

Disturbance, Diversity, and Invasion: Implications for Conservation

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Abstract: *Disturbance is an important component of many ecosystems, and variations in disturbance regime can affect ecosystem and community structure and functioning. The "intermediate disturbance hypothesis" suggests that species diversity should be highest at moderate levels of disturbance. However, disturbance is also known to increase the invasibility of communities. Disturbance therefore poses an important problem for conservation management. Here, we review the effects of disturbances such as fire, grazing, soil disturbance, and nutrient addition on plant species diversity and invasion, with particular emphasis on grassland vegetation. Individual components of the disturbance regime can*

have marked effects on species diversity, but it is often modifications of the existing regime that have the largest influence. Similarly, disturbance can enhance invasion of natural communities, but frequently it is the interaction between different disturbances that has the largest effect. The natural disturbance regime is now unlikely to persist within conservation areas, since fragmentation and human intervention have usually modified physical and biotic conditions. Active management decisions must now be made on what disturbance regime is required, and this requires decisions on what species are to be encouraged or discouraged.

Introduction

Preservation of natural communities has historically consisted of measures protecting them from physical disturbance. Timber harvests and livestock grazing are usually excluded from preserves, and fire suppression has been practiced—within the U.S. system of national parks, for example. Ecologists and conservationists have come to recognize, however, that many forms of disturbance are important components of natural systems. Many plant communities and species are dependent on

disturbance, especially for regeneration (Pickett & White 1985). Preserves should be large enough to allow the natural disturbance regime to operate and to support a mosaic of patches in different stages of disturbance, successional recovery, and community maturation (Pickett & Thompson 1978). In addition, both theory (the intermediate disturbance hypothesis, Connell 1978) and growing empirical evidence suggest that moderate frequencies or intensities of disturbance foster maximum species richness. To preserve biotic diversity and functioning natural ecosystems, then, conservation efforts must include explicit consideration of disturbance processes.

Disturbance acts in plant communities in another way, however, by promoting invasions by non-native

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and weedy plant species (Ewel 1986; Hobbs 1989, 1991; Rejmánek 1989). Invasive species have recently gained notoriety as major conservation and management concerns in natural ecosystems (see MacDonald et al. 1989; Soulé 1990; Westman 1990). The control of non-native plants has become one of the most expensive and urgent tasks of managers in several U.S. national parks, in island preserves such as the Galapagos, and elsewhere. Invasive plants can reduce or displace native species, both plant and animal, and may even alter ecosystem function (Vitousek 1986; Schofield 1989). They have become recognized, therefore, as significant conservation concerns.

Disturbance thus presents a conundrum to conservation management: the continued existence of particular species or communities often requires disturbance of some type—and hence disturbance regimes must be integrated with management plans—but disturbance may simultaneously lead to the degradation of natural communities by promoting invasions. Here we examine this problem by discussing the types of disturbance important in maintaining plant species diversity and those that encourage invasions. We identify particular cases where conflicts are most likely to arise. Our examples are drawn primarily from grassland vegetation, although we discuss other ecosystem types such as shrublands and woodlands. We close by suggesting guidelines for evaluating the proper role of disturbance in the management of a natural area or preserve.

Theoretical Background

There has been considerable debate on the definition of disturbance, and on what does and does not constitute a disturbance to any given community or ecosystem (see Rykiel 1985; van Andel & van den Berg 1987). Definitions of disturbance vary, from Grime's (1979) view of disturbance as a process removing or damaging biomass, to White and Pickett's (1985) definition of "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment." Petraitis et al. (1989) expand the definition further to include any "process that alters the birth and death rates of individuals present in the patch" by directly killing individuals or by affecting resource levels, natural enemies, or competitors in ways that alter survival and fecundity. Temporal and spatial scale are clearly important in our recognition of the "discreteness" of a disturbance event, as nearly any ecological or biogeochemical process might fall under the last, most inclusive definition. Pickett et al. (1989) define a disturbance as a change in structure caused by factors external to the hierarchical level of the system of interest; this is necessary to distinguish disturbance from other

changes in the system. In our discussion below, we will include both direct disturbances (those affecting the survivorship of individuals directly) and indirect disturbance (those affecting resource levels or other conditions that then influence individuals in the patch). Disturbances to plant communities thus include such events as fires, storms, and floods; but other changes such as altered grazing regimes or nutrient inputs would also be classed as disturbance if they affected resource levels and demographic processes.

Within a given patch, the response of any community to a disturbance (or to the disturbance regime, characterized by the natural distribution of disturbance sizes, frequencies, intensities, and timing) is determined by the attributes of component species. Disturbance frequency is also important; the time interval between successive disturbances can have significant effects on community response. This is because species composition changes with time since disturbance, and many species require some time after disturbance to reach reproductive maturity. If a second disturbance occurs before they reach that stage, there will not be any propagules available to recolonize the patch. The response of a community to disturbance is then predicted on the basis of the life history responses of those species available for recruitment or invasion (Noble & Slatyer 1980; Moore & Noble 1990).

There has been increasing recognition among ecological researchers of the importance of natural disturbance in the function of terrestrial ecosystems. Pickett and White (1985) provided a comprehensive review of the role of disturbance in the dynamics of many ecosystem types. They distinguished several components of natural disturbance regimes, including frequency, intensity, and size of disturbance (White & Pickett 1985), each acting in a distinctive way on communities and populations. Petraitis et al. (1989) presented a more detailed analysis of these components, and recognized that hypotheses about the relationship of disturbance and community response can be sorted into two groups: those postulating selective mortality or action for a specific target group, and those dealing with random or catastrophic mortality. Petraitis et al. (1989) suggested that selective mortality could maintain species diversity or richness at some equilibrium level, while random mortality would prevent the establishment of community equilibrium (for example, preventing the dominance of one superior competitor and the exclusion of other species). They pointed out that both equilibrium and nonequilibrium models of communities predict greatest species richness at intermediate levels of disturbance. Various versions of this "intermediate disturbance hypothesis" thus predict a similar result—highest species numbers when disturbances occur at intermediate frequencies or with intermediate intensities (Fig. 1)—despite different underlying theories of community

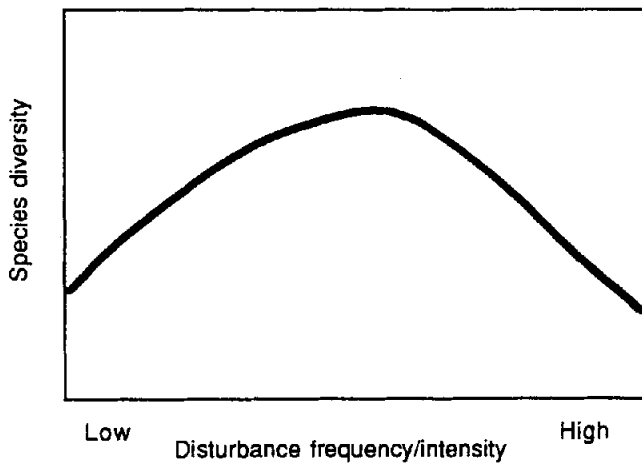


Figure 1. The intermediate disturbance hypothesis, which indicates that species diversity within a given patch should be highest at intermediate frequencies or intensities of disturbance (after Connell 1978).

function (see Fox 1979; Huston 1979; Sousa 1984). These arguments are often based on the fact that only a few species (ruderals) can persist in the face of frequent, severe disturbance; only a few species (the longest-lived, best competitors, and those able to regenerate without disturbance) can persist over the long term in the absence of disturbance; but many species (including some representatives of each of these, plus intermediates) can find some place to survive in a region comprising patches in various stages of recovery, arising at some intermediate frequency.

How is "intermediate" defined? It is perhaps easiest to relate the frequency of discrete events to the longevity of major species in the system. Approximately half the lifespan of the dominant species has been used as one estimation of intermediate disturbance frequency (Hobbs et al. 1984). Definitions of intermediate intensity may have fewer external referents, however; intensity can be evaluated in terms of percentage of individuals killed, or the degree of structural or resource alteration caused.

The above discussion concentrates on within-patch diversity (alpha diversity), but disturbance is also important for creating or maintaining diversity between patches or at the landscape level (beta diversity). By creating patches of different ages and successional stages, disturbance affects structural and habitat diversity as well as overall species diversity. While we concentrate on within-patch diversity in this review, the role of disturbance in creating landscape mosaics should also be noted (see Turner 1987).

While disturbance is important for maintaining diversity both within communities and at a landscape level, it has become increasingly recognized that disturbance may also have undesirable effects. Particularly important is the recognition that disturbance may act to increase

the likelihood of invasion of a community. For invasion to occur there must be available propagules of an invasive species capable of dispersing into a given plant community, and there then has to be a suitable microsite for germination and establishment to occur. That is, there has to be a suitable invasion "window" (Johnstone 1986). Disturbance usually acts primarily by affecting the availability of suitable microsites, although some forms of disturbance may affect the availability of invasive propagules. For instance, non-native herbivores may bring seed into an area either on their coats or in feces. Here we will discuss primarily the effect of disturbance on microsite availability.

The spatial and temporal distribution of disturbance in a region or an ecosystem gives rise to the disturbance mosaic of an area. Pickett and Thompson (1978) pointed out that the recurrence of disturbances necessitates the preservation of a "minimum dynamic area," or an area large enough to contain within it multiple patches in various stages of disturbance or recovery such that internal recolonization can contribute to the maintenance of the overall ecosystem. The dynamics of patch disturbance and of biotic exchanges among patches, which determine the pattern of recovery, are of major concern in defining the minimum critical size of ecosystems (see Lewin 1984), the size required to maintain characteristic species composition and system function. With increasing fragmentation of natural areas, it is likely that these minimum areas are now to be found only within the largest conservation units, and disturbance regimes and biotic exchanges between patches are liable to be significantly altered in smaller remnant areas (Hobbs 1987; Saunders et al. 1991). In particular, invasions are likely to become more important. How shall managers respond to or compensate for the changed nature of disturbance? We approach this question by surveying the major types of disturbance and reviewing their effects on plant species diversity and invasions. We mostly consider grasslands, but we also include illustrative examples from other vegetation types.

Empirical Evidence

1. Fire

The central role of fire in maintaining the open nature of the vegetation has been acknowledged for many grasslands, particularly in mesic regions. Further, research has documented that fire can stimulate or maintain high primary productivity. In tall-grass prairies of North America, fire enhances productivity by removing the thick litter layer and altering the microclimate and nutrient content of surface soil (see Knapp & Seastedt 1986). Fire also influences species diversity and the characteristic structure of these prairie communities. Classical work on fire ecology of prairies (Kucera &

Koelling 1964; Abrams et al. 1986) found that annual burning favored tall warm-season grasses and resulted in low abundance of typical prairie forbs after 5–10 years. Biennial burning resulted in the highest community diversity with mixed grasses and forbs. Areas with long fire-free periods resembled unburned areas in their heavy litter accumulation and decline in grasses.

Fires may favor the dominant "matrix" prairie grasses and thus can actually decrease diversity (Collins 1987). Apparently most prairie fires stimulate individual grasses and do not kill them; few openings are created for the establishment of new individuals or species. As we have noted previously, however, species diversity comprises two main components: species density or alpha diversity within a patch, and patch diversity or the number of types of different patches or microhabitats. Glenn-Lewin and ver Hoef (1988) reported that grasslands vary in the degree to which these two contribute to overall diversity. In three grasslands, patch diversity rather than species density was the major contributor to overall community diversity. Fire (and other disturbances) may create a heterogeneous patch structure, even if within patches it serves to decrease species density.

Life history, of course, determines the vulnerability and response of plants to fire. In annual grasslands in California, fire had only temporary effects on botanical composition (forbs increased and grass dominance decreased for a brief time). Here the restructuring of the community each autumn with germination quickly swamps any temporary effect on the seed bank or on germination conditions (Heady 1972).

Suppression of fires in ecosystems dominated by fire-adapted species can cause severe disruption of community and ecosystem processes, which may have implications for the conservation of native, fire-tolerant species. For example, Cowling et al. (1986) found that fire suppression has been responsible for the conversion of a South African open, grassy veld to a vegetation now dominated by undesirable non-native shrubs. They suggested frequent prescribed fires as the best mechanism for restoring the original open nature of the vegetation and for maintaining populations of the region's endemic geophytes. Strang (1973) similarly suggested that fire was an expensive but necessary part of reversing the conversion of moist grassland in south-central Africa to brush. Fire can also be used more precisely to favor the performance of one species over another. For example, in an attempt to restore prairie on the site of an abandoned agricultural site, fire was used successfully to create openings in a turf of non-native *Poa* species and to enhance the colonization and expansion of true prairie species (Curtis & Partch 1948).

As early work in tall-grass prairie confirmed, the overall fire regime rather than any single fire is the critical

factor in determining community response. Fires of differing intensity or occurring in different seasons are likely to affect species diversity in a variety of ways by altering the potential of individual species to regenerate. Hobbs et al. (1984) provide an example of how fire intervals can alter the diversity of species that are able to regenerate in heathland, and hence affect overall community diversity. An intermediate fire frequency resulted in the highest species diversity.

Fire has been discussed as a factor that can increase the likelihood of invasions (Christensen & Burrows 1986). Fire acts to remove much of the plant canopy and usually has a short-term fertilizing effect on the soil; hence both light and nutrient availability can be increased temporarily. Zedler and Scheid (1988) discuss the invasion of coastal chaparral by *Carpobrotus edulis* following fire. There is clear evidence, however, that not all fires result in increased invasion and that variations in fire regime can affect the extent of invasion. Hobbs and Atkins (1990) have illustrated how invasion of *Banksia* woodlands differs between fires burned in spring versus autumn. In some cases, fire per se does not affect the degree of invasion, or will do so only when combined with some other type of disturbance, such as mechanical disturbance of the soil or nutrient input. For instance, Hester and Hobbs (1992) studied burned and unburned shrubland patches within an area of remnant vegetation in the Western Australian wheatbelt and found that invasion by non-native annuals was restricted to the remant edges, even following burning. In adjacent woodland, the abundance of non-native species actually declined following the fire. Following another fire in the same area, this time in heathland vegetation, invasion increased only where the fire impinged on a road verge that had been subject to prior disturbance during road grading. This interaction is important when management of roadside vegetation corridors is considered (see Loney & Hobbs, 1991; Panetta & Hopkins 1991).

Because species vary in their response to fires, fire may favor one set of species over another; these relationships can explain the balance between native and non-native species in some fire-impacted systems. Where native species are sensitive to fire (because fuel loads were such that fires in the native ecosystem were of low frequency and intensity), fire can enhance the invasion of non-native fire-tolerant species. When these fire-tolerant species contribute to increased fuel loads and inflammability, the disturbance regime can be shifted toward more frequent and intense fires; these fires further enhance the dominance of non-native over native species. Just such a cycle has enhanced invasion of woody species in South African Mediterranean systems, and of annual grasses into other Mediterranean-climate regions (MacDonald et al. 1989). Similarly, invasion of fire-tolerant grasses in dry Hawaiian lowlands

has had severe effects on native species (Hughes et al. 1991).

2. Grazing

Grazing animals are conspicuous and important features of many grasslands; it has long been known that some plants are tolerant of grazing while others are not, and that grazing alters the appearance, productivity, and composition of grasslands. Milchunas et al. (1988) have reviewed the effects of grazing by large herbivores on differing types of grassland and relate these to the intermediate disturbance hypothesis. They suggest that grazing constitutes a disturbance only where the evolutionary history of grazing is short. This has also been discussed by Naveh and Whittaker (1980) and Peet et al. (1983). We suggest, however, that in any situation a significant change in grazing regime will constitute a disturbance. Thus, imposition of grazing animals (or different herbivores) on a system not previously subject to that type or level of grazing will constitute a disturbance. So, too, will the removal of grazing from a system with a long grazing history. Species diversity will be affected by the direction of change in grazing regime relative to the historical regime (Ranwell 1960; White 1961; van der Maarel 1971; Milchunas et al. 1990; Dolman & Sutherland 1991). Numerous authors have reported maximum species diversity under intermediate levels of grazing (Zeevalking & Fresco 1977; Milchunas et al. 1988; Puerto et al. 1990).

The most detailed understanding of how grazing affects community structure comes from the chalk grasslands of Britain and northern Europe; these infertile sites support a diverse mixture of grasses and forbs, with species adapted to openings of different kinds and scales (Grubb 1976). These communities, although admittedly artifacts of human activity (clearing, fires, or grazing), have long been prominent features of the landscape; today they are of major conservation value both for their diversity and for particular rare species. Repeatedly it has been demonstrated that grazing is an important factor in the maintenance of chalk grassland diversity; the cessation of grazing leads to dominance of a few grasses, and even to incursions by shrubs or other woody species (Wells 1969). Entire components of the flora may be lost; for example, During and Willems (1986) blamed the loss of most lichens and the impoverishment of the bryophyte flora in Dutch chalk grasslands on the absence of grazing.

Grazing maintains high species diversity in other grasslands, as well. Grazing management is an important and successful technique for preserving diversity and conservation value of old grasslands and pastures in England (Hopkins & Wainwright 1989). Sykora et al. (1990) found that grassland on embankments in the

Netherlands was converted to woody scrub in the absence of grazing; under light grazing, a species-poor grassland resulted from competition from a few competitive grasses. Under more intensive grazing, those grasses did not dominate, and a more diverse grassland was maintained. Mediterranean-climate grasslands may respond similarly to grazing management; in a California grassland on serpentine substrate, cessation of livestock grazing enhanced the dominance of non-native annual grasses and led to a rapid decline in abundance of the diverse native annual forb flora (Huenneke et al., unpublished data).

One straightforward effect of grazing is the elimination of trees and shrubs invading mesic grasslands. Without grazing, many North American prairie sites have been converted to woodland. Similarly, there are also documented cases of grazing preventing or reversing the succession of African savanna to woodland. For example, Smart et al. (1985) found that in Uganda the exclusion of elephants was even more important than fire suppression in encouraging acacia invasion, leading to the loss of many species including the original grassland dominants. In these regions, a long evolutionary history of grazing has led to the dominance of grassland plants adapted to and tolerant of grazing pressure. Caldwell's work (for example, Caldwell et al. 1981) has documented the many physiological traits that affect a plant's tolerance of grazing losses.

In contrast, regions with no recent history of grazing are often dominated by plants that lack these tolerance mechanisms. Extreme examples are presented by oceanic islands with no native mammalian herbivores, where the introduction of livestock or other grazers has usually been catastrophic in its effect on native vegetation—for example, the effect of feral goats on island floras (Coblentz 1978) and of introduced herbivores in the Galapagos on native vegetation (Hamann 1975, 1979). A less obvious but still major impact has been made on regions with few native grazers (at least since post-Pleistocene time), such as the intermountain West (Mack & Thompson 1982).

In semi-arid grasslands in the American Southwest, species diversity has declined and, in many cases, the physiognomy of the vegetation has been altered from perennial grassland to shrub-dominated desert scrub. The chief question of range management and ecology is the determination of the proper utilization rate: what level of grazing will maximize productivity and maintain the grassland's general character? Unfortunately, it is not known what utilization level maximizes plant species diversity or productivity, or whether the same level maximizes both. Westoby et al. (1989) outlined the differences in grazing management that would result from considering grazing in an equilibrium, successional context versus a nonequilibrium series of alternate states;

working with the second mental model requires much more active management to "seize opportunities and to evade hazards."

Given grazing's impact on community structure, it has been used as a management tool in conservation applications. One example is a grassland restoration project, where an abandoned, species-poor pasture in Holland was being grazed by cattle; seed inputs from cattle feces (together with openings created by grazing) contributed significantly to increasing species diversity (Bulow-Olsen 1980). In another case, sheep were used to restore abandoned fields (Gibson et al. 1987), again by importing seeds and creating openings for recruitment. Several grasses in the Middle East, wild cereal ancestors of conservation interest, are negatively affected by heavy grazing but also vulnerable to competition from tall perennial grasses. Therefore the two sets of species alternate on lightly grazed or protected sites (Noy-Meir 1990). Upland British grassland species of conservation value vary in their response. Some benefit from removal of grazing, while others are negatively influenced by the resulting increase in grass (Rawes & Welch 1972). Wells (1969) commented that grazing (or mowing) during the season when the dominant grass species is growing most rapidly is usually the most effective way to maintain diversity in chalk grassland. He stated that the cessation of grazing is the major conservation problem in those grasslands, eliminating many forbs and causing increases of litter and woody species. He added, however, that grazing should be timed to avoid the sensitive phases in the life cycle of species vulnerable to grazing.

This raises an important point: Effects of grazing are species-specific. That is, two species in the same community may vary in their response to grazing or to a specific grazing regime. For example, in an English high-elevation grassland on limestone, after sheep were excluded from one site, several rare shrubs benefited from protection, but one species declined (Elkington 1981). The optimal design of grazing management may thus be difficult. Vinther (1983) found that a mesic meadow was maintained as open meadow if it was heavily grazed—because tree seedlings were killed by browsing—or if it was not grazed at all—because seedlings couldn't establish in the dense herb layer. Intermediate grazing levels allowed woody regeneration and loss of the meadow's open character. Unfortunately, these same intermediate levels of grazing are those maximizing the richness of herbaceous species in the short term. An alternate means of preventing woody plant encroachment would then be necessary to allow continued management for maximum species diversity.

Grazing's impact presents an interesting contrast to mowing, which is often suggested as an alternative to grazing management. Mowing can reduce the growth of competitively dominant grasses, allowing the persis-

tence of less competitive species, but it does not create openings for recruitment of seedlings as grazing does. Sykora et al. (1990) emphasized the different results of the two, with grazing creating more microsites for establishment and greater heterogeneity, while providing seed dispersal in animal feces, hooves, and coats. As van den Bos and Bakker (1990) pointed out, grazers do not use an entire area evenly but always prefer some spots to others, so they create greater heterogeneity than does mowing. There is also a difference in the form in which nutrients are returned or retained in the system (Rizand et al. 1989). Grazing is thus an amalgam of different effects. Clearly, if mowing is to be used by managers in preference to grazing, more sophisticated methods involving variations in mowing time and pattern and degree of mulch removal should be investigated.

Grazing animals may frequently be implicated in the invasion of natural communities. Grazers may import non-native plant propagules into native vegetation, but they may also act to provide microsites for invasion. In particular, where grazing alters the vegetation structure or is accompanied by soil disturbance (trampling, digging, and so forth), conditions are modified in such a way that invading species can become established. For instance, Cross (1981) showed that grazing by the non-native sika deer facilitated the invasion of oak woodlands by *Rhododendron ponticum* by removing the herbaceous understory and providing more safe sites for establishment. The arrival of large numbers of livestock following European settlement has been implicated in the decline in native perennial grasses and their replacement with non-native annual grasses in several grassland areas in North America and Australia (Moore 1970; Mack 1981, 1989). Braithwaite et al. (1989) suggested that water buffalo activities aid in the establishment of *Mimosa pigra* in northern Australia. Pickard (1984) implicated grazing disturbance as one of the major factors influencing invasion on Lord Howe Island in the South Pacific.

3. Soil Disturbances

In grasslands, as in most plant community types, soil disturbance creates openings for establishment, frequently of weedy or ruderal species. It is unclear whether temporary increases in nutrients and other resources are directly responsible for this enhancement of establishment or whether reduced competition from neighboring plant canopies and roots is more important, and it is usually difficult to separate the two effects. Where such disturbance has long been a component of the ecosystem, there is likely a substantial fraction of the flora that is specialized or adapted to establishment there. Thus in the Mediterranean region, where human agricultural and other activity has long created such soil disturbance, there is a large and successful group of

weedy species. These are the colonists and invaders that have become so pervasive in disturbed sites elsewhere in the world, where agricultural activity has a much shorter history and where few native species are adapted to such a habitat (Naveh 1967; Hobbs & Hopkins, 1990).

Plowing is said to diminish species richness, especially that of dicots, in lowland grasslands (Fuller 1987). Even so, particular species may require plowing to persist (Preston & Whitehouse 1986). Smaller-scale disturbances may be equally important in providing opportunities both ecological and evolutionary; for example, in tall-grass prairies, mounds created by badger excavations support a distinctive and diverse flora of "fugitive" prairie plants that live only on those mounds (Platt 1975). This distinctive group of species contributes substantially to the overall diversity of those prairies, particularly to overgrazed ones in which the background or matrix is relatively species-poor. Other disturbances by prairie dogs, buffaloes, and gophers also have significant effects on prairie diversity (Coppock et al. 1983; Collins & Barber 1985; Huntly & Inouye 1988; Whicker & Detling 1988; Martensen et al. 1990). Mounds of bare soil formed by the activity of pocket gophers act in Californian annual grasslands to provide substrates for seedling establishment in an environment of lower density and altered microclimate and soil nutrient status (Hobbs & Mooney 1985; Koide et al. 1987). Coffin and Lauenroth (1988) used a modeling approach and found that the effect of soil disturbances (ant mounds and mammal burrows) on a shortgrass community was chiefly a function of disturbance frequency and secondarily of disturbance size.

While soil disturbances, especially by animals, often have important effects on the dynamics of native plant communities, there are also numerous examples of such soil disturbances facilitating invasion by non-native species. Disturbance by gophers was found by Hobbs and Mooney (1985, 1991) to be an important factor in the invasion of serpentine grassland by *Bromus mollis* and other non-native annual grasses following years of above-average rainfall. *Bromus mollis* became established in greater abundance on gopher mounds than in undisturbed grassland, and was virtually absent from areas where gophers were excluded. *Bromus mollis* was able to disperse seeds onto gopher mounds more effectively than some of the native species because of its taller inflorescence, and it then survived better on the more open microhabitat than in the undisturbed grassland.

Experiments in which artificial soil disturbances were created have had mixed results, with the effects varying among different plant communities. Hobbs and Atkins (1988) found that some communities were more readily invaded than others, and that soil disturbance did not necessarily increase the ease with which non-

native species could become established or survive. Disturbance had the largest effect in the communities that were already more susceptible to invasion.

Why does soil disturbance facilitate invasion? Disturbance may act primarily by providing a rougher surface on which seeds can lodge; in other words, the disturbance increases the availability of safe sites (Hobbs & Atkins 1988). Hobbs and Mooney (1985) found that plants of both native and non-native species grew much larger on gopher mound microhabitats than in undisturbed grassland, but Koide et al. (1987) found that nutrient availability was actually lower in gopher mound soils than in undisturbed soil. Hence removal of competitors may be the major factor in this case.

4. Nutrient Inputs

Another type of disturbance, which is often less obvious, is a change in the input and cycling of nutrients in an ecosystem. Input of additional nutrients, particularly nitrogen and phosphorus, in low-fertility sites can be as devastating as eutrophication in freshwater ecosystems. Fertilization has contributed to a marked decline in species richness in British and Dutch grasslands (Willis 1963; Bakker 1987; Fuller 1987). Grasses are often the species to respond and to dominate under nutrient enrichment, to the detriment of broadleaved plants. During and Willems (1986) suggested that continued input of pollutants and nitrogen were partially responsible for the floristic impoverishment of nonvascular flora in Dutch chalk grassland. Input of atmospheric nitrogen was apparently to blame for the increasing dominance of one grass species and the loss of many forbs and other grasses, regardless of management (mowing, grazing, burning) in chalk grassland (Bobbink & Willems 1987). Certainly the problem of increased deposition of nutrients from the atmosphere is likely to be chronic and widespread.

Gough and Marrs (1990) suggested that high phosphorus levels in the soil of abandoned pastures precluded the reestablishment of species-rich grassland there. Natural or successional losses of phosphorus were too slow from a management perspective; incursion of scrub or woody species apparently increased levels of extractable phosphorus. They suggested that managers use cropping (cutting and removing above-ground biomass each season) or heavy leaching to lower soil-extractable phosphorus levels more quickly. Marrs (1985) reported a similar effort to reduce soil fertility in a site where managers were attempting to reestablish an acid heathland. In another twenty-two-year experiment with cutting, Rizand et al. (1989) found that retaining clippings on the site kept phosphorus availability high, with a possible negative influence on species composition, compared with removal of clippings or with grazing. Green (1972) pointed out early

on that chalk grassland, dune grassland, and heath were all seral, low-fertility ecosystems with high conservation value. He suggested more study of nutrient budgets on those systems and pointed out that grazing, burning, and mowing all decreased the likelihood of nutrient accumulations. In North American old fields, nutrient-enriched fields supported lower species richness and retained a weedy annual, largely non-native flora (Carson & Barrett 1988) rather than the perennial grasses typical of fields of equivalent age.

In ecosystems with predominantly nutrient-poor soils, addition of nutrients can constitute a major disturbance, which has been shown in many examples to facilitate invasion by non-native species. Huenneke et al. (1990) have shown that a serpentine grassland dominated by annual forbs can be transformed in two years into one dominated by non-native grasses by the addition of nutrients, particularly nitrogen and phosphorus. Hobbs et al. (1988) produced similar results and showed that survival of non-native grasses was significantly enhanced on fertilized plots, while that of native forbs was reduced. In both these cases, invasion was not related directly to soil disturbance and, in fact, Hobbs et al. (1988) found that subsequent gopher disturbance actually reduced the dominance of non-native grasses and allowed the re-establishment of native forbs.

Nutrient input has also been shown to facilitate invasion of Australian plant communities. Heddle and Specht (1975) reported increased abundances of non-native herbaceous species in areas of heathland that had received fertilizer. Other studies have indicated a strong relationship between the degree of invasion by non-native species and soil nutrient levels, particularly of phosphorus (Cale & Hobbs 1991; Hester & Hobbs 1992). Experiments where nutrients were added to plots within a number of different plant communities in Western Australia showed that increased nutrients resulted in increased growth of non-native species in some plant communities but not others (Hobbs & Atkins 1988). Of particular interest was the finding that a combination of soil disturbance and nutrient addition had the greatest effect in enhancing the establishment and growth of non-native species.

5. Trampling

Like the other disturbances we have discussed, trampling can create openings in vegetation that provide opportunities for new individuals to become established, and it can slow the growth of dominant species sufficiently to allow the persistence of less vigorous species. Again, intermediate levels of trampling seem most effective at maintaining high species richness because of the suppression of competitive dominants (Liddle 1975). The season or timing of trampling has a significant effect on the chance, rate, and species composition

of recovery (Harrison 1981). There are species-specific responses to trampling: in one study most but not all species were negatively affected (Crawford & Liddle 1977): invertebrates seem far more sensitive than plants (Duffey 1975). We have encountered little information on the effects of trampling on invasions, although trampling effects are frequently considered together with those of grazing.

6. Fragmentation

The fragmentation and insularization of ecosystems is not a disturbance within an individual system but a landscape-level disturbance resulting in the rearrangement of the landscape matrix. By influencing edge effects and the likelihood of movement of nutrients, propagules, and fauna from adjacent patches, fragmentation affects disturbance regimes in individual patches of remnant vegetation (Hobbs 1987; Saunders et al. 1991). How does fragmentation affect the species composition and richness of grasslands? Simberloff and Gotelli (1984) surveyed patches of prairie and found that "archipelagoes" of small grassland patches supported more species than did single large patches of equivalent total area. Thus small patch size does not constrain total species richness. Quinn and Robinson (1987) and Robinson and Quinn (1988) used an experimental approach to this question, subdividing annual grassland into fenced patches separated by heavily grazed zones; species richness was substantially higher in the more subdivided treatments. Single species frequently came to dominate single plots, so a region with a greater number of patches supported both more dominant species (alternate dominants in different plots) and more edge species (growing along the greater perimeter). Murphy (1989) has pointed out that Robinson and Quinn's (1988) study was carried out at an inappropriate scale and in a grassland that is dominated by non-native annuals. However, the point that fragmentation will lead to an increase in edge species is important. From a conservation management perspective, one would want to know just which species are being favored by edge effects. A higher total species richness could be primarily due to an increased number of ruderal or weedy species of low conservation value (as found, for example for invertebrates by Webb & Hopkins [1984]), or to a higher number of legitimate community members.

7. Interaction of Disturbances

Of course, most ecosystems experience multiple disturbances and are shaped by multiple factors. In many cases the results are not merely additive, and disturbances can act synergistically. For example, grazing reduced fuel loads, reduced fire frequency, and allowed the invasion of woody species into many regions of semi-arid grassland (such as the historical expansion of

pinyon-juniper vegetation into western U.S. grasslands; Wright et al. 1979). In an experimental study, Collins (1987) found that fire significantly increased species diversity in grazed tallgrass prairie but not on ungrazed grassland; in some respects the effects of grazing and fire were additive. Collins and Gibson (1990) have further illustrated how grazing, fire, and small-scale soil disturbance all affect the matrix structure of these grasslands differently, and hence can interact to increase community diversity. Leigh et al. (1987) found that rabbit populations increased on burned areas of subalpine vegetation, while Noy-Meir (1988) found that elevated populations of voles had the greatest effects on grasslands where other grazing was minimized. Sykora et al. (1990) suggested that fire in Dutch grasslands increased nutrients and thus increased the likelihood of "ruderalization"—increasing dominance by a few grasses leading to a decline in diversity. Hodgkin (1984) found that woody encroachment increased soil fertility and changed the nature of British dune grassland. It was suggested that the myxomatosis-caused decline in rabbit populations had resulted in the increased establishment of woody vegetation, and that the resulting scrub had increased soil nutrients to the point that weedy plant species were favored.

Invasion by the nitrogen-fixing *Myrica faya* onto young lava flows in Hawaii has been shown to alter the nature of ecosystem development following volcanic eruptions (Vitousek et al. 1987; Vitousek & Walker 1989). In this and other cases, such as that of *Mimosa pigra* in Australia (Braithwaite et al. 1989), the invading plants themselves constitute a major disturbance to the systems they are invading.

Good Disturbances Turned Bad: Conflicts

Are there cases where disturbance is a necessary component of ecosystem and community dynamics, but also enhances the likelihood of invasion? From the foregoing, it would seem that virtually any type of disturbance can facilitate invasion under certain circumstances. Invasion is, after all, simply a subset of the possible recolonization response to disturbance. As an example, Griffin et al. (1989) have shown how periodic flooding can lead to the invasion of arid zone river systems by *Tamarix aphylla*. It is not the type of disturbance but rather certain aspects of its action in a particular system that shift the result toward enhancement of invasions at the expense of natives (see McIntyre et al. 1988). For example, it is not fire per se but the combination of fire with other disturbance, or the adoption of a fire regime inappropriate to the life histories of native plants, that favors non-native fire-tolerant species at the expense of natives. A primary consideration, then, must be the suite of adaptations and life histories found in the native plants, particularly those of conservation value.

The relationship between soil disturbance and invasion is also complex, and mechanical disturbance in the absence of nutrient addition may not necessarily lead to enhanced invasion (see Hobbs 1989). Frequently, however, physical disturbance and nutrient enrichment coincide, as when rabbits scrape the soil and defecate at the same time, or when disturbance enhances nitrogen mineralization. An important problem for systems with a naturally low nutrient status is the gradual nutrient enrichment that can occur via atmospheric input, wind-blown fertilizer, or input from livestock feces (Landsberg et al. 1990; Cale & Hobbs 1991). An increased baseline nutrient status will have important implications for the whole ecosystem, but in the short term it may exacerbate the likelihood of invasions by weedy pest species.

Conclusions

No system can remain immune from certain disturbances (such as nutrient input from the atmosphere); in the future, few areas will even be protected from direct human activity. Some disturbance types can be modified by on-site management (fire and grazing regimes) while others cannot (floods, storms). Human-induced disturbances such as road construction can also be minimized. "Natural disturbance regimes" may be desirable but are often impracticable in the altered settings of contemporary reserves. We need to acknowledge the actual disturbance regime operating currently in a reserve, and the current propagule rain, which determines the importance of coping with likely invasions. Further, managers need to take an active role in designing the disturbance regime, tailoring it to the landscape, the biotic community, and their specific conservation goals.

Denslow (1980) hypothesized that any natural community would be richest in species adapted to establishment in the type of patch most commonly created by disturbance. For example, where large scale disturbances are the norm, most species will establish there and species richness will decline through time and succession. In contrast, in an ecosystem where small-scale disturbances are normal, most species will establish in small scale gaps or in undisturbed sites, and diversity will increase with time after a large disturbance. Total diversity of native species at the landscape level will be greatest when disturbance occurs at its historical frequency and in the historical pattern (Fig. 2). Changes in the size of the frequency, as well as the type, of disturbance will mean that most native species will no longer be well adapted for recruitment or establishment.

In addition, even when disturbance regimes have not been significantly altered, the availability of weedy or invasive species may alter system response to disturbance. Management must consider not only alterations

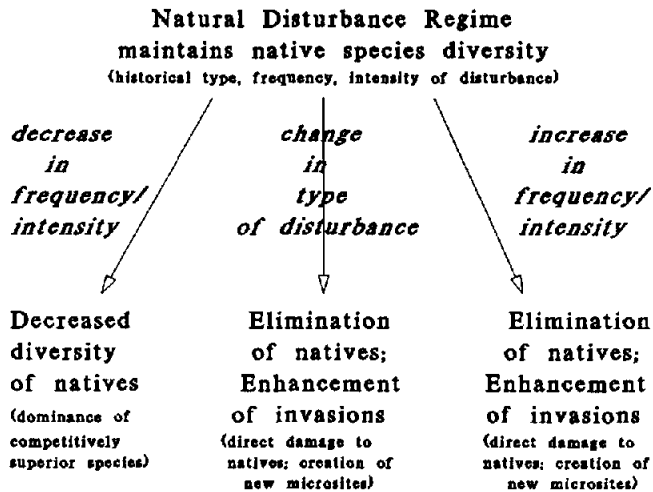


Figure 2. Any change in the historical disturbance regime of an ecosystem may alter species composition by reducing the importance of native species, by creating opportunities for invasive species, or both.

of the original disturbance regime, but also alteration in the pool of potential responding species (in other words, the availability of colonists or pests).

The response of invaders to disturbance is an extreme case of an underlying, unavoidable conflict—any disturbance and any management regime will be good for some species and bad for others. The decision may be easy (although the techniques for management may not be) when the choice is between natives and non-native pest species. The dilemma is thornier when non-natives have some appeal of their own (for instance in terms of grazing value), and it is still more difficult when the choice is between one set of native species and another. In the end, the wisest choice may be to use a diversity of management strategies, to encourage different species in different parts of the reserve or in different reserves within a region. There is no single optimal strategy; managers must make decisions based on the likely costs and benefits in terms of maintenance of diversity versus invasion by non-natives.

We draw the following conclusions from this review of scientific research on disturbance and species composition and diversity in grasslands.

- Disturbance plays an integral role in structuring plant communities, but some types or combinations of disturbance can increase the potential of invasion by non-native species.
- Background levels of disturbance, resource availability, and the pool of potential species in any ecosystem all differ now from primeval condition. This is true even in the largest parks and reserves (see Chase 1987). It is not enough to say that the original disturbance regime is the desired state.
- Species vary in their response to disturbance, requir-

ing managers to make deliberate choices of which taxa to favor.

- Managers may have to choose between specific conservation targets, such as preventing the spread of invasive species, and the more general goal of maintaining overall species diversity.
- Nearly all systems are likely to be nonequilibrium in the future; we must be activists in determining which species to encourage and which to discourage. We cannot just manage passively, or for maximal diversity, but must be selective and tailor management to specific goals.

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