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5. Fire, Grazing, and the Landscape Heterogeneity of a Georgia Barrier Island

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5.1 Introduction

Although the general role of ecological disturbance has received much recent attention (i.e., Lugo 1978; Barrett and Rosenberg 1981; Mooney and Godron 1983; Sousa 1984; Gerritsen and Patten 1985; Pickett and White 1985), the propagation and behavior of disturbance in landscape is not well understood (Risser et al. 1984; Wiens et al. 1985). Yet, it is the landscape level at which many environmental problems are managed. Many studies of disturbance are at too fine a scale for practical application. To gain a more complete hierarchical understanding of disturbance, we need to understand these processes at the larger scales.

At the landscape level, it is necessary to deal with heterogeneous systems. Previous studies have shown that responses to disturbance in homogeneous environments are complex, and at the landscape level this complexity may increase. However, the dynamics of heterogeneous environments have been, until recently, largely ignored by the ecological sciences (Risser et al. 1984).

When we move to the scale of the landscape, there are important questions regarding the spread of disturbance in landscapes that must be addressed. For example, how do disturbances move across the landscape? How does the heterogeneity of the landscape influence the propagation of a disturbance? Do effects vary with the type of disturbance or the type of landscape? How does the size or shape of patches influence the process?

This chapter explores three conceptual hypotheses which address some of these questions. We focus on how disturbances behave across a barrier island landscape, drawing examples from studies of disturbances, particularly fire and grazing, on Cumberland Island National Seashore, Georgia. The hypotheses are as follows:

1. Young, immature, resilient ecosystems may be energy sources for propagation of fire and grazing disturbances across the landscape. Mature, resistant, long-lived ecosystems may be recipients of severe impacts.
2. Increased landscape heterogeneity may increase the spread of disturbance between communities.
3. Multiple disturbances may have nonadditive effects and this tendency may be enhanced by increased landscape heterogeneity.

5.2 The Study Area

5.2.1 The Cumberland Island Landscape

Cumberland Island (30° 48′N, 81° 26′W) is the southernmost and largest of the Georgia sea islands (Fig. 5.1), measuring 28 km in length and 9 km across at its widest point. The major vegetation types in the Cumberland landscape are arranged in longitudinal bands that are primarily determined by physical factors such as tidal energy, salt spray, and topography. The island is composed of stable Pleistocene sediments, rarely subject to storm overwash and on which upland vegetation occurs, and more dynamic Holocene beaches, dunes, and marshes that are easily modified by major storm events. The interior forests are patchy, and patch size is generally small (Fig. 5.2). Some upland forests extend from the dunes to the sound on narrow parts of the island, whereas others are broken by sloughs, fresh water marshes, or large blocks of scrub. The island has been periodically farmed and logged since colonial times, and the patchiness of the upland forests is partly a result of these past disturbances.

The band of vegetation on the eastern, or ocean, side of the island consists of broad beaches backed by a row of foredunes. Interdune meadows and bayberry (*Myrica cerifera*) thickets separate these low, sparsely vegetated foredunes from higher secondary dunes on the north and south ends of the island. This habitat sequence is truncated in the middle of the island, where interdune meadows are poorly developed. On the western side of the island are extensive salt marshes composed primarily of monospecific stands of *Spartina alterniflora*.

The upland maritime forests stand between the secondary dunes and the salt marshes, and they are dominated by live oak (*Quercus virginiana*) and other hardwoods. As indicated earlier, these forests tend to be patchy. On the north end of the island, the oak forests occupy old dune ridges now separated by freshwater wetlands. The hydric sites support marshes primarily dominated by salt cordgrass (*Spartina bakeri*) or sawgrass (*Cladium jamaicense*). Behind this ridge and swale system lies more forest. Oaks predominate in some areas, whereas in others, pines, such as loblolly (*Pinus taeda*) or slash (*P. elliotii*),

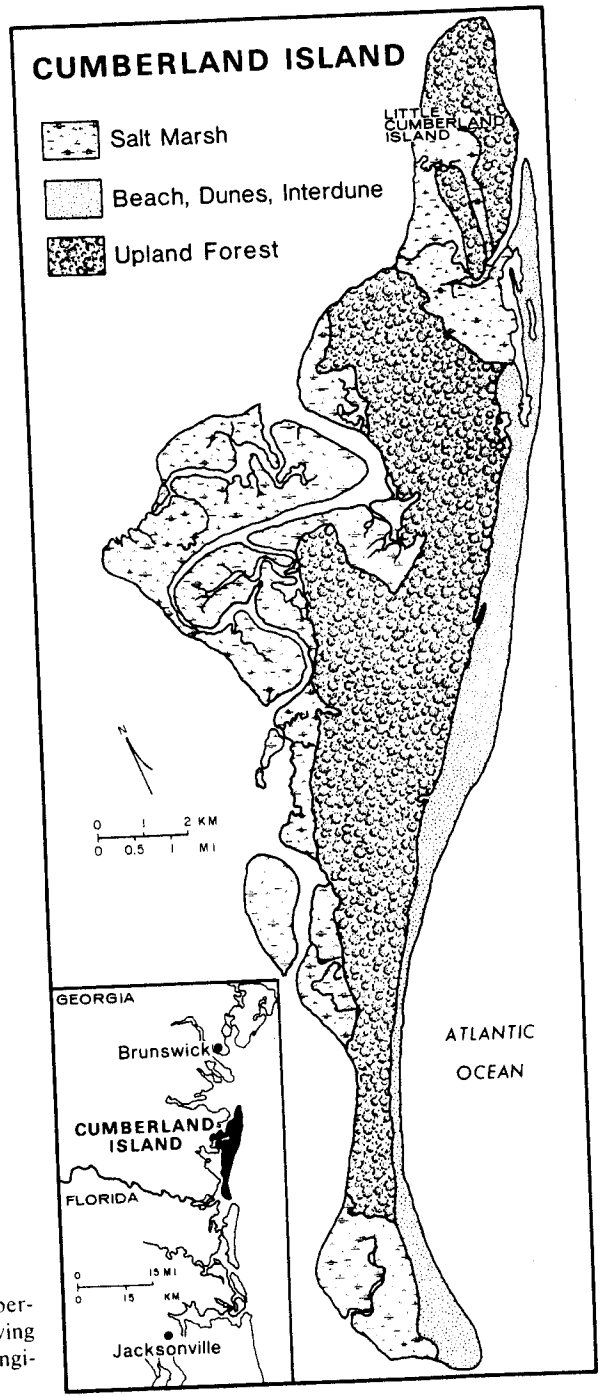

Figure 5.1. Map of Cumberland Island, Georgia, showing vegetation patterns of longitudinal bands.

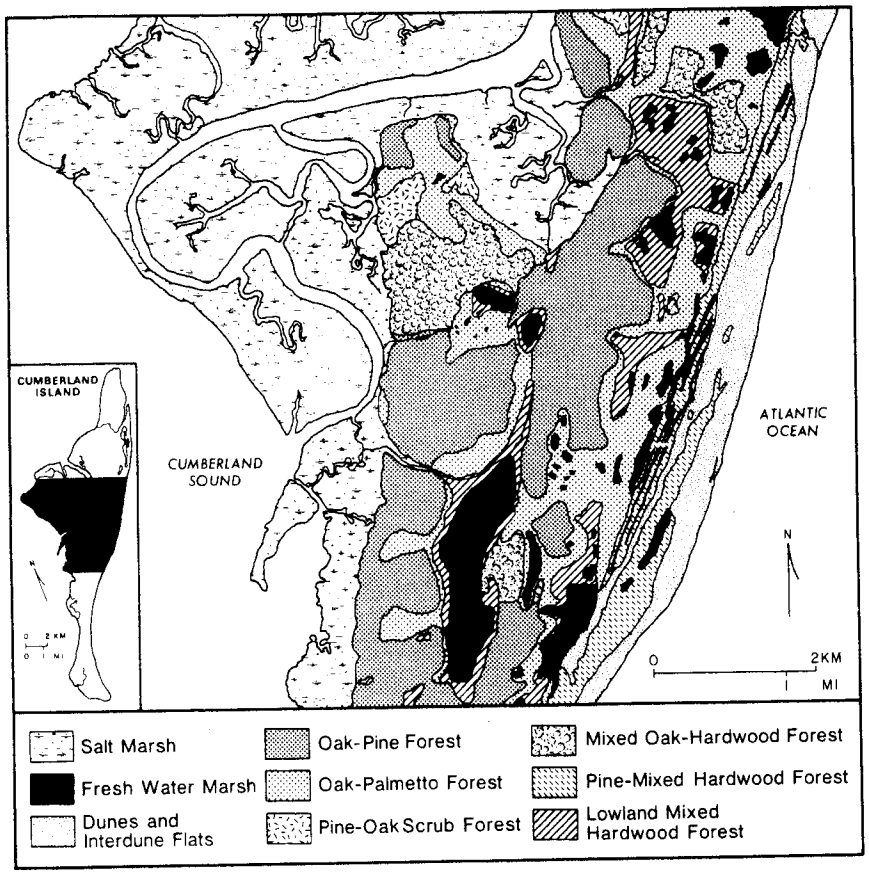

Figure 5.2. Central section of Cumberland Island illustrating the patchiness of the upland forests.

dominate or are mixed with hardwoods. Contiguous areas of pine and oak scrub are found in the north central part of the island and on Table Point. Small trees and ericaceous shrubs form a dense thicket on the most xeric interior soils.

The geology, soils, water resources, and fauna of Cumberland have been described by Hillestad et al. (1975). Designated as a National Seashore in 1972, the federal boundaries encompass approximately 14,500 hectares, about 9400 hectares of which is upland and marshes.

5.2.2 The Disturbances: Grazing and Fire

Physical forces or animals that move materials or energy in the landscape have been termed vectors (Forman 1981); Wiens et al. (1985) distinguished between

biotic and abiotic vectors. Grazing and fire, the disturbances we will use to explore our hypotheses, represent these two types of vector. They are further distinguished by their origins. Disturbances can originate from either outside the ecosystem or within it (Bormann and Likens 1971); that is, the perturbation may be foreign to the system, or it may be from within but applied at an excessive level (Barrett et al. 1976). Fire is an abiotic disturbance that originates externally and is a point source perturbation which can then spread across the landscape. Grazing, in contrast, is a biotic disturbance that originates internally and is a diffuse source of disturbance. Animals may be present across the landscape, but as their numbers increase their impacts spread from preferred, or focal, habitats into others.

During the last century horses (*Equus caballus*), cattle (*Bos bovine*), and hogs (*Sus scrofa*) have ranged free on the island. The U.S. National Park Service removed the cattle in 1974 and has greatly reduced the hog population via trapping. The horse population, however, remains unmanaged and presently includes 180 animals (Finley 1985). The native white-tailed deer population (*Odocoileus virginianus*) has also reached a high density following release from hunting and removal of predators. Intensive grazing has depleted forest understories and reduced interdune and high marsh vegetation to the height of a mowed lawn.

The most important source of large fires on Cumberland Island is lightning, and the fires tend to occur during dry summers. At least 1300 hectares of Cumberland have burned since 1900, much of this area more than once, and fire rotations of 20 to 30 years have been documented (Turner 1984). The size of the burns varies with community type. Fires in scrub are large, hot, and frequently burn into other vegetation types. Fires in mature pine stands or in freshwater marshes may also spread into surrounding areas, but do not support as intense a fire as the scrub.

Fire and grazing are important factors determining the landscape mosaic on Cumberland. We suggest that although they operate quite differently, there are some general tendencies governing their behavior in the landscape, and that this behavior is dependent upon landscape heterogeneity.

5.3 Spread of Disturbance Across the Landscape: Hypotheses

5.3.1 Resilient Ecosystems May Be Energy Sources for Disturbance

Hypothesis 1: Young, immature, resilient ecosystems may be energy sources for propagation of grazing and fire disturbances across the landscape. Mature, resistant, long-lived ecosystems may be recipients of severe impacts.

Although the processes of combustion and ingestion differ, both fire and grazing are disturbances that "consume" biomass as they proceed. Biomass is required as a fuel for the propagation of these disturbances. In the landscape, one ecosystem or patch may serve as a fuel source for the disturbances, encouraging further spread into other patches or the surrounding matrix. We suggest a pattern in this process.

5.3.1.1 Grazing by Horses and Deer

The feral horses on Cumberland depend primarily on salt marshes and interdune grassland for forage (Table 5.1). Salt marshes comprise 34% of the island and represent the single largest habitat available to the horses. Lenarz (1983) found that horses on the south end of the island spent 51.7% of their total foraging time in salt marsh and estimated the genus *Spartina* to be 25.5% of the horses' diet. Although the horses obtain a large portion of their energy from the salt marsh, they also use other ecosystems, such as the interdune meadows. Thus, between-patch interactions and transfers occur. Horses move between prime feeding areas and freshwater sources, traversing other communities, especially the maritime forest, in the process. Territorial conflicts may initiate movements of a kilometer or more, and frequently result in movements of several hundred meters (S. Bratton, field observations). Horses leave the marshes during high tides and to escape biting insects, using the forests as a high ground refuge from the tides, as shelter and, to a limited extent, for foraging. On the north end, where salt marshes are farther from the interdune meadows, horses may spend more time in the forest and may consume forest genera such as oak (*Quercus* spp.) and Spanish moss (*Tillandsia usneoides*).

Without the marshes and grasslands, the forests of Cumberland Island would probably not support a viable horse herd. The dense forest understories are dominated by unpalatable saw palmetto (*Serenoa repens*), and the more open communities are low in productivity. With the energy supplied by the marsh, however, horses use the forests, removing or trampling vegetation that probably includes young oaks, and depositing feces. Large piles of horse manure in buckthorn-sabal palmetto thickets adjoining Dungeness marsh indicate that the forest may be gaining nutrients (S. Bratton, field observations).

It is clear that the horses move across boundaries in the landscape. What effects do they have on the ecosystems they use? Horse grazing and trampling in the salt marshes drastically decrease the standing stock (Table 5.2) and net aboveground primary productivity of *Spartina alterniflora* (Turner 1985, 1987). Experimental studies indicate that two components of grazing, trampling and removal of biomass, both have significant, independent effects on the marsh. There is no shift in species composition, however, and *Spartina alterniflora* continues to dominate. After release from horse grazing, the marsh shows fairly

Table 5.1. Proportion of Foraging Time Spent in Each Habitat for Feral Horses on Cumberland Island, Georgia[a]

Habitat	Percentage of Observations	Percentage of Habitat
Salt marsh	51.7	34.1
Grasslands at marsh edge	22.5	2.6
Interdune meadows	15.3	6.3
Lawns	8.1	1.2
Foredunes	2.1	8.6
Other	0.3	47.2

[a] Lenarz 1983.

Table 5.2. Peak Biomass of *Spartina alterniflora* in Grazed and Ungrazed Plots, Cumberland Island, Georgia[a]

	Ungrazed		Grazed	Biomass Removed by Horses (%)
Plot A				
1983	120		52	57
1984	364		9	98
1985	528		8	98
Plot B				
1983	68		14	79
1984	232		7	97
1985	140		5	96
Plot C				
1983	388		292	25
1984	440		180	60
1985	472		28	94
Plot D				
1983	344	ns	382	0
1984	382	ns	372	0
1985	472		228	52

[a] Units are dry weight (g/m^2). Grazed and ungrazed are significantly different ($P<0.05$, Student's t-test, N = 8), except where indicated by ns. Study plots are arranged from nearest to the uplands (A) to farther in the marsh (D).

high resilience: *Spartina* begins to recover immediately (Turner 1985, 1987) and may regain the standing crop of ungrazed areas in three years.

To assess grazing effects in the forests, horse exclosures were erected on Cumberland in 1985, but no data from these are available yet. However, data from another barrier island with similar communities suggest processes that may also occur on Cumberland. Bratton and Davison (1985) compared understory species composition in maritime forest at Buxton Woods, Cape Hatteras National Seashore, NC, between 1937, when livestock were removed, and 1984. In 1937, there were practically no oak seedlings in the understory, and pine seedlings were prevalent. Since the removal of feral animals, oak seedlings have increased tremendously (Table 5.3). Decrease in grazing not

Table 5.3. Ratio of Percent Cover of Oak Seedlings to Pine Seedlings, Buxton Woods, Cape Hatteras[a]

Habitat Type	1937[b]	1984
Pine forest	0.10	7.11
Hardwood forest	0.48	31.50
Scrub	n/a	108.00

[a] Bratton and Davison 1985.
[b] Feral animals were removed in 1937.

only released the understories, but along with changes in fire frequencies, resulted in a decrease in pine seedlings and the edge zone species, persimmon (*Diospyros virginiana*) and beauty berry (*Callicarpa americana*), whereas oaks (*Quercus* spp.) and bays (*Persea* spp.) increased (Table 5.3). This suggests that the presence of feral ungulates may change the composition of the maritime forest from oak dominance to pine.

The overall pattern of horse impacts is illustrated in Fig. 5.3A. Horses obtain most of their energy from the salt marshes and grasslands, ecosystems which are both highly disturbed and resilient. However, the horses may have substantial effects on the maritime forest, which alone is not sufficient to maintain the herd. This suggests that on Cumberland, the marshes and grasslands are the energy sources for a perturbation which may change forest community structure and species composition.

Deer intensively graze the interdune meadows, open grassy fields, and upper edges of the salt marsh, but do not use the low marsh as do the horses. Deer will also browse almost all broad-leaved woody species on the island. Census data (unpublished) indicate that the density of deer may exceed 0.5 per hectare in the upland areas.

The overall pattern of the deer disturbance is shown in Fig. 5.3B. The disturbance results from an increase in the population density, causing impacts to spread from focal habitats into nonfocal patches within the landscape. Deer browsing is selective, and may slowly modify species composition in the forests.

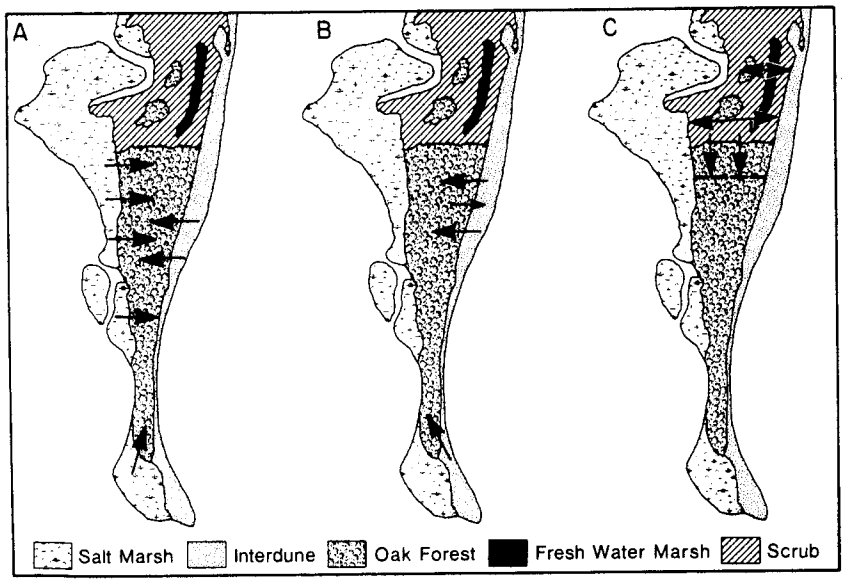

Figure 5.3. Energy flow of the three major disturbances across the barrier island landscape: (A) feral horses; (B) deer; (C) fire. Note that all affect the maritime forest.

Severe browse impacts may shift understory seedling composition from oak to pine (Bratton 1980), thus effecting changes similar to those caused by feral animals.

If grassland habitats were unavailable, deer would probably persist in low numbers in the forest. Thus, unlike the horses, a viable population might be maintained with decreased heterogeneity. However, the intensity of deer activity in the forests is increased by the availability of other habitats. The grassy, open communities appear to provide a source of energy that increases the grazing disturbance in the forest.

5.3.1.2 Fire

Fires will be initiated only in communities that contain adequate amounts of fuel. On Cumberland, fires generally originate in the scrub or freshwater marsh ecosystems where the vertical continuity of fuel encourages combustion of most available plant material. The fires are very hot and may spread completely across a patch of scrub or marsh once ignited. Scrub communities are probably "pyric disclimaxes" (Davison 1984) that accumulate fuels quickly and are prone to burning during periodic coastal droughts (Webber 1935).

Depending on weather, flammability, and the availability of fuel, fire may spread outward from its source. On Cumberland, fires may significantly affect communities that border the scrub or marshes. For example, a fire in the scrub will burn the edges of a mature oak forest, whereas the oak forest alone would not provide conditions conducive to burning.

During the summer of 1981, a severe fire burned from pine-oak scrub into surrounding communities on Cumberland. At the oak forest edge, oak trees within 3 m of the edge were usually killed by the fire, but the intensity of the fire decreased as it moved farther under the canopy. The effects of the fire did not extend into the forest as far as grazing did, usually penetrating only about 30 m. Patches of pine forest were more vulnerable to the fire, probably because of greater accumulations of litter. Patches of hardwoods surrounded by pine litter were killed completely and few sprouted. Live oak stands with basal areas greater than 13 m^2 suffered much less mortality than those with low basal area, such as those at the edge of the scrub (Davison 1984). A large stand of oaks will retard a fire and may protect small patches of other communities within its boundaries. However, small patches of mature oak forest probably cannot survive within larger patches of scrub.

The scrub tends to replace itself after fire (Webber 1935; Veno 1976; Davison 1984), showing high resilience. Small freshwater marshes are also fire tolerant and regenerate more quickly than the surrounding pine lands. The oak forest, in contrast, is fire resistant, and recovery in burned areas is slow. Thus, the presence of scrub patches within the landscape creates a focus for fire, which can move into the landscape and convert forest to scrub. Scrub vegetation is perpetuated by periodic destructive fires that will not permit further succession (Davison 1984).

The locations of the scrub and oak forests may be partially controlled by topographic factors, yet fires from the scrub encroach on the mature oak. The

boundary between these two communities may be determined by a relationship between edaphic conditions, fire intensity, and potential stand size. However, the physical disturbance of vegetation removal by fire can directly alter boundary locations, thereby influencing landscape patterns (Wiens et al. 1985). The scrub community may not be more productive than a live oak forest, but more biomass is consumed by fire, making it the energetic source of this disturbance in mature oak (Fig. 5.3C).

5.3.1.3 Discussion

Fire and grazing disturbances on Cumberland Island appear to be driven by resilient patches within the landscape, yet significantly affect resistant patches from which little energy is obtained. Why might this occur?

Vertical stratification differs between the source and recipient habitats on Cumberland. The source communities (marsh, meadow, scrub) are low and continuous, concentrating their productivity within the first few meters above the ground. Much of this energy is readily available to grazers and is susceptible to fire. In contrast, the recipient, live oak forest, has two or three vertical strata, and the mature trees possess characteristics that make them resistant to fire and grazing. Most of the internal energy of the forest system is unavailable to horses, deer, or fire, but the live oak forest is vulnerable to both fire and grazing in its understory. This vulnerability is important because if no young oaks survive, the forest will ultimately disappear.

Regeneration processes also differ between the source and recipient habitats, both in terms of temporal scale and reproductive strategy. The marsh, meadow, and scrub communities are composed of species that recover quickly from fire and grazing. The predisturbance structure of the community may be achieved again in a few years. The live oak forest, however, consists of long-lived species that recover very slowly. Depending on available light and other environmental factors, young hardwoods may take 15 to 20 years to grow out of the reach of grazers. Fire resistance in trees generally increases as trees grow taller and bark increases in thickness. The typical rotation for scrub fires is 10 to 20 years (Komarek 1974; Christensen 1981), suggesting they may recur before the oaks are protected.

The spatial arrangement of the habitats on Cumberland also contributes to the spread of the disturbances. The arrangement of the communities in longitudinal bands places different habitats in very close proximity across the width of the island. This increases the probability of a vector encountering and crossing a boundary. For example, grazers may move between preferred habitats easily, and in doing so traverse ecosystems that they might otherwise not use. Furthermore, patches in the upland forests tend to be small, thus having a high edge/area ratio and a relatively high proportion of boundary that can be crossed.

Forman and Godron (1984, 1986) suggested that in an undisturbed landscape, horizontal landscape structure tends progressively toward homogeneity, and vertical structure becomes higher and more heterogeneous. Disturbances usually rapidly produce opposite patterns of heterogeneity. The Cumberland landscape

appears to fit this pattern. In the absence of disturbance, the maritime oak forest would presumably form a homogeneous horizontal cover across the upland portion of the island, with a concomitant increase in vertical stratification.

Wiens et al. (1985) presented a conceptual framework for the study of boundary dynamics in landscapes. They suggested that the differences in between-patch and within-patch fluxes of energy, materials, or information create directional imbalances in the fluxes. Through such inequities, boundaries may shift in location or become blurred or sharpened through time. Our results support this concept, as well as Margalef's (1963) principle that when two systems of different maturity meet along a boundary that allows an exchange, energy flows toward the more mature system. However, our results are contrary to the second part of Margalef's principle, that the energy transfer favors the expansion of the mature patch into the immature patch. Instead, we observe an expansion of the less mature ecosystem. However, Margalef was specifically addressing stages of successional maturity, and not differences in the resistance and resilience of the patches. For example, although a pine forest and oak forest have differing successional maturity, the salt marsh and oak forest are both mature ecosystems. However, the marsh and oak forests differ in their abilities to resist or recover from specific disturbances.

The combination of differences in available energy, structure, stratification, resistance, and resilience of landscape components may have a substantial influence on both the spread of disturbance in the Cumberland landscape and the resulting landscape pattern. Transference of disturbance from one system to another may be a major determinant of long-term landscape dynamics.

5.3.2 Heterogeneity Increases the Spread of Disturbance

Hypothesis 2: Increased landscape heterogeneity may increase the spread of some disturbances.

We have observed that fire may burn from scrub into the surrounding mature forest matrix, and that grazing animals may move from preferred patches to less preferred habitats in the landscape. Given that fire and grazing do indeed spread from one habitat to another, what is the effect of changing the spatial heterogeneity of the habitats on the spread of these disturbances? As Wiens et al. (1985) note, it is part of conventional wisdom in ecology that disturbances are more likely to spread across a homogeneous area than one that is heterogeneous. We suggest, however, that the opposite also occurs. The movement of a disturbance from one habitat to another is amenable to modeling, and to address this issue, we developed a simple model to simulate different levels of heterogeneity in an idealized landscape.

The model assumed a square landscape that included two habitats, each of which comprised 50% of the landscape. A disturbance (i.e., fire on Cumberland Island) could travel unidirectionally for a fixed distance across the boundary from source habitat A (i.e., scrub) to recipient habitat B (i.e., oak forest). The landscape could then be divided into any even square number of boxes (4, 9, 16, etc.) with habitats A and B alternating systematically. The total area of the

landscape, the distance the disturbance could travel, and the heterogeneity of the landscape (the number of boxes) were varied. The amount of habitat B that was impacted by the disturbance was then determined.

Simulations were run using fire and grazing disturbances, and estimates of the distance the disturbances travel were based on data and field observations. Results illustrate that increased heterogeneity enhanced the spread of these disturbances. Simulating the spread of fire from the scrub community to the live oak forest, increased patchiness in a 10,000 m^2 landscape resulted in 100% of the oak forest burned when 25 squares were present (Table 5.4). In a 1,000,000 m^2 landscape, 100% of the oak forest was burned when the landscape was divided into 625 squares, each of which had an area of 1600 m^2. In both cases the curve of percent oak forest affected versus the number of squares was hyperbolic; the percent affected increased with the amount of edge (total area of each habitat remained constant).

Table 5.4. Results of the Model Simulating the Spread of Disturbance with Increasing Landscape Heterogeneity

Disturbance:	Fire	Source Habitat:	Scrub
Landscape Area:	10,000 m^2	Recipient Habitat:	Oak
Disturbance Travels:	20 m		

No. squares	Size per square (m^2)	% Habitat affected
4	2,500	64
9	1,111	96
16	625	96
25	400	100

Disturbance:	Fire	Source Habitat:	Scrub
Landscape Area:	1,000,000 m^2	Recipient Habitat:	Oak
Disturbance Travels:	20 m		

No. squares	Size per square (m^2)	% Habitat affected
4	250,000	8
9	111,111	15
16	62,500	22
36	27,777	36
64	15,625	48
100	10,000	60
400	2,500	94
625	1,600	100

Disturbance:	Grazing	Source Habitat:	Marsh
Landscape Area:	100,000,000 m^2	Recipient Habitat:	Oak
Disturbance Travels:	500 m		

No. squares	Size per square (m^2)	% Habitat affected
4	25,000,000	19
9	11,111,111	36
16	6,250,000	51
36	2,777,777	64
64	1,562,500	91
100	1,000,000	99
121	826,446	100

Similar results were observed for grazing effects. Assume an area of 100,000,000 m^2 consisting of marsh and live oak forest with grazers moving 500 m from the marsh to the forest (Table 5.4). With four squares, only 19% of the forest is affected; 16 squares results in impacts in 51% of the forest. By 64 squares, more than 90% is impacted, and this then increases gradually to 100%.

In the Pacific northwest, Franklin and Forman (1986) found a similar relationship between clearcut and remnant patches of forest and the spread of windthrow into the remnant patches. As the size of the remnant patches decreased after a checkerboard pattern, susceptibility to windthrow increased.

In general, the trends of these simple simulations indicate that with large areas considerable subdivision of the landscape is required before the recipient habitat is severely impacted. With small areas, few subdivisions will have large effects. Although this model is simplistic, it illustrates some potential effects of landscape heterogeneity on the spread of disturbance. Further refinement could be added to simulate random arrangements of patches, variable areas of each habitat, different shapes and sizes of patches, and even accounting for a gradient in the intensity of the disturbance as it spreads.

These results are consistent with a principle of landscape ecology proposed by Forman and Godron (1984, 1986), that the flow of heat energy and biomass across boundaries between patches, corridors, and matrix increases as landscape heterogeneity increases. The fire and grazing disturbances on Cumberland represent exactly these types of flows across a landscape. However, there are other cases in which increased heterogeneity may retard the spread of disturbance. Pine bark beetle attacks fall into this category, along with the spread of pests in agroecosystems, some wildfire perpetuation, the spread of Dutch elm disease, and erosional patterns (Risser et al. 1984). Thus, the geometry of the landscape alone does not determine the nature of the relationship between heterogeneity and disturbance. Ecological characteristics and differences between patches will determine this. The relative importance of geometry and biological factors in determining the spread of disturbance remains to be determined.

Whether landscape heterogeneity enhances or retards the spread of the disturbance depends on the interaction among several factors, including (1) the type and scale of the disturbance, (2) the spatial arrangement of components within the landscape, (3) the characteristics of those components and their permeability to the disturbance, and (4) the similarity of adjacent patches with respect to the disturbance.

5.3.3 Nonadditive Effects of Multiple Disturbances

Hypothesis 3: Multiple disturbances may have nonadditive effects on the landscape, and this tendency may be enhanced by increased landscape heterogeneity.

Thus far, only fire and grazing disturbances acting separately in the landscape have been addressed. However, landscapes are responding to complexes of disturbances that occur at different spatial and temporal scales. It has been suggested that multiple disturbances may have nonadditive effects in ecosystems (Lugo 1978; White and Pickett 1985; Schowalter 1985; Turner 1985). We suggest that multiple disturbances may also have nonadditive effects in the landscape, and that this tendency may be enhanced by increased heterogeneity.

When more than one perturbation occurs simultaneously, there are several alternative responses that may be observed. First, there may be no response observable because the perturbations act in opposite directions and cancel each other. Or, the response may be additive, being the sum of the responses to the individual perturbations. Finally, the response may be synergistic (greater than additive) or antagonistic (less than additive). Measuring the effects of both combined and single factors in the same study is critical to identify the interactions of multiple factors.

Nonadditive effects of multiple disturbances were documented in a single ecosystem on Cumberland Island by Turner (1985). The impacts of multiple disturbances (clipping, trampling, and fire) on the salt marsh were studied to determine whether some combinations of disturbance could elicit nonadditive responses from the vegetation. Responses of standing stocks of *Spartina* to combinations of burning plus clipping and burning plus trampling were significantly antagonistic: the response to these perturbations in combination was not as severe as expected based on the disturbances applied singly (Turner 1985). The study demonstrated that multiple disturbances could indeed elicit nonadditive responses from components of an ecosystem. We hypothesize that such interactions may also occur across a landscape, and that increased heterogeneity of the landscape may enhance the opportunity for synergistic or antagonistic effects.

Fire and grazing may have opposite effects on the landscape over relatively short time scales. For example, fire may decrease the heterogeneity of the landscape, burning through small patches of maritime forest and increasing the amount of scrub. Grazing, in contrast, may decrease fire frequency by removing available fuel, reducing the effect of fire. Thus, in the short term, the disturbances are antagonistic and their combined effect is less than expected. However, grazing may encourage the development of pine stands in openings in the upland forests by selective foraging on oaks. These pine stands will burn more readily than the oak forest. By encouraging the occurrence of patches of pine forest, grazing will enhance the spread of fire and reduce any potential oak recovery. Thus, over the long term, grazing may interact synergistically with fire to enhance the spread of the fire-resilient scrub. This interaction may reduce the forest matrix to remnant patches which are then susceptible to extinction.

As discussed earlier, increased heterogeneity of the landscape tends to increase the spread of fire and grazing disturbances. Similarly, increased heterogeneity provides more opportunities for nonadditive interactions among disturbances to occur. It is likely that a landscape consisting of fewer large patches will have fewer synergistic disturbances than a landscape that contains many small patches.

To fully understand the dynamics occurring within a landscape, the entire disturbance regime must be considered along with potential nonadditive interactions among disturbances. On Cumberland Island, for example, the vegetation mosaic is also influenced by feral pigs, the activities of human visitors to the island, and storms. Major storms may dramatically alter the landscape in a very short time, perhaps less than a day. The effects of these disturbances on shifting boundaries and transfers across the landscape must also be assessed to fully understand the landscape dynamics.

5.4 Conclusion

On Cumberland Island, the heterogeneity of the landscape strongly influences the behavior of grazing and fire disturbances. In turn, the boundaries between components of the landscape may change as a result of disturbance. Our analysis suggests some additional questions for research. It is unclear, for example, to what extent the community boundaries are a function of environmental conditions and to what extent they are determined by disturbance dynamics. The environmental factors may determine the absolute limits of a community type, whereas the disturbance regime controls the arrangement within that ultimate constraint. Furthermore, is antagonism among disturbances a common phenomenon that acts as a stabilizing force in the landscape?

We also suggested that one ecosystem or patch may serve as a fuel source for the disturbances, encouraging further spread into other patches or the surrounding matrix. In general, does small patch size and the prevalence of resilient or successional patches indicate large energy transfers across the landscape? Conversely, does large patch size and the dominance of resistant or mature communities indicate lower energy transfer?

This study also suggests that management of particular patches (i.e., for wildlife) or disturbances (i.e., fire) in the landscape may have a substantial effect on community boundaries and thus the structure of the landscape. The importance of assessing management actions in the context of the whole landscape is underscored.

In a heterogeneous landscape such as Cumberland Island, differences in structure, stratification, available energy, resistance, and resilience between landscape components may have a substantial influence on the spread of disturbance and the resulting landscape pattern. Transference of disturbance from one system to another may be a major determinant of long-term landscape dynamics. To fully understand the dynamics occurring within a landscape, the entire disturbance regime must be considered along with potential nonadditive interactions among disturbances. Whether landscape heterogeneity enhances or retards the spread of disturbance will depend on the interaction of several factors, including (1) the type and scale of the disturbance, (2) the spatial arrangement of components within the landscape, (3) the characteristics of those

components and their permeability to disturbance, and (4) the similarity of adjacent patches with respect to the disturbance.

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