Restoration and Rehabilitation of Degraded Ecosystems in Arid and Semi-Arid Lands. I. A View from the South

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Abstract

A general model is presented describing ecosystem degradation to help decide when restoration, rehabilitation, or reallocation should be the preferred response. The latter two pathways are suggested when one or more "thresholds of irreversibility" have been crossed in the course of ecosystem degradation, and when "passive" restoration to a presumed predisturbance condition is deemed impossible. The young but burgeoning field of ecological restoration, and the older field of rehabilitation and sustainable range management of arid and semiarid lands (ASAL), are found to have much in common, especially compared with the reallocation of lands, which is often carried out without reference to pre-existing ecosystems. After clarifying some basic terminology, we present 18 vital ecosystem attributes for evaluating stages of degradation and planning experiments in the restoration or rehabilitation of degraded ecosystems. Finally, we offer 10 hypotheses concerning ecological restoration and rehabilitation as they apply to ASAL and perhaps to all terrestrial ecosystems.

In the nations of the "North," where restoration ecology has mostly been pursued thus far, aesthetic or intrinsic values (Naess 1986) have motivated most efforts to date. The primary goal has been to create "living museums," or to put things back as they once were. On the other hand, the vast literature of ecology applied to agriculture, forestry, and range management in the "South," particularly in arid and semiarid lands (ASAL), takes for granted that people will continue to be the dominant force in both natural and agro-ecosystems. The main issues are, first, whether primary and secondary productivity can be increased or sustained by new management techniques and, second, what effects these techniques might have on biodiversity and ecosystem stability. The models and ideas guiding these applied fields have mostly come from sources other than restoration ecology and conservation biology. Nevertheless, we believe that range managers, agronomic engineers, conservation biologists, and restoration / rehabilitation ecologists could all benefit from greater exchange of ideas and methodology, both in the rich North and the poorer South (see Dyksterhuis 1949; Bradshaw 1983; Jordan et al. 1987).

At a higher level, it is the fragmentation and degradation of entire landscapes that both restorationists and rehabilitators must combat. When economic and cultural practices are modified in the direction of ecological sustainability and conservation of biodiversity, and when restoration or rehabilitation is applied to all partially degraded ecosystems, with the help of all the necessary and appropriate scientific disciplines, the result would be-to borrow a phrase from Hobbs and Saunders (1991)—an attempt at "reintegration of fragmented landscapes" (Fig. 1).

After clarifying some basic terminology, we will discuss 18 vital ecosystem attributes for evaluating degradation and planning experiments in the restoration or rehabilitation of degraded ecosystems. Finally, we offer 10 hypotheses concerning ecological restoration and rehabilitation.

Basic Terminology

Restoration Sensu Stricto and Sensu Lato. Restoration of degraded ecosystems can be likened to the restoration of a Renaissance painting that has deteriorated over time but still reveals its initial lines and colors sufficiently for the fine arts restorator to do his or her work. Analogously, ecological restorationists seek a complete or near-complete return of a site to a pre-existing state. The Society for Ecological Restoration (SER) defines restoration as "the intentional alteration of a site to establish a defined indigenous, historic ecosystem. The goal of this process is to emulate the structure, functioning, diversity, and dynamics of the specified

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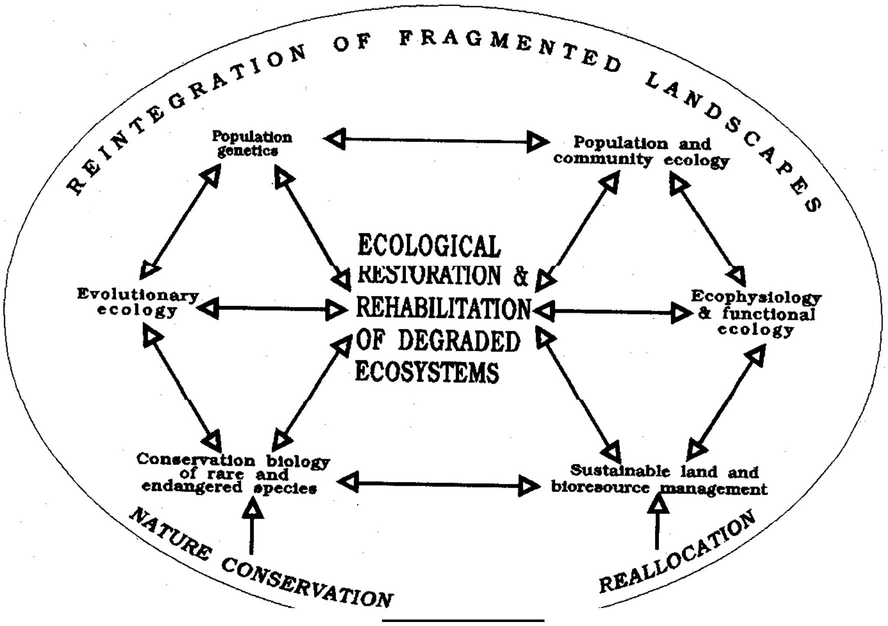

Figure 1. Relationships and potential pathways for exchange among ecological restoration and rehabilitation of degraded ecosystems and various branches of ecology, conservation biology, and sustainable land and bioresource management, including soil science.

ecosystem.” Implicit in this definition is the notion that restoration seeks to reassemble, insofar as possible, some predefined species inventory.

However, since it is rarely possible to determine exactly what historic or prehistoric ecosystems looked like or how they functioned, let alone establish the full species list of indigenous communities, restoration efforts may be plagued by ambiguities in both their goals and criteria of success (Cairns 1989, 1991; Simberloff 1990). We suggest using the term “restoration *sensu stricto*” to describe endeavors corresponding to the SER definition, as opposed to restoration *sensu lato,* which seeks simply to halt degradation and to redirect a disturbed ecosystem in a trajectory resembling that presumed to have prevailed prior to the onset of disturbance.

Despite this difference, the primary goal of both *sensu stricto* and *sensu lato* restoration is the conservation of indigenous biodiversity and ecosystem structure and dynamics. They thus differ from a third possible response to ecosystem degradation, which we call rehabilitation.

Rehabilitation. Rehabilitation, in our sense, seeks to repair damaged or blocked ecosystem *functions,* with the primary goal of raising ecosystem *productivity* for the benefit of local people. Moreover, it attempts to achieve such changes as rapidly as possible. However, a rehabilitation project resembles a restoration attempt in adopting the indigenous ecosystem’s structure and functioning as the principal models to be followed, insofar as they can be determined or guessed. That is, they both aim at recreating autonomous or self-sustaining ecosystems, which are characterized by biotic change or succession in plant and animal communities, and the ability to repair themselves following natural or moderate human perturbations. Thus, restoration and rehabilitation projects must also share as explicit or implicit working goals the return to former paths of energy flow and nutrient cycling, and the reparation of conditions necessary for effective water infiltration and cycling throughout the ecosystem’s rhizosphere (Allen 1988, 1989; DePuit & Redente 1988). However, whereas restoration *sensu stricto* invariably seeks a direct and full return to the indigenous, historic ecosystem, restoration *sensu lato* and, particularly, rehabilitation may settle on one of many possible alternative steady states, or a synthetic “simplified ecosystem” as an intermediate step in their long-term goals (Fig. 2). The alternative steady states might or might not have occurred in the process of degradation of the original, predisturbance ecosystem. In any case, they are-like our so-called “simplified ecosystems”-a practical method for designing, managing, and evaluating ecosystem-level experiments (Fig. 2).

What we call rehabilitation has often been called reclamation, particularly in conjunction with mine-tailing revegetation (Bengson 1977; Bradshaw 1987). But reclamation has also been used synonymously with both restoration and with some examples of what we call reallocation.

Reallocation. A general term is needed to describe what happens when part of a landscape, in any state, is assigned a new use that does not necessarily bear an intrinsic relationship with the predisturbance ecosys-

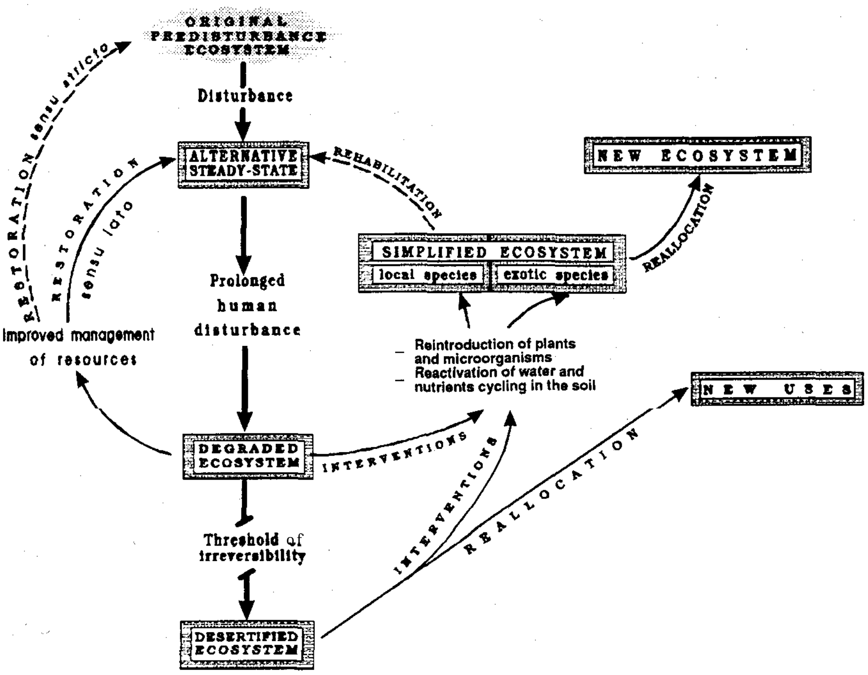

Figure 2. General model of ecosystem degradation and the possible responses to it. The original predisturbance ecosystem is pictured in a cloudlike space to indicate that it is frequently ambiguous.

tern's structure or functioning. We call this reallocation. For simplicity's sake, reallocation pathways in Figure 2 are indicated only after various stages of ecosystem degradation have taken place and one or more thresholds of irreversibility have been crossed. In reality, it can occur in the case of a slightly disturbed ecosystem or even an undisturbed (predisturbed) one. Problems arise when reallocated sites sprawl over landscapes in a more or less anarchic fashion.

In contrast with restoration and rehabilitation, reallocation assumes a permanent managerial role for people and normally requires ongoing subsidies in the form of energy, water, and fertilizers. The huge plantations of the fodder shrubs in North Africa, such as *Atriplex, Acacia,* and *Opuntia* spp., are examples of reallocation. By contrast,. the native perennial grasses we have introduced or reintroduced there (Chaïeb 1990; Chaïeb et al. 1992*a*, 1992b) survive direct grazing, reproduce sexually, and eventually become naturalized. They form part of a rehabilitation experiment.

Ecosystem of Reference. As Cairns (1991), Simberloff (1990), and Sprugel (1991) point out, it's often not clear what ecological yardstick is being used when a restoration or rehabilitation experiment is being set up. Yet for purposes of project design and evaluation, it is desirable to establish ahead of time some standard of comparison and evaluation, even if it is arbitrary. We call this the ecosystem of reference. In restoration, this will normally correspond to the SER's "indigenous, historic ecosystem," but in some rehabilitation (and, of course, reallocation) projects, it may be something entirely different, depending on the state of advancement of the ecosystem's degradation and on the needs of landowners or local people.

Alternate Steady-States. It is often assumed that if ecosystem degradation has not progressed too far, a return to an "indigenous, historic" state is possible simply by removing anthropic stresses (intentional fires, wood clearing, overgrazing, etc.) and allowing natural processes to do the rest. Yet in ASAL, this is rarely the case (Smeins et al. 1976; West et al. 1984; Westoby et al. 1989; Omar 1991). In the ASAL, including Mediterranean climate regions (Naveh 1988), it seems more reasonable to seek a return to an intermediate or alternative steady-state, such as a quasi-metastability that can be created and maintained by continual but relatively light human disturbance. Some disturbances are, of course, created in the absence of people, such as natural fires, hurricanes, volcanos, epidemics, but these appear to be rare in the ASAL. This still implies introducing new attitudes, insights, and-above all-enlightened management techniques to local people (Goodloe 1969; Lange 1969; Janzen 1986), particularly if indigenous ecosystems have already crossed one or more thresholds in the course of their degradation.

Threshold of Irreversibility. The concept of "thresholds" of environmental change is well established in ecology (Holling 1973; May 1977; Wissel 1984), and has recently been applied to range management as well (Friedel

1991; Laycock 1991). Still, "thresholds of irreversibility" are not easily detected or quantified, but once having passed through one, most ASAL ecosystems apparently cannot cross back without interventions designed to correct the specific changes that led to the threshold being crossed. For example, reconstitution of seed banks might be needed, or the restocking of soil organic matter and microorganisms that promote higher plant establishment and growth. Where truncation of upper soil layers, sedimentation, salinization, or other processes have drastically modified surface and sub-soils, reconditioning of soils or reactivation of their hydrological functioning may be required.

Restating one difference between rehabilitation and restoration, we can now say that the former often needs to jumpstart a new ecosystem trajectory and combat the conditions that constitute any existing thresholds of irreversibility. By contrast, most restoration projects begin in situations where no thresholds of irreversibility have yet been passed.

Resistance and Resilience. Resistance is an ecosystem's inertia in the face of change (Margalef 1969; Holling 1973), and resiliency is its ability to return to a former successional trajectory after being degraded or deflected by outside disturbances (Connell & Slatyer 1977). Resilience may be the best indicator of ecosystem health or integrity (Leopold 1948). Stability is the general concept embracing both resistance and resilience (Westman 1978).

May (1977), Westman (1978), Willis (1963), and others have proposed mathematical models of dynamic resistance and resilience for a number of theoretical systems, but practical ways of measuring it are seldom discussed. Walker et al. (1981) proposed as two possible measures the coefficient of variation of productivity in different trajectory phases and the rate of return to a former level of productivity following specific interventions (see Noy-Meir & Walker 1986; Westoby et al. 1989). Clearly, these measures are more relevant to rehabilitation than to restoration. For the latter, some measure of ecosystem structure, including its biodiversity, will be needed as well.

One point worth emphasizing is that resilience and resistance are often unconnected (Noy-Meir 1974; Naveh & Lieberman 1984). Moreover, we argue that no generalization or equation about either one can apply to the entire diachronic process of an ecosystem trajectory. Instead, they should be employed only in the context of a specific phase of retrogressive or progressive succession bounded by a "ceiling" and a "floor." We suggest that within a given phase of degradation, increase of resistance and of resilience can be inversely related.

Vital Ecosystem Attributes

Noble and Slayter (1980) defined several categories of vital attributes of life history useful in determining the response of a species to recurrent disturbance. Here we modify Noble and Slayter's concept. We define as vital ecosystem attributes (VEA) those characteristics or attributes that are correlated with and can serve as indicators of ecosystem structure and function. They should help in formulating predictions and designing experiments in both restoration and rehabilitation. One may object that many of these VEA are not readily obtainable under normal project conditions. Many of them are interrelated however, and determining one may allow an accurate estimation of other more difficult ones. Quite some time ago, Odum (1969) also constructed a list of ecosystem attributes to compare "developmental" and "mature" stages of ecological succession. Disappointingly little has been done since then to test his ideas of the "strategy of ecosystem development."

I. Vital Ecosystem Attributes as Related to Ecosystem Structure. Given the dramatic changes in many ecosystems' physiognomies from summer to winter, or, in many ASAL, from wet to dry seasons, this first group of VEA should be measured or calculated at the end of the main growing season-typically in late spring for arid, temperate ecosystems, or the end of the main rainy season in the tropical and subtropical arid zones-when maximum expression of alpha, beta, and gamma diversity is found. Ideally, they should be recorded for several successive years. These attributes are as follows:

(1) perennial species richness,
(2) annual species richness,
(3) total plant cover,
(4) aboveground phytomass,
(5) beta diversity,
(6) life form spectrum,
(7) keystone species,
(8) microbial biomass, and
(9) soil biota diversity.

Both (1) *perennial species richness* and (2) *annual species richness* are relatively easy to obtain through replicated relevés and, when combined, reveal structural differences among phases in an ecosystem's succession or retrogression. Perennials appear to occupy a dominant position in most terrestrial and aquatic ecosystems under relatively stable conditions (Frank 1968). By contrast, some successional stages of many semiarid ecosystems are characterized by very large numbers of annual species. Thus, where possible, it is useful to have data on the species composition of the ecosystem of reference. Similarly, low soil fertility is sometimes associated with high annual species diversity-in certain temperate grasslands (Gough & Marrs 1990) and savannas (Scholes 1989), for example. Finally, some perennials become abundant, pesty invaders under conditions of prolonged disturbance.

Among perennials, *it* is useful to distinguish between herbaceous and woody species, since the interactions of woody and herbaceous layers are important factors in many of the ecosystems most subject to prolonged use and anthropic degradation (such as savannas, semi-arid grasslands, arid shrublands) (Walker & Noy-Meir 1982; Ovalle & Avendaño 1987; Archer et al. 1988). The ratio of annuals to perennials can be revealing as well.

(3) Total plant cover is a good integrator of VEA 1 and 2, but may vary significantly within and among years (Whittaker 1972). In some cases, such as Sahelian savannas, total ligneous plant cover is a more useful indicator. Moreover, absolute cover alone, even when combined with species richness, does not provide much insight into ecosystem productivity. Thus, two important corollaries are (4) *Aboveground phytomass* (kg dry matter per 10 or 10,000 m^2) which is best measured at the end of the main growing season, and biomass productivity, which will be described below.

(5) *Beta diversity* is defined as the "extent of species replacement or biotic change along environmental gradients" (Whittaker 1972). MacArthur (1965) and Wilson and Shmida (1984) have established the importance of determining beta diversity in addition to alpha diversity (the number of species within community samples) as components of overall diversity. In one study (Frank & McNaughton 1991), plant community diversity was found to be positively correlated with resistance to change in species composition when perturbed by drought.

(6) Life form spectrum, first defined by Raunkiaer (1934), is an additional indicator of ecosystem structure and, probably, of functioning as well. As for beta diversity, the range of life forms in an ecosystem usually decreases with degradation.

(7) *Keystone species* are those species critical to ecosystem structure and functioning. The concept is known primarily from the literature of food webs and conservation biology (such as Paine 1969; Gilbert 1980), yet it seems appropriate in restoration ecology as well. Thus, an attempt to reorient the trajectory of a disturbed ecosystem may be facilitated by carefully reintroducing or increasing the density of keystone species and, where necessary, by the de-emphasis of the survival of other species (Simberloff 1990).

Given the growing body of empirical evidence of the importance of perennial, nitrogen-fixing legumes in undisturbed ASAL ecosystems (Jenkins et al. 1987; Jarrell & Virginia 1990) as well as in alternative steady-state systems found in Mediterranean-climate regions and savannas (Knoop & Walker 1985; Ovalle & Avendaño 1987; and others), we assume that perennial, nitrogen-fixing legumes are among the keystone species in many ecosystems, including those in our study areas in central Chile, southern Tunisia, and northern Cameroon (Aronson et al. 1992).

Once identified or at least specified in a working hypothesis, keystone species may logically be among the first candidates for experimental reintroduction to disturbed ecosystems. However, since plant reintroduction is an expensive, risky option that commits personnel to long-term monitoring and management, it is well to assess the methods to be employed and the risks they present (Hughes & Styles 1987). Different provenances of introduced nitrogen-fixing legumes can vary dramatically in their impact on herbaceous plants and soils (Reetu Sharma & Dakshini 1991).

If nitrogen-fixing trees and shrubs are keystone species, then their associated rhizobial and other microsymbionts must be so considered as well (Dommergues & Krupa 1978). Although they are less well documented and understood than higher plants, it seems likely that many of the spatial and temporal considerations mentioned for keystone plant species will be found to apply to microsymbiont keystones as well.

Accordingly, *(8) microbial biomass* and, particularly, *(9) soil biotu diversity* should both be estimated when possible. Soil microorganisms have a tremendous impact on vegetation in ASAL and other terrestrial ecosystems (Whitford & Elkins 1986; Carpenter & Allen 1988; Virginia 1986). For example, soil bacteria, especially *Rhizobium* play a critical role in plant competition in a grass-legume community (Turkington et al. 1988). Mycorrhizae can regulate competition between plants of different successional stages (Allen & Allen 1984; also see Nelson & Allen in this volume).

The most probable number technique allows estimates of microbial biomass. Soil biota diversity is also amenable to quantification; just as information on aboveground abundance and diversity is critical, it is important to carry out inventories of heterotrophic nitrogen-fixing bacteria and other microorganisms such as rhizobia and endo- and vesicular-arbuscular mycorrhizae.

II. Vital Ecosystem Attributes Related to Ecosystem Function. The second group of attributes are as follows:

(1) biomass productivity,
(2) soil organic matter,
(3) maximum available soil water reserves,
(4) coefficient of rainfall efficiency,

(5) rain use efficiency,
(6) length of water availability period,
(7) nitrogen use efficiency,
(8) microsymbiont effectiveness, and
(9) cycling indices.

(1) *Biomass productivity* (kg biomass $ha^{-1}yr^{-1}$), a complement to total cover, is of concern to rehabilitation projects. These indicators are nonetheless insufficient to give all the information required by an ecosystem manager, despite Margalef's (1969) generalization that the ratio of standing biomass to annual productivity increases with increased maturity of an ecosystem. Some ecosystems are actually more productive (in terms of kg per unit area per unit time) during early stages of degradation (Odum et al. 1979) than in the predisturbance state. This is due to the rapid colonization by nitrophilous weeds, typically including annual Asteraceae and grasses, but occasionally some woody legume species as well. In advanced stages of degradation, productivity invariably declines drastically. Thus, additional vital ecosystem attributes are needed to describe ecosystem function.

(2) Soil organic matter content is a readily accessible and highly revealing attribute that complements vital ecosystem attributes (5) and (6). For example, there is a positive correlation between organic carbon content and aboveground phytomass in some subtropical soils (Lugo et al. 1986). Low levels of organic matter also directly influence soil features critical to seedling establishment and to water and root infiltration in arid and semiarid lands (Le Houerou 1969; César 1989). Accordingly, there is great interest in the study of leaf litter, detritivores, and other potential contributors to organic matter in these systems (Schaeffer & Whitford 1981).

(3) Maximum available soil water reserves have great importance in ASAL where rainfall is irregular, even if they are not always readily obtainable. For example, in the Tunisian and Cameroonian case studies of Floret & Pontanier (1982) and Seiny-Boukar et al. (1992), soil profiles are shallow and water reserves can be easily measured and have been correlated with productivity. The differential influence of water reserves on the aboveground biomass productivity of several native shrub and perennial grass species of the steppes of southern Tunisia is quite dramatic (Chai'eb et al. 1990), and their measure has been used in the design of ecosystem projects in that region (Chai'eb et al. 1992*a*, 1992b). Similar data on North American grassland species have been used in the experimental restoration and management of prairies (Burton et al. 1988).

(4) *Coefficient of rainfall efficiency* is defined as the amount of water infiltrating to middle and deep soil layers, and it is thus an indicator of soil surface conditions and of the absorption capacity of soils (Chaïeb et al. 1992a). All water infiltrating past the soil surface is of course not necessarily used by plants. Yet, as for maximum available soil water reserves, coefficient of rainfall efficiency is a useful indicator of soil conditions in ASAL and elsewhere. It is closely tied to the presence or absence of surface crusts, which form in degraded systems and tend to seal off soils against efficient infiltration of rainfall (Skujins 1991).

(5) Rain use efficiency equals the slope of the relationship between annual rainfall and aboveground phytomass production (Le Houerou 1984). In dryland systems and elsewhere, it serves as an excellent indicator of soils and, hence, of ecosystem productivity. Water use efficiency, expressed in terms of kg of aboveground biomass produced per mm of evapotranspirated water, is more accurate than rain use efficiency (Floret et al. 1983; Seiny-Boukar et al. 1992). However, rain use efficiency is easier to obtain in most situations and more useful for inter-regional comparisons.

(6) Length of water availability period in the soil is easily measured by successive tensiometer readings at different soil depths. When evaluated in conjunction with rain use efficiency, water availability period allows predictions of the seasonality, duration, and extent of plant growth, and helps guide species selection in early stages of restoration or rehabilitation projects (Chai'eb et al. 1992*a*, 199227).

(7) *Nitrogen* use *efficiency* is a vital attribute since, even in arid environments, available nitrogen and phosphorus (and other nutrients) can limit plant and animal growth as much as deficiencies in water can (Penning de Vries et al. 1980). There may be an inverse relationship between the amount of standing biomass in a system at a given moment and the amount of nitrogen in that biomass (Penning De Vries & Djiteye 1982; Vitousek 1982).

As currently defined for individual plants or populations, nitrogen use efficiency (NUE) combines (1) the instantaneous rate of carbon fixation per unit of nitrogen, and (2) the mean residence time of nitrogen in the plant (Berendse & Aerts 1987). Thus, NUE = A/L_n, where A is nitrogen productivity and $1/L_n$ is the mean residence time of nitrogen. The first component is essential, since a close linear relationship exists between relative growth rate and nitrogen concentration in plants (Ingestad 1979). The second component is important because nitrogen can reside in a plant for varying lengths of time before being discarded through the shedding of organs (Berendse & Aerts 1987). Under nutrient-poor conditions, a long mean, residence time may be favorable to the plant (Berendse 1985), whereas under nitrogen-rich conditions, high nitrogen uptake and rapid circulation are favored (Vitousek 1982).

However, clear differences in both nitrogen conversion rates and mean residence times exist in co-occurring species (Brown 1978; Berendse & Aerts 1987; Berendse et al. 1987). Although Vitousek (1982) suggested that nutrient use efficiency for a forest is the inverse of nutrient concentration in the aboveground litterfall, it remains to be clarified how exactly to apply the concept of nutrient use efficiency generally, to a complex ecosystem. One factor to consider is clearly the relationship between nutrient use efficiency and life form. For example, Muller and Garnier (1990) and Joffre (1990) have shown that some perennial grasses make more efficient use of nitrogen than congeneric annual grasses.

(8) *Microsymbiont effectiveness* is no less critical than biomass or diversity. Legume-Xhizobium couples represent the most widely used plant-bacterium association. However, introduced rhizobial strains often fail to survive in competition with indigenous strains, particularly under adverse soil conditions (van Elsas & Heijnen 1990; Asad et al. 1991). Thus, the successful use of a rhizobial inoculant requires knowledge of the abundance, diversity, and competitive ability of the indigenous strains as well as of the growth limitations of the inoculants selected for introduction.

Jarrell and Virginia (1990) suggest that soil cation accumulation in the soil root zone can be used to calculate both total water use during the lifetime of a given ecosystem and cumulative symbiotic A&-fixation. This suggests that empirical variables could be identified that would allow estimates of soil biota effectiveness, given a fixed amount and diversity of standing vegetation over a period of constant climate conditions.

(9) *Cycling indices* measure the ratio of the amount of energy or an element recycled in an ecosystem to the amount of energy or elements moving straight through the system (Finn 1976). Species richness and many other structural and functional attributes are correlated with soil nutrient levels and cycling (Willis 1963; Gough & Marrs 1990). For example, soil fertility has been found to have a controlling influence on rain use efficiency in savannas (Penning de Vries et al. 1980; Scholes 1989). Furthermore, since the degree to which a nutrient circulates freely in an ecosystem depends partly on its physical state, and is thus closely linked with hydrological conditions, cycling indices of N, P or other nutrients will also reflect on such vital ecosystem attributes as water reserves, water availability period, and coefficient of rainfall efficiency. Comparing the cycling index of nutrients (especially phosphorus and nitrogen) at different phases of an ecosystem's trajectory may thus be useful for evaluating relative perturbation or attempts at restoration or rehabilitation. Since ecosystems in a "mature" stage are thought to have a greater capacity to entrap and hold nutrients for internal cycling than in less mature, developing stages (Odum 1969), the achievement of tighter mineral cycles and reduced nutrient exchange rates between organisms and the environment should reveal that restoration or rehabilitation is being achieved. Furthermore, in efforts aimed at the reintegration of fragmented landscapes, cycling indices could measure interactiveness among interlocking ecosystems.

Discussion

As Bradshaw (1987) noted, the time has come to study the ecology of ecosystems. Both restoration and rehabilitation projects offer good opportunities to do so. It is also time to study the evolution or the trajectories of ecosystems in the process of degradation, restoration or rehabilitation. We have argued that restoration *sensu stricto* seeks to re-establish a full inventory of preexisting species, while restoration *sensu lato* is satisfied to reorient a disturbed ecosystem's trajectory in a direction ressembling its predisturbance state. Rehabilitation seeks the repair of ecosystem function above all, in the search for sustained productivity. Reallocation, when applied to agriculture or silviculture, assumes dependence on external subsidies and represents an unnatural situation of "perpetually interrupted succession" (Jarrell 1990).

If it is to distinguish itself from traditional forest or range management and rehabilitation agronomy (Malcolm 1990) on the one hand, and conservation biology on the other, restoration and rehabilitation ecology must show itself to be a maturing science by generating its own models and by testing hypotheses on ecosystems in retrogression or renewed succession. To begin, below are ten hypotheses.

Ten Hypotheses for Restoration and Rehabilitation Ecology.

- Beyond one or more thresholds of irreversibility, ecosystem degradation is irreversible without structural interventions combined with revised management techniques.
- The more thresholds passed, the more time and energy will be required for an ecosystem's restoration or rehabilitation.
- Without massive intervention, restoration will proceed only as far as the next highest threshold in the process of vegetation change or succession.
- Beta diversity and life form ranges decline with ecosystem degradation, while alpha diversity temporarily increases.
- The loss of keystone species speeds degradation more than the loss of other species. Such losses tend to occur simultaneously with the crossing of thresholds of irreversibility.

- The reintroduction of keystone species should accelerate rehabilitation of an ecosystem by facilitating the reintroduction and establishment of additional native species.
- Water and nitrogen use efficiency and nutrient cycling times decrease with ecosystem degradation.
- Diversity of soil biota and their compatibility with extant higher plants decrease with ecosystem retrogression.
- Between a floor and a ceiling of a given phase of retrogression, resistance increases but resilience decreases.
- The rate of recovery in restoration or rehabilitation pathways is inversely related to the structural and functional complexity of the ecosystem of reference.

Conclusion

As W. M. Schaffer (1985) pointed out, ecologists will probably never be able to write down the complete governing equations for the order in chaos that is any natural system. Experimental restoration and rehabilitation projects do, however, offer excellent opportunities for the elucidation of structural and functional dynamics of ecological systems. Our hypotheses will be difficult to test. We have included them here to stimulate discussion and empirical tests. Being rather simple and extensive, ASAL ecosystems and their biota seem ideal for such tests.

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LITERATURE CITED

Allen, E. B., editor. 1988. The reconstruction of disturbed arid lands. Westview Press, Boulder, Colorado.

Allen, M. F. 1989. Mycorrhizae and rehabilitation of disturbed arid soils: processes and practises. Arid Soil Research and Rehabilitation 3:229–241.

Allen, E. B., and M. F. Allen. 1984. Competition between plants of different successional stages: mycorrhizae as regulators. Canadian Journal of Botany 62:2625–2629.

Archer, S., S. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111–127.

Aronson, J., E. Le Floc'h, C. Floret, C. Ovalle, and R. Pontanier. In review. Restoration and rehabilitation of degraded ecosystems. II. Case studies in southern Tunisia, central Chile and northern Cameroon. Restoration Ecology.

Asad, S., K. A. Malik, and F. Y. Hafeez. 1991. Competition between inoculated and indigenous *Rhizobium/Bradyrhizobium* spp. strains for nodulation of grain and fodder legumes in Pakistan. Biology and Fertility of Soils 12:107–111.

Bengson, A. 1977. Drip irrigation to revegetate mine ~~wastes in~~ an arid environment. Journal of Range Management 30:143-147.

Berendse, F. 1985. The effect of grazing on the outcome of competition between plant species with different nutrient requirements. Oikos 44:35–39.

Berendse, F. and R. Aerts. 1987. Nitrogen-use efficiency: a biologically meaningful definition? Functional Ecology 1:293-296.

Berendse, F., H. Oudhof, and J. Bol. 1987. A comparative study on the nutrient cycling in wet heathlands ecosystems. I. Litter production and nutrient losses from the plant. Oecologia 74:174–184.

Bradshaw, A. D. 1983. The reconstruction of ecosystems. Journal of Applied Ecology 20:1–17.

Bradshaw, A. D. 1987. The reclamation of derilict land and the ecology of ecosystems. Pages 53-74 in W. R. Jordan, M. E. Gilpin, and J. D. Aber, editors. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge, England.

Brown, R. H. 1978. A difference in N-use efficiency in C-3 and C-4 plants and its implications in adaptation and evolution. Crop Science 18:93–98.

Burton, P. J., K. R. Robertson, L. R. Iverson, and P. G. Risser. 1988. Use of resource partitioning and disturbance regimes in the design and management of restored prairies. Pages 46-88 in E. B. Allen, editor. The reconstruction of disturbed arid lands. Westview Press, Boulder, Colorado.

Cairns, J., Jr. 1989. Restoring damaged ecosystems: is predisturbance condition a viable option? Environmental Professional 11:152- 159.

Cairns, J., Jr. 1991. The status of the theoretical and applied science of restoration ecology. Environmental Professional 13:1–9.

Carpenter, A. T., and M. F. Allen. 1988. Responses of *Hedysarum boreale* to mycorrhizas and *Rkizobium:* plant and soil nutrient changes in a disturbed shrub-steppe. New Phytologist 109:125–132.

César, J. 1989. L'influence de l'exploitation sur la pérennité des pâturages de savane. II. Role du système racinaire dans la degradation du patûrage. Fourrages 120:382–392.

Chaïeb, M., C. Floret, E. Le Floc'h, and R. Pontanier. 1990. Les graminees perennes, un recours pour la rehabilitation des terres de parcours degrades en zone aride tunisienne. Ecologia Méditerranea 16:415–425.

Chaïeb, M., C. Floret, E. Le Floc'h, and R. Pontanier. 1992*a*. Life history strategies and water resource allocation in five pasture species in the Tunisian arid zone. Arid Soil Research and Rehabilitation 6:1-10.

Chaieb, M., C. Floret, E. Le Floc'h, and R. Pontanier. 1992b. Rehabilitation d'écosystèmes pastoraux de la zone aride tunisienne par reintroduction d'especes locales. Proceedings of the IVth International Rangelands Congress. CIRAD, Montpellier, Vermont. In press.

Connell, J. M., and R. 0. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1144.

DePuit, E. J., and E. F. Redente. 1988. Manipulation of ecosystem dynamics on reconstructed semiarid lands. Pages 164-204 in E. B. Allen, editor. The Reconstruction of disturbed arid lands. Westview Press, Boulder, Colorado.

Dommergues, Y. R., and R. Krupa, editors. 1978. Interactions between non-pathenogenic soil microorganisms and plants. Elsevier, Amsterdam, The Netherlands.

Dyksterhuis, E. J. 1949. Condition and management of range land based on quantitative ecology. Journal of Range Management 2:104–115.

Finn, J. T. 1976. Measures of ecosystem structure and function derived from analysis of flows. Journal of Theoretical Biology 56:362–380.

Floret, C. 1981. The effects of protection on steppic vegetation in the Mediterranean arid zone of Southern Tunisia. Vegetatio 46:117–119.

Floret, C., and R. Pontanier. 1982. L'aridité en Tunisie présaharienne. Climat, sol, végétation et aménagement. Travaux et Doctorat de l'ORSTOM, no. 150.

Floret, C., E. Le Floc'h, and R. Pontanier. 1983. Phytomasse et produccion en Tunisie présaharienne. Acta Oecologia 4:133–152.

Frank, D. A., and S. J. McNaughton. 1991. Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. Oikos 62:360–362.

Frank, I'. W. 1968. Life histories and community stability. Ecology 49:355–356.

Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44:422–426.

Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11-33 in M. E. Soulé, and B. A. Wilcox, editors. Conservation biology: an evolutionary-ecological perspective. Sinauer, Massachusetts.

Goodloe, S. 1969. Short duration grazing in Rhodesia. Journal of Range Management 22:369–372.

Gough, M. W., and R. H. Marrs. 1990. A comparison of soil fertility between semi-natural and agricultural plant communities: implications for the creation of species-rich grassland on abandoned agricultural land. Biological Conservation 51:83–96.

Hobbs, R. J., and D. A. Saunders. 1991. Re-integrating fragmented landscapes-a preliminary framework for the Western Australian wheatbelt. Journal of Environmental Management 33:161–167.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Hughes, C. E., and B. T. Styles. 1987. The benefits and potential risks of woody legume introductions. International Tree Crops Journal 4:209–248.

Ingestad, T. 1979. Nitrogen stress in Birch seedlings. II. N, I', Ca and Mg nutrition. Physiologia Plantarum 45:149–157.

Janzen, D. H. 1986. Guanacaste National Park. Tropical ecological and cultural restoration. Editorial EUNED, San José, Costa Rica.

Jarrell, W. M. 1990. Nitrogen in agroecosystems. Pages 385-412. In C. R. Caroll, J. H. Vandemeer, and I'. M. Rosset, editors. Agroecology. McGraw Hill, New York.

Jarrell, W. M., and R. A. Virginia. 1990. Soil cation accumulation in a mesquite woodland: sustained production and long-term estimates of water use and nitrogen fixation. Journal of Arid Environments 18:51–56.

Jenkins, M. B., R. A. Virginia, and W. M. Jarrell. 1987. Rhizobial ecology of the woody legume mesquite *(Prosopis glandulosa)* in a Sonoran Desert arroyo. Plant and Soil 105:113–120.

Joffre, R. 1990. Plant and soil nitrogen dynamics in mediterranean grasslands: a comparison of annual and perennial grasses. Oecologia 85:142–149.

Jordan, W. R., M. E. Gilpin, and J. D. Aber, editors. 1987. Restoration ecology: a synthetic approach to ecological research. Cambridge University Press, Cambridge, England.

Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. Journal of Ecology 67:565–577.

Lange, R. T. 1969. The piosphere: sheep track and dung patterns. Journal of Range Management 22:396–400.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. Journal of Range Management 44:427–433.

Le Houérou, H. N. 1969. La végétation de la Tunisie steppique. Annals de l'Institut National de Recherche Agronomique de la Tunisie 42:1–622.

Le Houérou, H. N. 1984. Rain-use efficiency: a unifying concept in arid-land ecology. Journal of Arid Environments 7:213–247.

Leopold, A. 1948. A Sand County almanac. Oxford: Oxford University Press.

Lugo, A. E., M. J. Sanchez, and S. Brown. 1986. Land use and organic carbon content of some subtropical soils. Plant and Soil 96:185–196.

MacArthur, R. H. 1965. Patterns of species diversity. Biological Review 40:510–533.

Malcolm, C. V. 1990. Rehabilitation agronomy-guidelines for revegetating degraded land. Proceedings of the Ecological Society of Australia 16:551–556.

Margalef, R. 1969. On certain unifying principles in ecology. American Naturalist 97:357–374.

May, R. M. 1977. Thresholds and breaking points in ecosystems with a multiplicity of stable states. Nature 269:471–477.

Muller, B., and E. Garnier. 1990. Components of relative growth rate and sensitivity to nitrogen availability in annual and perennial species of *Bromus*. Oecologia 84:513–518.

Naess, A. 1986. Intrinsic value: will the defenders of nature please stand up? Pages 504-516 in M. Soulé, editor. Conservation biology. The science of scarcity and diversity. Sinauer, Massachusetts.

National Research Council. 1986. Ecological knowledge and environmental problem solving: concepts and case studies. National Academy Press, Washington, D.C.

Naveh, Z. 1988. Multifactorial reconstruction of semiarid Mediterranean landscapes for multipurpose land uses. Pages 234-256 in E. B. Allen, editor. The reconstruction of disturbed arid lands. Westview Press, Boulder, Colorado.

Naveh, Z., and A. S. Lieberman. 1984. Landscape ecology: theory and application. Springer-Verlag, New York, New York.

Noble, L. R., and R. 0. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5–22.

Noy-Meir, I. 1974. Stability in arid ecosystems and the effect of man on it. Pages 220-225 in A. J. Cove, editor. Structure, functioning and management of ecosystems. Proceedings of the first International Congress of Ecology, Pudoc, Wageningen.

Noy-Meir, I., and B. H. Walker. 1986. Stability and resilience in rangelands. Pages 21-25 in P. J. 'Joss, P. W. Lynch, and 0. B. Williams, editors. Rangelands: a resource under siege. Australian Academy of Science, Canberra, Australia.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262–270.

Odum, E. I'., J. T. Finn, and E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. Bioscience 29:349-352.

Omar, S. A. S. 1991. Dynamics of range plants following 10 years of protection in arid rangelands of Kuwait. Journal of Arid Environments 21:99–112.

Ovalle, C., and J. Avendaiio. 1987. Interactions de la strate ligneuse avec la strate herbacee dans les formations d'*Acacia caven* (Mol.) Mol. au Chili. I. Influence de l'arbre sur la composition floristique, la production et la phenologie de la strate herbacee. Oecologia Plantarum 8:385–404.

Paine, R. T. 1969. A note on trophic complexity and community stability. American Naturalist 103:91–93.

Penning de Vries, F. W. T., J. M. Krul, and H. van Keulen. 1980. Productivity of Sahelian rangelands in relation to the availability of nitrogen and phosphorus from the soil. Pages 95-113 in T. Rosswall, editor. Nitrogen cycling in West African ecosystems. Kluwer, Amsterdam.

Penning de Vries, F. W. T., and M. A. Djiteye., editors. 1982. La Productivité des pâturages Sahéliens. Pudoc, Wageningen.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. Oxford University Press, Oxford, England.

Reetu Sharma, A., and K. M. M. Dakshini. 1991. A comparative assessment of the ecological effects of *Prosopis cineravia* and *P. juliflora* on the soil of revegetated spaces. Vegetatio 96:87–96.

Schaeffer, D. A., and W. A. Whitford. 1981. Nutrient cycling by the subterranean termite *Gnathamitermes tubiformis* in a Chihuahuan desert ecosystem. Oecologia 48:277–283.

Schaffer, W. M. 1985. Order and chaos in ecological systems. Ecology 66:93–106.

Scholes, R. J. 1989. The influence of soil fertility on the ecology of southern African dry savannas. Journal of Biogeography 17:71–75.

Seiny-Boukar, L., C. Floret, and R. Pontanier. 1992. Degradation of savanna soils and the reduction of water use efficiency: the case of northern Cameroon vertisols. Canadian Journal of Soil Science In press.

Simberloff, D. 1990. Reconstituting the ambiguous-can islands be restored? Pages 37-51 in D. Towns, C. H. Dougherty, and I. A. E. Atkinson, editors. Ecological restoration of New Zealand islands. New Zealand Department of Conservation, Wellington, New Zealand.

Skujins, J., editor. 1991. Semiarid lands and deserts: soil resources and reclamation. Marcel Dekker, New York, New York.

Smeins, F. E., T. W. Taylor, and L. B. Merrill. 1976. Vegetation of a 25-year exclosure on the Edwards Plateau. Journal of Range Management 29:24–29.

Sprugel, D. G. 1991. Disturbance, equilibrium and environmental variability: what is "natural" vegetation in a changing environment? Biological Conservation 58:1–18.

Turkington, R., F. B. Holl, C. P. Chanway, and J. D. Thompson. 1988. The influence of microorganisms, particularly *Rhizobium* on plant competition in grass-legume communities. Pages 344-367 in A. J. Davy, M. J. Hutchings, and A. R. Watkinson, editors. Plant population ecology. Blackwell Scientific Publications, Oxford, England.

van Elsas, J. D., and C. E. Heijnen. 1990. Methods for the introduction of bacteria into soil: a review. Biology and Fertility of Soils 10:127–133.

Virginia, R. A. 1986. Soil development under legume tree canopies. Forest Ecology and Management. 16:69–79.

Virginia, R. A., L. M. Baird, J. S. La Favre, W. M. Jarrell, B. A. Bryan, and G. Shearer. 1984. Nitrogen fixation efficiency, natural ^{15}N abundance, and morphology of mesquite (*Prosopis glandulosa*) root nodules. Plant and Soil 79:273–284.

Vitousek, I'. M. 1982. Nutrient cycling and nitrogen use efficiency. American Naturalist 119:553–572.

Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology 69:473–498.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556-590 in B. H. Huntley and B. H. Walker, editors. Ecology of tropical savannas, Springer-Verlag, Berlin, Germany.

Weltsin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation in northwestern Kenya. Journal of Vegetation Science 6:325–334.

West, N. E., F. D. Provenza, P. S. Johnson, and M. K. Owens. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. Journal of Range Management 37:262–264.

Westman, W. E. 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28:705–710.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management 42:266–274.

Whitford, W. G., and N. Z. Elkins. 1986. The importance of soil ecology and the ecosystem perspective in surface mine reclamation. Pages 151-187 in C. C. Reith and L. D. Potter, editors. 1972. Principles and methods of reclamation science. University of New Mexico, Albuquerque, New Mexico.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21:213–251.

Willis, A. J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. Journal of Ecology 51:353–374.

Wilson, M. V., and A. Shmida. 1984. Measuring beta diversity with presence-absence data. Journal of Ecology 72:1055–1064.

Wissel, C. 1984. A universal law of the characteristic return time near thresholds. Oecologia 65:101–107.