

Species-Area and Fragmentation Effects on Old-Growth Forests: Prospects for Longleaf Pine Communities

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ABSTRACT

Deforestation and fragmentation afflict old-growth forest communities around the world. Conservationists have raised concerns that fragmentation and area loss will entail species extinction and degradation of ecosystem functions. Ecological theory provides only a rough rule-of-thumb for predicting the effects of area loss and virtually no guidance on the effects of fragmentation. However, a growing body of empirical information on the effects of fragmentation in several kinds of forests on particular species and processes suggests that fragmentation will often present a major threat in addition to that posed by loss of area. Further, certain effects, such as increased predation on particular species, seem to arise in numerous fragmented systems. However, there is a major need for detailed field studies of particular forest systems to expand our understanding of the effects of fragmentation and how to ameliorate them.

Longleaf forests may be unique in terms of conservation prospects in the face of exploitation. From the standpoint of area loss, even accounting for second growth, they have suffered more drastically than other more widely publicized forests, such as tropical rain forest or North American temperate rain forest. And there are indications that some of the same sorts of effects of fragmentation that afflict other forests are also operating in fragmented longleaf forest. However, the structure of longleaf forests and the organization of biological diversity within them characteristically differ from those of other types of forest. These differences suggest optimism that longleaf forests can be exploited, within limits, without the catastrophic effects envisioned for other forest types. They also indicate that restoration of damaged longleaf forest communities may be more feasible than restoration of other forest communities.

The key differences are: 1) The majority of biological diversity in longleaf forests is associated with the groundcover rather than the canopy; the canopy is often virtually a monoculture. 2) Second-growth trees can perhaps provide, to some extent, structural aspects of the system provided by canopy trees. 3) The sparseness of trees, nature of the soil, and gentle terrain permit economical selective logging of a type that would be much more difficult in, for example, the mountainous rain forest of our Pacific Northwest or the moist and rugged terrain of many tropical rain forests.

However, in order to test hypotheses about the effects of fragmentation and area loss in longleaf forests, about ways to reduce this loss, and about the prospects for substantial restoration, a great increase in the scope and scale of controlled experimentation will be necessary. Large tracts will be required for both experimental treatment and control, focus will have to be on many components of the community in addition to game animals and dominant trees, and the overview will have to be comprehensive and community-wide. Anecdotal notions and small-scale experiments have been valuable in generating insights but these must now serve as the basis for a major experimental approach if longleaf communities are to be saved.

INTRODUCTION

Old-growth forests all over the world have been diminished and fragmented. The classic example in most American ecology and conservation textbooks is from Curtis (1956), who documented progressive deforestation in Cadiz Township, Wisconsin, over 120 years. Similar situations have now been depicted for many regions (e.g., Thorpe 1978, Järvinen and Miettinen 1987). This destruction has two components--area loss and fragmentation—and they often accompany one another, making it difficult to understand the separate effects of each (Haila and Hanski 1984). Area loss has received by far the most attention from ecologists and conservationists. This is probably because there is a venerable theoretical framework for the effect of area loss, but a much skimpier one for fragmentation. However, in many forests, including longleaf, fragmentation effects on the forest may rival those of area loss.

By "effects on the forest" I mean effects on the entire forest community. Foresters' almost exclusive focus on wood production has often made it difficult for foresters and ecologists to understand one another, because they have used the same words but meant different things. To ecologists and adherents of the "new forestry" (e.g., Franklin 1989, Swanson and Franklin 1992), the forest consists of an entire community of organisms embedded in an abiotic matrix. Until recently, to many foresters a forest was essentially a system for producing wood (Franklin 1989). To this day, such a view is not unusual; Atkinson (1991) dismisses the new forestry as "hobby silviculture." Large forest products companies such as MacMillan-Bloedel define "clear-cutting" as "a forest regeneration system" (Anon. 1990). This definition reflects the view that a forest is the dominant trees, and a healthy forest is one that produces many trees. But adherents of this view do not see the forest for the trees (Davis 1989)! The trees may provide much of the physical structure for the community but often constitute only a small part of the biodiversity. From an ecological standpoint, a healthy climax forest is one that maintains the species and processes of the entire community (Kessler et al. 1992).

Old-growth forests that have attracted the most attention are tropical and temperate rain forests. In fact, in many ways the situation for both forest types appears better than it is for longleaf. There were ca. 16,200,000 km² of moist tropical forest, mostly in South America, Africa, and Asia. Of this expanse, 40% is already gone (Simberloff 1986). The rate at which the remainder is being cut is a

matter of dispute; at the least, 0.62% is being clearcut annually, and as much or more is greatly damaged. So an area at least the size of Scotland is clearcut every year (Myers 1988, 1989; Whitmore and Sayer 1992).

Huge tracts of pristine moist tropical forest survive; for example, much of central Amazonia is intact. But the remaining forest is increasingly fragmented, islands of forest in a sea of pasture or brush (e.g., Oedekoven 1980). Many of these fragments and their populations are very small, leading to fears of extinction of some species on some or all fragments because populations have fallen to a point below which rapid extinction is assured--the "minimum viable population" (cf. Shaffer 1981, 1987). For the last decade a massive experiment has been conducted in Brazil in which small islands of rain forest were left surrounded by large clearcuts (Lovejoy et al. 1984). For the species studied most closely--birds, frogs, and mammals--a number of species have disappeared already from various fragments. The exact reasons for these extinctions are being studied, but it is already known that some of them are due to the absence of critical habitat in particular fragments (Zimmerman and Bierregaard 1986).

An even greater fraction of the temperate rain forests has been destroyed than of tropical rain forest. I cannot find comprehensive data on the extent of destruction world wide, although for New Zealand and Australia it is enormous. The largest remaining temperate rain forest covers the northwest coast of North America. For the United States, of an original 7,700,000 ha, about 1,012,000 ha now remain (13.2%) (cf. Morrison 1988). In Canada, of an original 4,000,000 ha, one recent unreferenced estimate is that about 1,400,000 ha now remain (34.9%). So in total, perhaps 20.6% of the old-growth remains. Dominant trees in these forests are often more than 1,000 years old, and second-growth does not approximate old-growth for more than 200 years (Morrison 1988). Since this forest was cut no more than a century ago, no significant production of new growth has yet replaced what was destroyed, in terms of the entire plant and animal community.

As in the tropical rain forest, this rapid deforestation has left remaining old-growth increasingly in fragments--islands in a sea of clearcuts and regenerating stands (Thomas et al. 1990). The effect of deforestation and fragmentation of the Northwest rain forest on animal species is just beginning to be studied. The well-known cases are the marbled murrelet, which nests in coastal redwood,

and the federally listed northern spotted owl. Other species associated with the same habitat, such as the northern goshawk, Vaux's swift, silver-haired bat, red tree vole, northern flying squirrel and several amphibians, are likely threatened because of habitat loss (U.S.D.A. Forest Service 1988, Carey 1989, Welsh 1990).

Longleaf pine originally covered about 28,325,000 ha of the Southeast (Means and Grow 1985). Of the old-growth, no more than 600 ha remains, scattered in small, isolated stands (S. Hermann, pers. comm.). In other words, only 2/1,000 of 1% remains of one of America's major ecosystems. This is much, much less than for tropical or temperate rain forest. The largest figure I have heard for second-growth longleaf forest is 4,050,000 ha (Croker 1979), and the great majority of this second-growth differs radically from the original because the groundcover was largely destroyed. And, of course, much of it is very young. But even if we were to tally all of it as equivalent to original old-growth longleaf, it would still add up to only 14% of the original area, which is much less than either tropical or temperate rain forest.

Several species associated with longleaf pine have federal and/or state status as threatened, and more probably should. Because many papers and panels at this conference deal with such matters (e.g., Guyer and Bailey, 1993; Walker, 1993), I will not belabor the point here. Suffice it to say that the fraction of the total biota that is threatened may exceed that for either tropical or temperate rain forest.

CONSEQUENCES OF AREA-LOSS AND FRAGMENTATION

The species-area relationship

Possibly ecology's oldest "rule," the "species-area relationship" states that, for stable, old, ecologically similar sites of different size, such as islands in an archipelago, the number of species increases with area. It increases less than linearly. Some data sets are better fit by exponential or other functions than by the power function, but the power function often fits, and the exponent is often ca. 0.25 (Connor and McCoy 1979).

This equation generates a prediction about how many species will remain for a given area.

Predicting in this way entails many assumptions. The relationship takes no account of the mix and quality of habitats at a site; it assumes all sites are identical except for area. However, sites are never truly identical, and the habitat at a site has an enormous effect on which species will be found there. In fact, this habitat effect probably accounts for a substantial fraction of the wide scatter of points in typical species-area relationships; Connor and McCoy (1979) found that log area explained, on average, only 44.8% of the variation in log species number for 100 published species-area relationships. So a small site with just the right habitats can have surprisingly many species, while a large site with inadequate habitats can have surprisingly few.

Another limitation of predicting from the species-area relationship is that, if a large area is suddenly reduced to a small remnant, the species-area relationship predicts a reduced equilibrium number of species, but no useful theory predicts how long it will take for the new equilibrium to be achieved (Simberloff 1992).

So at best the species-area relationship can be used as a very rough rule of thumb to give a ballpark estimate of how many species might be maintained, at some unknown time in the future, in a park or refuge of given size. The main point from this prediction is that the species-area relationship is not linear, so a small area might have a disproportionately large number of species. Darlington (1957) and MacArthur and Wilson (1967) suggested that, in many instances, a site reduced to about 1/10 of its area might at equilibrium contain around 1/2 the original number of species. The precise fractions could vary widely from system to system, but the non-linear relationship should obtain. This fact is cause for some optimism--even rather small remnants might be useful in conserving biodiversity.

However, it is important not to get too optimistic. At some point, a fragment becomes too small to maintain populations of most species. As populations get smaller and smaller, they are less likely to persist for many reasons. This is the notion of "minimum viable population size"--when populations fall below some threshold, swift extinction is very likely from demographic, genetic, environmental, and other factors (Shaffer 1981, 1987; Simberloff 1988). Thus at some point, tiny refuges will not be useful and even having very many of them, with substantial total area, would not be a valid conservation strategy.

Fragmentation

The species-area relationship assumes the entire area is contiguous. As noted above, deforestation typically leads not to a single contiguous remnant, but to many smaller, more or less isolated fragments. All the species-area relationship says is that each fragment will, at equilibrium, have fewer species than the original. It says nothing about what the total ensemble of small fragments will contain (Simberloff and Abele 1982). This is a question of how much overlap there is among the species sets of the small fragments. If they all contain the same set of species, even if it is a rather large set, then the whole ensemble will have many fewer species than the original continuous forest. If, on the other hand, different fragments have substantially different species, the ensemble of fragments might contain a large fraction of the original biodiversity.

Of course, even if no one fragment is large enough to maintain a population of some species for long, an ensemble of fragments might be able to maintain the population. Such maintenance would require that there be sufficient movement among the fragments that one of two conditions holds:

- 1) The forces leading to extinction within each fragment are opposed by sufficient recruitment from other fragments that the population never disappears from any fragment (the "rescue effect" of Brown and Kodric-Brown [1977]).
- 2) Extinction does occur occasionally on individual fragments, but never on all of them at once. After extinction occurs on fragment A, immigration from fragments B,C,D, etc. re-establishes the population on A before the other populations have all gone extinct. There is a shifting network of populations, all winking in and out, but with some of them always extant at any instant (the "metapopulation" of Levins [1970]; cf. Hanski and Gilpin 1991).

There is no general theory or even venerable empirical relationship, such as the species-area relationship, for the effects of fragmentation. There has not been much direct study of fragmentation. A recent review (Hanski and Gilpin 1991) describes a variety of models, none of them applied often. There is not even unanimity about a set of processes to look for, such as one looks for demo-

graphic or genetic factors coming into play as populations dwindle when area decreases. Several field studies, however, suggest that fragmentation might be very important. Each of these studies is idiosyncratic, because each was a careful study of a specific system. Nevertheless, general patterns emerge from collections of careful field studies, not from abstract theory. Some sorts of processes seem to occur over and over again in the few studies to date and seem like they might well pertain to longleaf forest communities.

Saving the northern spotted owl is the most controversial conservation issue in the U.S. (Simberloff 1987, Thomas et al. 1990). The owl is federally listed; about 2,000 pairs remain in Northwest old-growth forest. Each owl pair needs thousands of hectares of old-growth to forage for its food, mostly rodents. When it is restricted to fewer hectares or lives in other kinds of forests, its reproduction tends to decline. It is this area requirement that, until recently, received almost all the attention. But another problem may be equally critical.

The owl used to inhabit continuous old-growth of millions of hectares, so dispersing yearlings rarely had to cross non-forested areas. They increasingly inhabit a patchwork quilt of fragments of old-growth interspersed with clearcuts, various stages of second-growth, and agriculture. When they disperse through this matrix, as many as 80% of the young males and 30% of the young females are killed by predators, mostly great-horned owls and goshawks (R. Gutierrez, pers. comm.). As old-growth remnants get sparser, this mortality is likely to increase. In addition, it is possible that increasingly fragmented habitat favors barred owls, a potential competitor of the spotted owl that has recently invaded its range (Thomas et al. 1990). These considerations caused the federal interagency team charged with developing a strategy to conserve the spotted owl to shift the recommendation from spotted owl habitat areas (SOHAs) or spotted owl management areas (SOMAs), of a few thousand suitable hectares each, to much larger habitat conservation areas (HCAs) (Thomas et al. 1990).

In the forest patch project in Brazil, several understory bird species have disappeared from smaller fragments, though the habitat looks appropriate. These birds do not willingly cross a cleared gap of even 80 yards to get to a fragment. When such birds fly over clearings, they are almost always chased and often killed by bat falcons (*Falco ruficularis*) (R. Bierregaard, pers. comm.).

Nest predation may be greatly enhanced in a fragmented landscape. Wilcove (1985, 1990) studied this possibility in eastern U.S. forests by placing artificial nests with quail eggs at different distances from the edge of forest fragments of different areas. He found that, in the biggest forest, the Great Smoky Mountains National Park, only 2% of the nests were destroyed after a week. On the other hand, in rural 4-10 ha woodlots, predation averaged 48%. In woodlots in the suburbs, predation was 70%. Similar temperate forest results have been reported by Andren and Angelstam (1988), Small and Hunter (1988), and Yahner and Scott (1988). In addition to the area effect, nests closer to a forest edge were more likely to be destroyed.

Wilcove hypothesized, but has not yet proved, that some major nest predators—raccoons, squirrels, blue jays, crows, and dogs and cats—are greatly increased in the disturbed habitat surrounding the forest patches, and that these are the source of the predation. He argues that, centuries ago when forests were continuous, large predators such as wolves, mountain lions, large hawks, and owls were far more numerous and that these predators kept populations of the smaller predators low.

There has been no analogous tropical study, but Loiselle and Hoppes (1983) used artificial nests with quail eggs to look at a related problem. They found that ground nest predation was far greater on Barro Colorado Island in Panama than at a mainland site with similar vegetational structure. They attribute this increase to increased populations of small predators. Karr (1982), in turn, attributed the increase in small predators either to decrease in large predators or to decrease in hunting on the island. Terborgh (1988) suggested that top predators may play a large role throughout neotropical forests in maintaining species diversity. Similarly, Brash (1987) argued that abundances of the pearly-eyed thrasher (a nest parasite of the Puerto Rican parrot and other birds) and the warble fly *Philornis pici*, a parasite of chicks of the same bird species in Puerto Rico, are inversely proportional to forest fragment size. As with Wilcove's research in eastern U.S. forests, the next step is to find out exactly what the densities of predators and parasites are in fragments of different size. Controlled experimental removal of large predators would be even more definitive (da Fonseca and Robinson 1990).

Alverson et al. (1988) have studied fragmentation of northern Wisconsin forests. Originally ca. 80% of this region was old-growth, with occasional

pockets of early successional stages. Now the situation is exactly the opposite: old growth covers less than 5% of the region and comprises islands of 8-200 ha in a sea of early successional plants, especially aspen. White-tail deer populations have more than doubled in this mosaic of clearcuts and successional areas, because the successional areas produce abundant browse.

The forest now supports much lower densities of other species, such as moose, and increased browsing by deer affects the entire structure and composition of the forest. The deer wander into the fragments of old-growth as well as the more open areas, and they browse particularly on many of the old-growth ground cover plants as well as seedlings of typical old-growth trees such as eastern hemlock, white cedar, and Canada yew. Frelich and Lorimer (1985) similarly found a succession from hemlock to sugar maple driven by enhanced deer browsing in Michigan. Alverson et al. feel that, even if the Forest Service wanted to maintain many small fragments as old-growth, they would be unable to because the deer would change successional patterns. If the old-growth forest is to be preserved there, it may require much larger tracts.

FRAGMENTATION EFFECTS IN LONGLEAF FOREST

There has not been controlled research on the effects of fragmentation on longleaf pine forests analogous to the studies just described. But good preliminary research has done three things:

- 1) It hints that there may be some similar problems for species of longleaf pine communities.
- 2) It sets the stage for controlled experiments to determine whether these effects do, in fact, occur.
- 3) It suggests ways to ameliorate these effects through ecologically sound management.

Longleaf pine

Of course one way fragmentation affects longleaf forest is by interrupting the spread of fire, but enough will be said about fire at this conference (R. Myers, pers. comm.; Rebertus et al., 1993) that I need not belabor the point.

Another probable effect of fragmentation on longleaf pine has not received much attention. Wahlenberg (1946) described hog damage to longleaf seedlings, especially in flatwoods, that sounds analogous to the deer damage to Wisconsin old-growth. Hogs favor large grass-stage seedlings and the cortex of the main taproot. They have been observed to kill more than 17,000 2-year seedlings per ha at rates of more than 200 seedlings per day, so one hog can obliterate a hectare of planted pines in two days. On the De Soto National Forest, hogs greatly damaged seedlings 5-120 cm and saplings 1.5-4.5 m high. Chapman (1943) and Bruce (1947) described equally devastating damage by hogs in experimental plots in Louisiana. Hogs are known to travel 25 km, so it seems clear that small fragments embedded in land favorable to hogs will sustain major damage of this sort, and fencing, hunting, and other special measures will be required to prevent it. In areas where longleaf pine forests are naturally fragmented, such as parts of the St. Marks National Wildlife Refuge, hogs are similarly problematic (S. Hermann, pers. comm.).

Pocket gophers may cause major damage to longleaf seedlings, though not as great as that caused by hogs (Wahlenberg 1946). Because pocket gophers thrive in some agricultural settings, it would not be surprising if small stands of longleaf interspersed with agricultural fields would sustain greater pocket gopher damage than would large intact forests. However, no experimental work has been done to test hypotheses about either hog or pocket gopher damage.

Pityopsis graminifolia

S. Brewer (poster abst. 1993) has been studying the interaction of season of burn with herbivory on *Pityopsis graminifolia*, an abundant groundcover plant in some longleaf forests. He has found that, when fires occur in the dormant season, herbivory by deer on the meristem of the unopened inflorescences is massive, quite possibly rendering seed numbers a limitation on regeneration. Although this work is still in progress, it seems likely that this effect is enhanced in fragmented longleaf patches embedded in mixed matrices, rather than very large stands, because of increased deer populations, much as in the Wisconsin forest study.

Quail

Although no specific study has been con-

ducted on nest predation of quail in forest fragments vs. nest predation in continuous longleaf forest, data from southwest Georgia (Simpson 1976) suggest that differential nest predation could be extremely important. About 20% of nests were successful, and, of those that failed, 94% were preyed upon. In the Thomasville-Tallahassee area 36% of nests succeeded, and, of the failures, 69% were caused by predation (Stoddard 1931).

In Simpson's study, the two skunk species accounted for at least 30% of the nest predation, rodents (especially cotton rats) at least 15% at one study site, and opossums about 5%. Many other species destroyed small numbers of nests. The nearby cultivated food plots were thought to be responsible for the much greater predation by rodents at one site than at another. Skunks, rodents, and opossums all thrive in a mixed landscape with second-growth and agriculture, so it seems likely that a study similar to Wilcove's would show fragmentation to have a major impact on quail nest predation. Carefully designed research on the foraging ambit of these predators should also help.

The fact that a particular stage of the life cycle (nesting, in this instance) typically sustains substantial mortality need not mean that spatial variation in density in nature is due to spatial variation in this mortality. For example, a territorial species with high fecundity could have most mortality occurring on juveniles, yet still have population densities that vary from site to site depending on the numbers of adequate territories possible at the different sites. In other words, no matter what fraction of juveniles survived, a predetermined number would get to reproduce, and that number would be independent of the fraction that survived early life. However, in the absence of some conventional population regulation of this sort (contest or interference competition, in the case of territorial species), it seems quite likely that massive mortality of juveniles would severely limit adult density and that variation in this mortality would be reflected in variation in density. At the least, such mortality would seem to be a promising locus for research.

Turkey

Speake's study (1980) of predation on turkeys in Alabama was not specifically designed to test the effects of fragmentation, but the results are suggestive. Adults were virtually immune to predation, except for hens during the nesting and early

brooding season. Nest predation, on the other hand, was high, ranging over five study areas from 31.5% to 64.7%. Raccoons were the most important nest predators, followed by dogs. Williams et al. (1980) studied turkeys in Florida and found a similar rate of nest predation, with the two skunk species, raccoons, and opossums implicated in most of the predation. Raccoons, dogs, skunks, and opossums are all likely to be more numerous in a fragmented landscape, though critical data are lacking.

Fox squirrel

Fragmentation could threaten fox squirrels even if the total area of suitable habitat were large (Weigl et al. 1989). Their prime habitat is longleaf pine-turkey oak forests, and they are able to use longleaf pine cones that are too big for gray squirrels. Fox squirrels are very mobile and can move between isolated longleaf pine fragments and use the intermediate habitats to some extent, so long as there are some longleaf pine fragments and these are not too isolated. They are also greatly aided by the cavities that large longleaf pines provide.

Weigl et al. (1989) argue that, in large expanses of uninterrupted longleaf forest, predation will have little effect on fox squirrels. The longleaf forests and their animal populations are too sparse to support substantial populations of predators. However, as longleaf forests decline they are replaced by earlier stage forests and agricultural lands that suit gray squirrels very well, and dense gray squirrel populations can serve as alternate prey for predators, especially nest predators, that might feed on fox squirrels.

This effect has points of similarity with the nest predation work of Wilcove. In addition, ecologists know several examples of introduced predators sustained on common alternate hosts and driving down populations of rarer ones, perhaps to the verge of extinction (Howarth 1991). Weigl et al. do not yet have data for this scenario, and it will be hard to gather controlled data without large expanses of longleaf pine. However, the research to date almost demands that someone study predation on these squirrels and their nests.

Red-cockaded woodpeckers

Not only is the red-cockaded woodpecker an endangered species, but it is important to numerous other community inhabitants through the nestholes it constructs in longleaf trees (Engstrom,

1993). The woodpecker has difficulty with fragmentation, but it is a different difficulty than that of species discussed so far. Nest predation probably is not a major factor because of the pitch around the openings (cf. Jackson 1974, 1978). But the big problem is that they need large, old trees (Hooper et al. 1980), so they must find a new site if all large trees are occupied or destroyed. And they do not routinely disperse more than about 8 km (F. James, pers. comm.), so that an isolated vacated site often is not recolonized for a very long time.

Bachmann's sparrow

Bachmann's sparrow has declined to the point where it probably deserves threatened or endangered status. This bird traditionally nests in the grassy groundcover of mature longleaf pine forests, but it is found in enough habitats that the decline is puzzling because it appears that much suitable habitat is unused. Some habitats that appear suitable are not, either because the understory is too dense or the groundcover is too sparse (Dunning and Watts 1990). The isolation of suitable patches is problematic because patches in second-growth remain suitable only briefly, and the bird may not be able to find other patches because it disperses too poorly (Dunning and Watts 1990).

Research on the dispersal of the sparrow is needed. It seems to me that another tenable hypothesis is that, in the fragmented landscape, nest predation is increased in much the same way that Wilcove found in more northern forests. Predators destroy about half of all eggs and nestlings (Dunning 1993). Nest predation information in longleaf patches of different size and with different surrounding habitats would be interesting.

Gopher tortoises

The gopher tortoise is crucial to xeric-mesic longleaf pine communities, of course, because at least 332 other animal species use its burrows (Jackson and Milstrey 1989). Some, such as several scarab beetles, are obligate commensals. For other species, such as the pine snake and the gopher frog, the burrows are optimal habitat (Franz 1984). The exact effect of fragmentation on gopher tortoises is unknown, but as with quail and turkey, data on predation strongly suggest that this would be an important topic for study. Landers et al. (1980) found 89% of nests in southwestern Georgia to be preyed on by skunks, raccoons and crows, all of which would be facilitated by a fragmented landscape.

Diemer (1986) cited similar data from other studies, pointing to raccoons as leading egg and nestling predators. Research in Florida and Alabama showed adults to be preyed upon by feral dogs (Douglass and Winegarner 1977, Causey and Cude 1978), which thrive in a fragmented landscape.

Landers et al. (1980) also found several hatchlings destroyed by fire ants. The introduced fire ant is numerous in agricultural fields and disturbed forest but virtually absent from undisturbed longleaf except along access roads (Tschinkel 1988).

In addition to predation in fragments, there must be enhanced mortality when young tortoises, at 5 - 10 years, wander long distances. For example, road kills must be elevated. Road kills were the greatest mortality factor at one site in rural Georgia (Landers and Buckner 1981). Certainly larger contiguous areas would lessen this mortality (Diemer 1986).

Indigo Snakes

The very close association of the indigo snake with gopher tortoise burrows (Diemer and Speake 1983) bodes ill for this animal; as the tortoise population is inimically affected by fragmentation, so will snake populations be threatened. In addition, indigo snakes have very large home ranges--up to a square mile (Speake et al. 1978). Thus small fragments of even optimal habitat have insufficient food, and there must be increased mortality from road kills as the snakes wander. Again, it would be interesting to compare sources of mortality for populations in different sized sites.

MANAGEMENT TO AMELIORATE EFFECTS OF FRAGMENTATION ON LONGLEAF COMMUNITIES

Longleaf pine forest seems particularly well adapted to sustain thoughtful, carefully planned harvest. And well-managed second growth may be able to support almost as many species as old-growth. This would not be true for many other forest types. It certainly would not be true for tropical or temperate rain forest.

First, there is the matter of where the biodiversity and the physical structure are. Longleaf forests are very diverse, and the plant diversity is all in the groundcover plants (Walker

1990, 1993). Animal diversity also is primarily on the ground. The canopy is basically a sparse monoculture. The understory is sparse and not very diverse. Thus just removing some individual trees does not remove all the physical structure of the system and does not by itself lower the diversity much.

For old-growth rain forests of the Northwest, there is relatively little diversity among the groundcover plants, and much of the animal diversity is up in the canopy. More than 1,500 invertebrate species can inhabit the canopy of one old-growth stand (Anon. 1989). A huge number of animal species inhabits the soil, but comparative data are not available for longleaf pine forest or tropical rain forest (Luoma 1991). The canopy trees provide the basic physical structure of the system. Thus, when blocks of trees are removed, the structure disappears and many of the associated species are lost.

For old-growth tropical rain forest, not only is the physical structure produced almost entirely by the trees, but the trees themselves are incredibly diverse. In Borneo, 700 species of trees inhabit only 10 ha (Wilson 1988). Most of the animals live in the trees. A single tree species may have hundreds of insect species living in its canopy (Erwin 1988, Wilson 1988). There is little ground cover, so there is little diversity of groundcover plants (Richards 1952). Finally, almost all the nutrients are in the trees themselves, not the soil (Wilson 1988). So when trees are cut, structure, biodiversity and nutrients all disappear.

Topography is the second reason for some optimism that thoughtful harvest of longleaf might not be a conservation disaster. Single tree selection in our Northwestern rain forest often is very difficult and expensive. The terrain is mountainous, often wet and remote. And trees are relatively close together. To fell trees and get them out on the ground is very difficult. In tropical rain forest, the situation is often worse. The trees frequently are huge and close together, the ground is moist and soft, and equipment on the ground causes great damage, even removing a single large tree.

The sparse nature of longleaf pine forests and the gentle terrain make selective logging much more feasible. Of course damage to the ground must be avoided, but this may not be an insurmountable problem. And enough large trees have to be left to support the woodpecker and the fox squirrel. This seems feasible; L. Neel (pers. comm.) describes such an approach. In other words, maintaining the essential character of longleaf pine for-

est in a large fraction of the landscape is likely to be the most effective way to maintain the community and its inhabitants. An alternative approach that is much touted nowadays—narrow corridors for movement between habitat patches—seems far less likely to succeed. It is surely expensive, and no empirical data support its efficacy in longleaf pine forests; few exist for any habitat type (Simberloff et al. 1992). The most frequent effect in the above sketch of possible effects on longleaf pine inhabitants is predation of animals or herbivory of plants, and it is difficult to see how corridors could alleviate this problem. In fact, several authors have suggested that corridors could increase predation within the connected forests because their high content of edge habitat might attract species favoring edge that would forage within the forests (references in Simberloff et al. 1992). Whether red-cockaded woodpeckers would effectively use corridors is very doubtful (Simberloff et al. 1992).

Most of the literature on the “new forestry” focuses specifically on the Pacific Northwest (e.g., Franklin 1989). However, the key goal—management for the entire ecosystem rather than simply wood production—applies equally to longleaf pine and some specific suggestions from this literature may prove useful in the Southeast (e.g., Sharitz et al. 1992). Franklin (1989) suggests that a successful new forestry will not derive simply from increased set-asides, but that even forests from which timber is extracted must be conceived as part of a matrix supporting the entire ecological community. A thorough cost-benefit analysis is required for any forest management system. For example, if we

consider simply forest patch size, traditional forestry analyses focus almost exclusively on the economic cost of removing timber and profit derived from the timber crop (e.g., Cabbage 1983). On the other hand, there are myriad ways in which timber operations leaving landscapes containing different forest patch size distributions may have differing ecological effects (Franklin and Forman 1987). Both Cabbage (1983) and Franklin and Forman (1987) rely on extremely simple and general simulation models that would be difficult to apply to a specific situation on the ground. They are forced to this reliance partly by lack of adequate empirical data on real-world situations. Additionally, it has proven notoriously difficult to assign economic values to various ecological entities, processes, and phenomena (Norton 1987). It is quite likely that dollars are not even the right currency with which to evaluate costs and benefits; certainly they cannot be the only currency. However, in spite of the technical difficulties, an advance in rational forest management will require much more comprehensive and detailed assessments of costs and benefits.

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