 1962. Used with permission.

Urban perturbations are completely new, representing selective forces not encountered previously by the biota. We know so little about urban ecology, that it is difficult to know what is possible or even desirable with regard to management.

Mining. Mining for minerals and fossil fuels in the United States is a lucrative and often necessary human endeavor. In the 19th century, mines of all sorts tended to be underground using shafts for access to the mineable materials. Since the bulk density of mined material is less than in its pre-mining condition, the total volume increases and tailing piles characterize shaft mines.

For both shaft-mined minerals and some fossil fuels, especially oil, the most landscape-destructive phase of use is the period of exploration, wherein roads are constructed, often in remote areas, and large
numbers of test areas are established with their attendant human support facilities. The actual mining process severely alters local areas, but the total extent of this is usually small and the consequences are local and often repairable at moderate cost. Frequently, the severest outcome of mining of the type we are discussing is when the material is delivered and used. Thus, the transport, the manufacturing, and the use of petroleum products have altered ecosystems more than the mining process per se.

Recently there has been a tendency to use larger open pit or strip mines to retrieve a variety of minerals and coal. This form of mining has become economically feasible as the cost of minerals increases and the cost of removing the overburden materials drops compared to market prices. This type of mining often impacts large areas, tens of square miles or more. Currently 40 billion metric tons of coal can be mined in this way, and deeper mines could yield an additional 90 billion metric tons.

Strip mining effects vary from place to place. In the moist, temperate eastern portions of the United States, the growth of plants on mine spoils is feasible if there are no problems of phytotoxic substances in the materials. However, the very water that aids plant growth often leaches some pyrite materials, forms sulphuric acid which enters groundwater and may create problems in both terrestrial and aquatic ecosystems. In the arid West, where large reserves of coal exist, as well as alternative energy sources such as oil shale, the low precipitation, high evaporation environments impede the reestablishment of plants on spoils. Areas that are not managed remain visual blights and are sources of dust pollution and possibly toxic wastes via movement of trace elements into soil and groundwater. This last problem is exacerbated for coal. After combustion, the residual coal ash may represent up to 20% of the original amount of coal. Ash often contains high concentrations of toxic heavy metals and its disposal is a difficult problem—currently unsolved.

Mining, then, may have effects of varying extent, but usually of high intensity where it occurs. It is a one-time perturbation, but its effects may last for long periods of time, especially in ecosystems that occur in extreme environments. The alteration of chemical processes and substrates in soils, which have been mined, exposes plants and animals to environments that are often beyond their tolerance capacities.
Reconstructing Disturbed Ecosystems

Since we have catalogued ways that ecosystems may be disturbed by human intervention, it is appropriate to ask now if our general knowledge of succession might suggest effective ways to manage disturbed areas. Obviously, there are different goals of management, different types of ecosystems to be managed, different perturbations that have occurred, etc. All of the alternatives in their various combinations dictate different management strategies. I cannot address a significant proportion of these possibilities, but some general, perhaps novel, approaches can be suggested, all of which derive from an ecological perspective.

**Defining the desired endpoint.** The first problem in reconstructing any altered ecosystem is to decide what is desired as a final product. In some cases, rightly or wrongly, the decision is made for us. For example, the current surface mining rehabilitation practices are mandated by the Surface Mining Control and Reclamation Act of 1977. This requires that a site be returned to "...a diverse, effective and permanent vegetative cover...capable of self-regeneration and plant succession" (PL 95-87.91 STAT 491, para. 19). The common manner for doing this is to choose, before mining, an area similar to the mine site and to use this as a post-mining reference, a standard by which to judge the success of mined-land reclamation. Generally, some native seed mix is applied to initiate "succession." This scenario infers that because the reference site and the pre-disturbance mine site had similar ecological characteristics, at some level of measurement resolution, that they actually are the same ecosystem.

At least three potential problems exist with this approach. First, our discussion of the historical aspects of land use suggests that the "reference area" approach may be faulty. The existing vegetation on a plot of ground is not necessarily what would be there under undisturbed conditions. The reference vegetation may have been perturbed by Indians and Europeans, off and on in various ways for 10,000 years. It is difficult to establish "potential vegetation" of a plot in an historical sense.

Second, succession is fickle, following various trajectories in the same general area due to local site differences as well as to a series of stochastic processes associated with any successional or other
ecosystem process. What if these two sites, reference and disturbed, represent two different trajectories whose compositions cross only at the time of initial measurement? To force the mined site to mimic the reference site is costly, highly artificial, and might be useless without constant site management. One needs to know more about the total successional trajectory of both sites to be sure that, through time, all of their points are coincident and that they do not merely intersect at an instant in “ecological time.”

Third, it is possible that the intensity and extent of the perturbation of a site may have altered the very nature of that site and its capacity to support an ecosystem. In this sense, the site represents the potential for the development of a novel ecosystem, and attempts to enforce establishment of the old type, in an altered universe, can only be costly and doomed to failure.

Another interesting and related problem, one with a uniquely human basis, involves perception of good versus bad, healthy versus sick, natural versus unnatural, or other states that rest on a value judgment. The same vegetation, seen by two individuals, supposedly imparts the same empirical knowledge to the observer. However, these “data” are filtered through each person’s experience, ideals, etc., and thus may be interpreted differently. This flavors decisions in such a way that they are made on untenable premises. For example, implicit in the mining law is the perception that returning a site to a state where it is homomorphic with the reference area is “good,” that native species are “good,” and that anything that differs is “bad.” As I contend below, there may be alternatives, new ecosystems, that while different in terms of appearance and composition, may be more ecologically and economically sound and, in my perception, “better.”

Biome specific-reconstruction. Elsewhere I have argued that the most critical process in any successional sequence may differ from biome to biome (MacMahon 1981). Thus, while ecesis might be the bottleneck to revegetation in deserts with their low and unpredictable rainfall, this is not likely to be the case in the humid, temperate southeastern United States. Similarly, animals are often important

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1A biome is simply a unit of landscape that repeats itself worldwide and that has a particular appearance (physiognomy). This appearance is inferred to be caused by the occurrence of organisms in a similar climatic regime. Examples of biome types are deserts, grasslands, deciduous forests, tundra, etc.
vectors of plant propagules in forests, particularly rain forests, while this is seldom the case in tundra. In the two systems then, we might manage differently the migration process to suit human needs.

The implication is that the entire management strategy should consciously incorporate an analysis of the real bottlenecks, i.e., critical successional processes to ecosystem reconstruction. Why should we, on a particular site, manage a process that will occur in a suitable manner without management while ignoring another process just because that process is not important elsewhere? A high degree of site-specific planning is required. General ecological principles and their global applicability may offer more insight than do strict management principles which are tailored to and highly successful in a different biome.

Native versus non-native species. The exclusive use of native species to reconstruct disturbed ecosystems is an error. If the site is highly altered, non-native (foreign to that site) species might enhance reconstruction efforts. The counterargument to this position is that the introduction of non-native species has caused many management problems in the past. We need only observe parts of Cache Valley in the spring to see species like Dyers woad (Isatis tinctoria) or cheatgrass (Bromus tectorum) which dominate the aspect of our hillsides and often the functioning of hillside ecosystems to reinforce this view. In fact, while there are often problems with species introductions, an examination of facts and some ecological concepts suggests that we need not reject this possibility totally.

First, contrary to popular opinion, introductions do not always lead to the extinction of the native species (Table 2). Second, not all introductions lead to uncontrolled population explosions of the introduced species. A backyard is an example of a place where numerous non-native species are introduced, but where they remain in check for various reasons, including:

1) The species is appropriately managed by man.
2) The species cannot reproduce or is very slow to reproduce.
3) The species' range of tolerance to the environment limits its distribution and it cannot "escape" very far from its point of introduction.
TABLE 2. Effects of species introductions on native species. Includes data on plants through vertebrates. Obviously the values are crude estimates.*

<table>
<thead>
<tr>
<th>Introductions = Effects + No effects</th>
<th>854</th>
<th>176 (20.6%)</th>
<th>678 (79.4%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effects = Extinction + Other Effects</td>
<td>176</td>
<td>71 (40.3%)</td>
<td>105 (59.7%)</td>
</tr>
<tr>
<td>Extinction = Predation + Habitat Change + Competition + Other</td>
<td>71</td>
<td>50 (70.4%)</td>
<td>11 (15.5%)</td>
</tr>
</tbody>
</table>


Clearly then, we can take these leads to establish non-native species as components in the reconstruction of disturbed ecosystems. This is possible if species are carefully screened for certain key characteristics, for example:

1) Annuals are usually less desirable than perennials—the extremely high reproductive capacity and physiological tolerance of annuals, as mentioned earlier, may permit them to escape and "get out of hand." Perennials, once established, will persist for long periods of time, even without reproduction, and they can be replaced as they senesce.

2) Only species for which there is already an appropriate control mechanism should be chosen. A species which is introduced may require control if it is to be successful in the sense of being confined to the area of intended use. Most importantly, the control should be developed before introduction—not after.

3) Introduced species should have environmental tolerance ranges which are broad enough to suit them to the target area, but narrow enough to limit them to the target area. In this context, creative breeding of exotic species may allow us to develop "species" ideal for our purposes. Certainly, the grass breeding program of the United States Department of Agriculture Laboratories at Utah State is a good example of this type of genetic manipulation.
4) Introduced species should be relatively independent of other species, i.e., if a species depends inextricably on other species, its probability of extinction is its own innate extinction probability times that of its associate and thus survivorship becomes a less likely event. If series of species each requires all the others, the effect is even more obvious (Fowler and MacMahon 1982).

The above caveats do not form an exhaustive list, but they suggest that proper ecologically based selection of species might permit us to form artificial ecosystems, or at least ecosystems with non-native components, that might suit altered landscapes better than purely native mixes. Such ecosystems with minimum management inputs might meet measurable human needs as well as our less easily defined desires relating to aesthetics.

Community architecture. Commonly, architecture refers to the structure and design of things. Here it is used to refer to the geometric structure of ecosystems without regard to the component species. I specifically include two components, the vertical and the horizontal. The vertical component includes layers of vegetation, forms of branches, leaves, etc., in the layers. The horizontal component includes the organism-organism distance (dispersion) and the geometric complexity and style of the horizontal component. In a sense, the architecture of an ecosystem is the three-dimensional detail of its vertical or horizontal components projected onto a plane, much like a photograph.

My simple contention is that architecture is often more important in determining the reconstruction of ecosystems than is the exact species composition per se. This is linked to the use of non-native plants for reconstruction, i.e., the proper ecosystem architecture may be obtained with several different species, native and non-native.

Our own work shows that, for communities of spiders and birds, whether in the desert or in subalpine or southwestern oak forests, architecture is an important determinant for species occurrences. The implication is that in one of two ways architecture determines animal community composition. First, a certain animal species may require a certain form of tree in which to breed, e.g., one where holes can occur. Trees that do not provide holes cannot support the bird—but the bird can use a hole in any tree species, native or non-native. This type of relationship is well known and has been summarized for insects.
Another example is that birds frequently use man-made objects for breeding sites when clearly they did not use these before European man, e.g., nesting under bridges, in barns, etc. Each of these cases shows a general response of an organism to a particular form, rather than to a particular species or even just to a living organism.

The horizontal component is more difficult to work with. However, we know that while desert mammals do not respond to vertical architecture, they do respond to plant cover and spacing (MacMahon 1976). These responses are not limited to animals. Plants are known to occur in characteristic dispersion patterns, and it is even possible that these patterns change predictably as succession progresses. The cause of these patterns could be competition for water keeping individuals spaced apart or, in other cases, plants might be clumped so that their aggregated stems act as a drift fence to accumulate wind- or water-borne particles of organic matter.

When reconstructing ecosystems, if we plant according to final horizontal architecture, we may shorten successional time—the period to reestablish the normal pattern. If we use non-native species, species which will develop an architecture which mimics native species, these are likely to work better—enhance establishment of native animals and plants more readily—than native species which provide an inappropriate architecture.

It turns out that these relationships have importance at several scales in addition to that of the local plot we have discussed. Previously, I alluded to urban effects on bird species. Urban areas support mainly non-native trees. Some native birds use them—but not in the same species mixes as in native forests. This may be due not to the fact that these are non-native trees but to the fact that trees in residential areas are scattered on a lot and thus the lot-to-lot, neighborhood-to-neighborhood effect is to have an open, very broken canopy—not very forest-like. It has been proposed that merely rearranging house lot layout would create extensive “forest” islands and thus support a near native bird species mix (Figure 3) (Goldstein et al. 1981). The same would be true for insects, mammals, or any plant or animal, which has specific architectural requirements.

Finally, at yet another scale, the broad spatial architecture by which we preserve our wildlands is important. Above I argue that it
Some tree planting schemes for lots of different geometries:

A. Horizontal block (grid) subdivision pattern of developing 0.1 ha (approximately 1/4 acre) single family building lots;

B. & C. Circular and square subdivision patterns which allow clumping of privately owned woodland patches into a large circular breeding bird habitat;

D. Hexagonal subdivision pattern of eighteen 0.1 ha single family building lots. This pattern allows a large circular breeding bird habitat plus the efficient assembly of large residential developments since hexagons pack efficiently together into a honeycomb shape.

From Goldstein et al. 1981. Used with permission.
might be possible to use non-native species for reconstruction of disturbed ecosystems. This does not imply that I suggest elimination of native species. Quite the contrary, every species represents a unique gene pool that might be needed someday. But our planning of nature reserves usually is based on expediency rather than on a clear idea of what shape or size or number of reserves is needed to maintain the integrity of ecosystems. Small or linear tracts of land have a high ratio of impact from surrounding areas. Circular areas have the last perimeter/area ratio and would appear to be geometrically more sound. Often, since species might become extinct, replicate areas might be better than one huge area and so on. Thus, at all scales, from the angle of the insertion of a leaf upon a stem as a proper insect nest site to the geometry of native reserve site plans, architecture is an important, underutilized domain of ecological interest and of potential importance.

To summarize, my message is similar to a current television commercial where a man says, "You can pay me now to do 'X' or suffer the consequences of your oversight and pay me more later." In the case of ecosystem disturbance, we may spend time and money to carefully study the history, status, and dynamics of an ecosystem in order to develop a sound management plan, one that will produce a self-sustaining system meeting human needs and desires, or we may pay the constant, ongoing, extensive costs of continuous management of a system that is inherently unstable and that must have its very persistence enforced by human intervention. Obviously, I am biased since I believe that nothing succeeds like succession and that attention to this process is the only reasonable scheme for managing our human lot.
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