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Fragmentation of pine flatwood and marsh communities converted for ranching and citrus

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Abstract

Patterns of change are documented for pineland and marsh, two habitats that are significant for 273 of the 326 native terrestrial vertebrates within the Immokalee Rise region of Florida. Area of both habitats, average patch sizes, and association of patches with patches of the same type and different types changed dramatically from ca. 1900 to 1989. Patterns of change were slightly different from ca. 1900 to 1973 and 1973 to 1989, with more large-scale removal of patches occurring in the former time period. Fragmentation of remaining patches was greatest from 1973 to 1989. In addition to loss and fragmentation of habitat, the association of the two habitat types has been altered. Pineland and marsh have become separated from each other thereby altering, if not destroying, the important upland–wetland linkages naturally present in the region. Drawing from previous studies of species–habitat associations and fragmentation impacts on wildlife in other areas, we form some general conclusions on the implications of these changes on regional biodiversity. Species most severely impacted by the change are most likely those requiring large contiguous areas, requiring interior pineland habitat, and those that use both uplands and marsh. It is probably not a coincidence that 65% of the species rare in the region use pineland or marsh. Continued chipping away at the remaining habitat without regard for the importance of the spatial arrangement and regional context will continue to impact regional biodiversity. A regional perspective to agricultural development is needed to maintain the native biodiversity in the region. Efforts should be made to preserve the remaining large tracts of habitat and seek to restore connections between critical habitats. Maintance of biodiversity will require a regional perspective to agricultural development. Large tracts of remaining habitat must be preserved and connections between critical habitat restored. © 1997 Elsevier Science B.V.

Keywords: Pine flatwood; Terrestrial vertebrates; Regional biodiversity; Florida; Critical habitat

1. Introduction

Wildlife ecologists recognize that utilization of available habitat frequently depends upon patch size and spatial configuration. The regional effect of human development in a landscape is often not just the overall lost of acreage, but also its fragmentation.

The Immokalee Rise region in southwest Florida provides habitat for 380 vertebrate species (Mazzotti et al., 1992), including 22 amphibians, 47 reptiles, 34 mammals, 234 birds, and 43 fishes. When habitat importance was ranked by the authors for 14 southwest Florida cover types, pine flatwoods and fresh-

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water marshes had the most number of species needing those cover types as critical habitat. This paper examines the history of fragmentation of those two cover types.

Our objectives are to: (1) characterize landscape changes in pineland communities as a result of agricultural development; (2) examine changing spatial relationships between pineland and freshwater marsh communities; and (3) present ecological correlates that suggest potential impacts of these landscape changes on selected wildlife species.

1.1. Study area

The study area encompasses 509,260 ha in the Immokalee Rise in southwest Florida (Fig. 1). The natural vegetation is predominately wetland depressions and sloughs with pineland (*Pinus elliotti* and *Serenoa repens*) dominating the uplands. Seasonally flooded, isolated depressions ('temporary ponds') are numerous throughout the pineland matrix. Sloughs are overland sheet flows of slowly moving water that cut across the uplands, creating hydrologic linkages from north to south. The Okaloacoochee Slough is a prevailing wetland in the Immokalee Rise. Isolated depressions or sloughs may be occupied by diverse freshwater marsh grasses or cypress (*Taxodium distichum*) and hardwood swamp. Sandy soils with depths of up to 200 cm on the uplands give way to muck over limestone as the elevation drops slightly to the east and south of the Immokalee Rise (Drew and Schomer, 1984). Extensive sawgrass (*Cladium jamaicense*) marsh occupied the eastern low elevations in their natural state and cypress is the predominant land cover in the southern region. The sawgrass has been completely replaced with sugarcane farms.

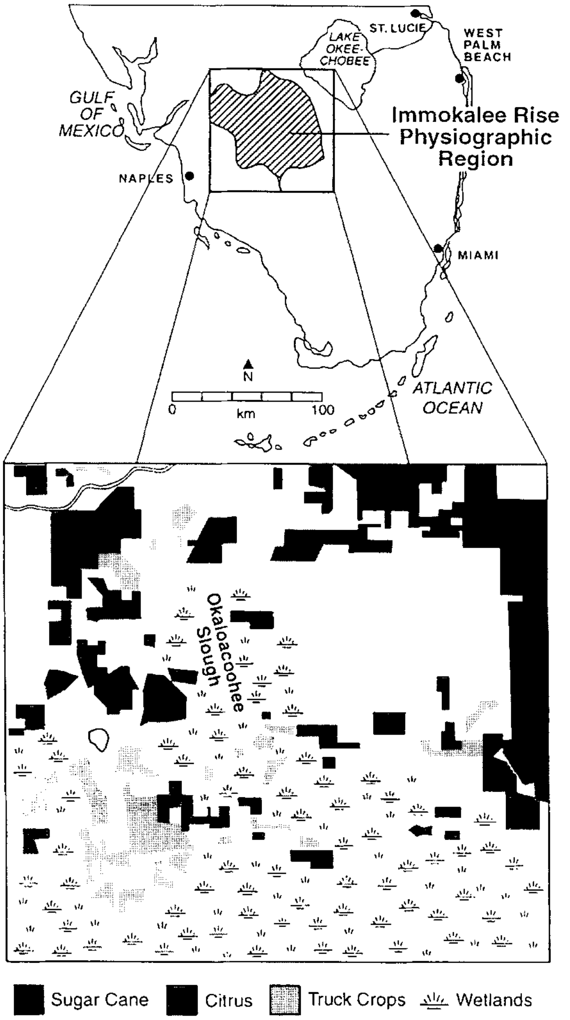

Fig. 1. Location map of the study area illustrating agricultural development in 1989. The background matrix is rangeland.

It is the sandy soils of the uplands that attracted first cattle grazing and then, in the early 1980s, citrus growers to the region. Following a series of devastating freezes, growers began relocating to the Gulf Coast region of the state. By 1989, citrus acreage had grown to 60,000 ha. Behr (1989) estimated the on-tree value of this production to be US$380 million annually. Therefore, this industry is a major contributor to the economic well-being of southwest Florida. However, there is concern that the scale of these developments will significantly affect the ecological integrity of the region. Much of the current and proposed citrus development is occurring in an area occupied by a diverse native flora and fauna including 31 species listed by state and federal agencies as endangered, threatened, or a species of special concern (e.g., the Florida panther, *Felis concolor coryi*).

1.2. Effects of fragmentation

Few published studies have specifically addressed the effects of pineland fragmentation on in the southeast United States. Dunning et al. (1995) observed that isolated patches of managed pine woodlands in South Carolina were less likely to be colonized by Bachman's sparrow (*Aimophila aestivalis*). Conner and Rudolph (1991) demonstrated that fragmentation of pine habitat within 400 m of Red-cockaded Woodpecker (*Picoides borealis*) clusters has a negative effect on the probability of clusters remaining active and on group size. They suggest that reduced dispersal efficiency, rather than loss of foraging habitat, is the primary cause of this relationship. Neither study provides an adequate corollary to the low-elevation, mesic pinelands interspersed with marsh that are characteristic of the Immokalee Rise.

As the pineland on the Immokalee Rise has been cleared for cattle grazing and then citrus, the remaining pineland has been severely fragmented. Large contiguous areas (i.e., patches) of pine in ca. 1900 are now broken into many small remnants. The most obvious effects of fragmentation are decreased core area and increased edge. Core area is the interior area unaffected by environmental influences associated with patch edge. The edge of a patch often receives more light than the interior, is more influenced by wind, and experiences changes in the flux of nutrient and water transport (for review, see Saunders et al., 1991). Because of these environmental characteristics, edges often have a biotic community that is different from the patch interior. Harris (1988) and Yahner (1988) argue that while edges are historically viewed as beneficial (Yoakum and Dasmann, 1971) because their position between adjacent habitats frequently results in more biodiversity, edges can have negative impacts on wildlife. The increased diversity is primarily from generalist species. Too much edge can be at the expense of species needing contiguous habitat. Edge diversity is gained at a loss to interior species that do not tolerate edges and are often of special concern (Simberloff, 1993). Edges, particularly when associated with the disturbance often create habitat for opportunistic exotics and invasive species. Therefore, establishment of invasive and edge species can increase species numbers, but the number of species originally found in the area may decline (Verner, 1986; Murphy, 1989; Webb, 1989; Harris and Scheck, 1991).

Another critical consequence of fragmentation is increased isolation of the remnant habitat patches (Lovejoy et al., 1984, 1986; Haila and Hanski, 1984; Wilcove et al., 1986). As patches get further apart, the ability of some species to disperse may be restricted (Mader, 1984; Saunders and de Rebeeira, 1991). Additionally, the matrix surrounding the habitat patches, such as cleared agricultural fields, may create behavioral barriers to movement (Saunders et al., 1991). Size of the remaining habitat is, of course, also important. As fragments of habitat decrease in size, species using those habitats may crowd together (Lovejoy et al., 1986), altering competition and predation interactions, causing overexploitation of available resources (Saunders et al., 1991) and possibly resulting in dramatic changes in species composition.

2. Methods

Mylar maps were obtained from the University of Florida Center for Wetlands depicting 12 classes of land use and vegetation cover for ca. 1900, 1973, and 1989. These 1:80,000 (approximately) scale maps of Lee, Hendry, and Collier counties were the products of photo-interpretations of 1:63,360 aerial photography. The interpretation of the ca. *1900* land cover was extrapolated from photography taken from 1946 to 1953, US Natural Resources Conservation Service (formally Soil Conservation Service) general soils maps, and previously compiled vegetation maps. Interpretations of the 1973 and 1989 land cover was from photography from those single years.

Each of the nine county maps was scanned into a digital product and rasterized to a output pixel size of 30 × 30 m. The counties were then joined into overall land coverages for each date and the land boundaries were clipped at the study area boundaries. A final majority analysis in a circular moving window was used to recode small slivers which occurred between county boundaries. The ERDAS geographic information systems software matrix routine was used to document changes in the land cover found in the images between years by recording each unique combination of previous to current land cover.

To examine the patch characteristics of increasingly fragmented pineland and their changing relationship to wetlands, only the pineland and marsh classes were considered in the analyses. Marsh is an aggregation of freshwater marsh and slough, sawgrass, and wet prairie from the original classification.

All other classes were treated as background. Fragstats spatial pattern analysis software (McGarigal and Marks, 1995) was used to calculate landscape metrics for each year. The metrics we used from the Fragstats program are presented in Tables 1 and 2. Algorithms are detailed in the Fragstats manual (McGarigal and Marks, 1995). While some of the metrics used, such as Number of Patches, are self-explanatory, a few require more description.

'Patches', in this paper, refers to contiguous areas of the same cover type. Core areas were described in the introduction. We define core area as any patch area remaining after moving in 90 m from the edge of the patch. 'Mean area per disjunct core' is the sum of the core areas in the image divided by the number of core areas in the image. This is similar to 'mean core area per patch', the sum of the core areas in the image divided by the number of patches, except that it accounts for the likely possibility that single patches will have more than one discontiguous core area. Because we are mostly interested in core area as it relates to minimum habitat size requirements for wildlife, we will use 'mean area per disjunct core' metric in this paper.

'Nearest neighbor distance' is the shortest distance from the edge of a patch to the edge of an adjacent patch of the same class. Variability of the nearest neighbor distance relative to the mean is a measure of the spatial distribution of patches in the landscape. This metric is the 'nearest neighbor coefficient of variation' and it is multiplied by 100 to express it as a percent. The 'coefficient of variation' is small (< 100) if patches tend to be uniformly or regularly distributed across the landscape and the metric is a large value (> 100) if the patches are aggregated or clumped in the landscape.

Proximity analysis in ERDAS geographic information systems software was used to report changes in the distance from the edge of pineland patches to the edge of marsh patches. We discuss wildlife dispersal implications of changing distances between these cover types.

Brandt et al. (1995) constructed a matrix of species habitat relationships and a relative abundance ranking for 326 vertebrates in the Immokalee Rise area based on the literature, fieldwork conducted during 1990 and 1991 (Mazzotti et al., 1992) and surveys of expert opinion. We summarized these data for pineland and marsh to examine the importance of these cover types in relationship to the changes reported here. Four groups were considered: (1) species using pineland as habitat, (2) species using

Table 1
Class-level landscape metrics for pineland in the southwest Florida study area. SD = standard deviation, CV = coefficient of variation

	Pine			Pine % change		
	Year 1900	Year 1973	Year 1989	00–73	00–89	73–89
Total area (ha)	509263.0	509263.0	509263.0	0.0	0.0	0.0
Class area (ha)	142999.0	81170.0	16728.0	−43.2	−88.3	−79.4
Percent of landscape (%)	28.0	16.0	3.0	−43.1	−88.3	−79.4
Number of patches	1174.0	621.0	18392.0	−47.1	1466.6	2861.7
Patch density (#/100 ha)	0.2	0.1	3.6	−47.0	1469.6	2859.0
Mean patch size	121.8	130.7	0.9	7.3	−99.3	−99.3
Patch size SD (ha)	3314.1	760.0	9.1	−77.0	−99.7	−98.8
Patch size CV (%)	910.4	581.4	1005.2	−36.1	10.4	73.0
Total edge (m)	5851890.0	4748130.0	7792770.0	−18.9	33.2	64.1
Edge density (m/ha)	11.5	9.3	15.3	−19.0	33.2	64.2
Core % of landscape	22.4	10.2	0.4	−54.5	−98.3	−96.3
Number of core areas	739.0	960.0	528.0	29.9	−28.6	−45.0
Total core area (ha)	114187.0	51919.0	1904.0	−54.5	−98.3	−96.3
Mean area per disjunct core (ha)	154.5	54.1	3.6	−65.0	−97.7	−93.3
Area per disjunct core SD (ha)	1967.2	426.2	19.3	−78.3	−99.0	−95.5
Area per disjunct core CV (%)	1273.2	788.0	536.2	−38.1	−58.0	−32.0
Mean nearest neighbor distance (m)	255.8	355.7	60.2	39.1	−76.5	−83.1
Nearest neighbor SD (m)	451.5	785.3	134.2	74.0	−70.3	−82.9
Nearest neighbor CV (%)	176.5	220.8	223.1	25.1	26.4	1.1

Table 2
Class-level landscape metrics for marsh in the southwest Florida study area. SD = standard deviation, CV = coefficient of variation

	Marsh			Marsh % change		
	Year 1900	Year 1973	Year 1989	00–73	00–89	73–89
Total area (ha)	509263.0	509263.0	509263.0	0.0	0.0	0.0
Class area (ha)	213742.0	100455.0	88103.0	-53.0	-58.8	-12.3
Percent of landscape (%)	42.0	12.0	17.3	-53.0	-59.0	-12.3
Number of patches	2757.0	1220.0	19869.0	-55.8	620.7	1528.6
Patch density (#/100 ha)	0.5	0.2	3.9	-55.6	622.2	1525.0
Mean patch size (ha)	77.5	82.3	4.4	6.2	-94.3	-94.6
Patch size SD (ha)	2873.2	734.0	137.5	-74.5	-95.2	-81.3
Patch size CV (%)	3706.0	891.4	3100.6	-76.0	-16.3	247.9
Total edge (m)	6796620.0	5232180.0	18414450.0	-23.0	170.9	252.0
Edge density (m/ha)	13.4	10.3	36.2	-23.1	170.9	252.1
Landscape shape index	24.8	19.3	65.5	-22.1	164.1	238.9
Area weighted mean shape	11.8	5.5	12.7	-53.3	7.2	129.5
Core % of landscape	34.4	13.6	4.5	-60.4	-87.1	-67.3
Number of core areas	1311.0	1354.0	4188.0	3.3	219.5	209.3
Total core area (ha)	175402.0	69477.0	22712.0	-60.4	-87.1	-67.3
Mean area per disjunct core (ha)	133.8	51.3	5.4	-61.7	-96.0	-89.4
Area per disjunct core SD (ha)	3737.9	554.4	125.1	-85.2	-96.7	-77.4
Area per disjunct core CV (%)	2793.8	1080.5	2306.9	-61.3	-17.4	113.5
Mean nearest neighbor distance (m)	163.1	262.1	78.9	60.7	-51.6	-69.9
Nearest neighbor SD (m)	176.3	444.3	102.1	151.9	-42.1	-77.0
Nearest neighbor CV (%)	108.1	169.5	129.4	56.8	19.7	-23.7

marsh, (3) species using pineland and marsh, and (4) species using pineland or marsh. The last group is different from simply summing groups 1 and 2 because the same species in group 1 and in group 2 are not double counted. Within each group the species are further subdivided into: (1) the total number of species using that cover type, (2) species for which the cover type is critical habitat, (3) species that are rare in the region using the cover type, and (4) species rare in the region that require the cover type as critical habitat.

3. Results

Fig. 2 illustrates the acreages of all the cover types at the three dates as interpreted by the Center for Wetlands. The cover types that decrease the most are pineland and two of the marsh communities, sawgrass and wet prairie. There also was a substantial increase in grassy scrub and the development of agricultural crops. The fluctuation of acreage in the hammocks and fresh marsh and slough communities is primarily the result of interpreter differences among the images as discussed below. 'Hammock,' incidentally, is a mostly Florida term used with hardwood communities which are frequently, but not always, associated with slight elevation rises such as limestone outcrops (Harper, 1905).

Pineland and marsh cover types are the classes of interest, in part, because of the high observed loss of acreage. Thirty-one percent of the pineland from ca. 1900 to 1973 were converted to grassy scrub which represents the conversion to rangeland for cattle grazing. Seven percent was converted to citrus development (Tree Crops). From 1973 to 1989, 29% of the pineland was converted to grassy scrub and 11% was citrus.

Trends in the spatial pattern of pineland and marsh (combining fresh marsh and slough, sawgrass, and wet prairie) change between the 3 yrs of observation (Fig. 3). Pineland area decreased by 62,000 ha between the beginning of the century and 1973 and then another 64,000 ha in the next 16 yrs (Table 1). Pineland's coverage of the landscape decreased 126,000 ha (−88%) from 28% of the landscape in ca. 1900 to 3% of the landscape in 1989. Although pineland area decreased both from ca. 1900 to 1973 and 1973 to 1989, impacts on the structure of the

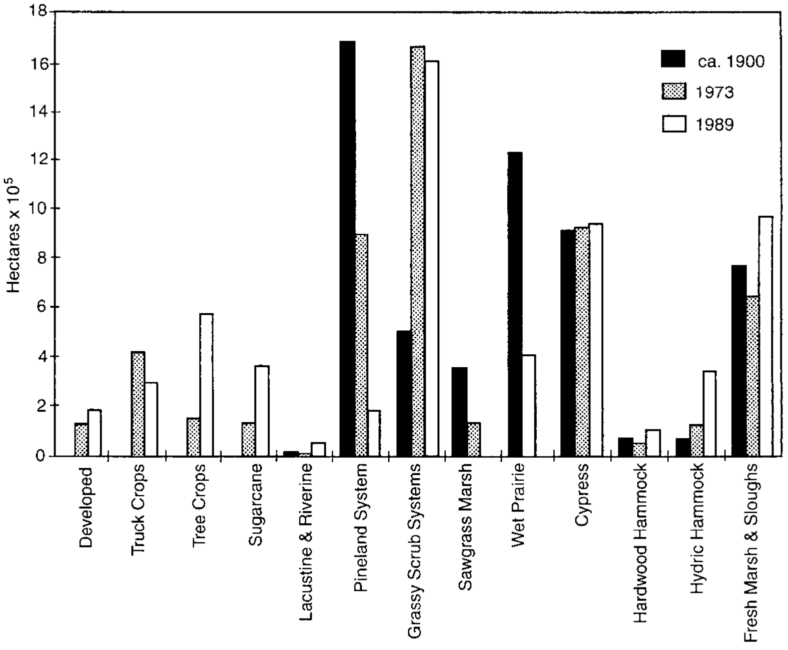

Fig. 2. Acreages of cover types in the study area for ca. 1900, 1973 and 1989. Photointerpretations produced by the Center for Wetlands, University of Florida.

landscape were different from 1900 to 1973 than they were from 1973 to 1989. The principal process resulting in loss of pineland acreage in the earlier images is large-scale clearing that completely removed many patches. Thus, the number of patches, patch density, and total edge decreased. Consequently, the mean nearest neighbor distance between patches increased from 255 to 355 m (39%) and the variability in nearest neighbor distances greatly increased from a standard deviation of 451 to 785 m.

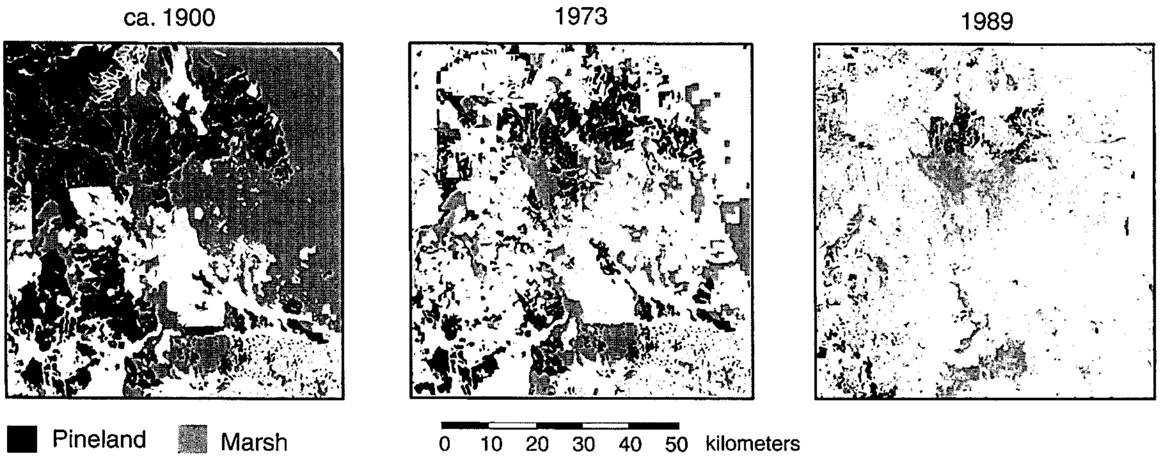

Fig. 3. Spatial arrangement of pineland and marsh in the study area for ca. 1900, 1973 and 1989. Photointerpretations by the Center for Wetlands, University of Florida.

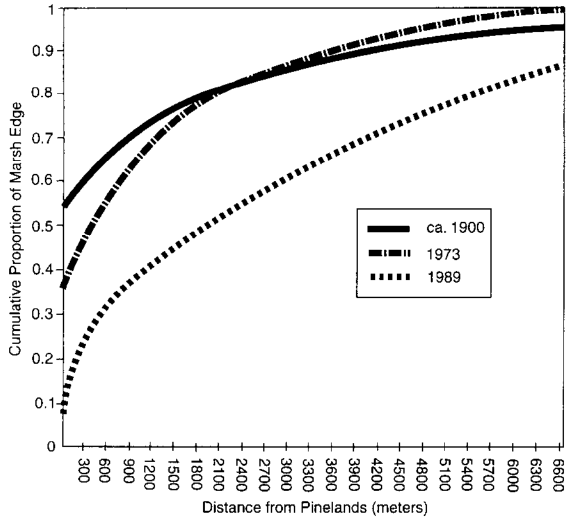

Fig. 4. Proportion of marsh cover type edge at increasing distances from pineland.

Fragmentation rather than complete removal also was occurring in the landscape, so while the overall number of patches decreased, the number of core areas increased, but the area per core decreased.

Between 1973 and 1989, fragmentation rather than removal of pineland patches became the principal process. The effect on the landscape was a 2800% increase in the number of pineland patches while patch size decreased 99% thereby reducing the number of core areas (−45%) and the mean area of each core (−93%). Fragmentation of the pineland resulted in small patches that are clumped close together, so mean nearest neighbor distances decreased 83% to 60 m ± 134 m. The nearest neighbor coefficient of variation indicates a clumped pattern of pineland patches in all years.

A greater proportion of marsh was converted to other uses between ca. 1900 and 1973 than pineland (Table 2). Much of the 113,000 ha was converted from sawgrass marsh to sugarcane, almost completely removing that marsh community type from the landscape. Sawgrass marsh was completely replaced with sugarcane by 1989. Unlike pineland, however, the loss of marsh slowed between 1973 and 1989 (−12,000 ha). Pineland and marsh have similar patterns of a decreased number of patches and total edge between ca. 1900 and 1973 and then a greatly increased number of patches and total edge between 1973 and 1989 because the same processes of clearing and fragmentation were affecting both cover types. Between ca. 1900 and 1989, marsh acreage had decreased from 42% to 17% of the landscape, a loss of more than half its acreage. Mean patch size and the mean area per core both declined approximately 95%.

Mean nearest neighbor distances in the pineland and marsh have a similar trend with distances increasing due to clearing and then becoming very small by 1989 as patches are fragmented. Nearest neighbor coefficients of variation suggest that the marsh patches were more randomly distributed in the landscape in ca. 1900 and became somewhat more clumped with agricultural development.

Proximity between pineland and marsh habitats also changed between the three dates. When the cumulative proportion of marsh edge was plotted as a function of distance from the edge of pineland (Fig. 4), 55% of the marsh was within 30 m of adjacent pineland in ca. 1900. That same proportion of marsh edge in 1973 required a search distance of 630 m. In 1989, the search distance required from pineland to reach the edge of 55% of the marsh in the landscape increased to 2460 m.

Fig. 5 illustrates the results of summarizing wildlife utilization data collected by Brandt et al. (1995). From a total of 326 terrestrial vertebrate species in the Immokalee Rise area, 273 species or

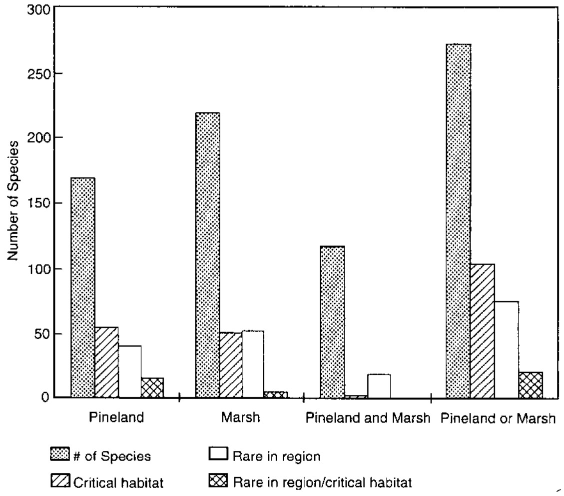

Fig. 5. Summary of data collected by Brandt et al. (1995) for wildlife utilization of pineland and marsh habitats.

84% occur in pineland or marsh habitats and 117 of those species use both pineland and marsh as habitat. One hundred and five species use pineland or marsh as critical habitat.

One hundred and fifteen vertebrate species are present but rare in the Immokalee Rise area. Of those rare species, 65% or 75 species use pineland or marsh habitat. Nineteen rare species use both pineland and marsh as habitat.

4. Discussion

Fahrig and Merriam (1994) stress that landscape spatial structure is critical to understanding effects of fragmentation. Wildlife use of landscapes depends on: (1) spatial relationships among landscape elements used by the population for habitat and through which they disperse, (2) dispersal characteristics of the organism, and (3) temporal changes in the landscape (Fahrig and Merriam, 1994). Changes in the landscape of the Immokalee Rise over the last century provide a dramatic look at habitat fragmentation in an increasingly human-dominated system. A regional perspective to agricultural development may have been able to preserve large tracts of pineland and marsh mosaic and the wildlife they support. However, the cumulative impacts of site-by-site development without consideration of the landscape as a whole have left only remnants of isolated pineland and marsh habitat.

Pineland and marsh decreased by approximately 126,000 ha each between ca. 1900 and 1989. Clearing and land conversion for agriculture account for the lost of acreage through two mechanisms: (1) large-scale clearing that completely removes large areas of the cover type, and (2) smaller-scale fragmentation of the cover type into smaller patches. Both processes contributed to landscape change through the study period. However, the first process was more important between ca. 1900 and 1973 as seen in the removal of patches, decreased patch density and decreased edge. Between 1973 and 1989, the second process became dominate, resulting in greatly increased numbers of patches, patch density and edge while core area was substantially lost.

Despite the 88% decrease in pineland and 59% decrease in marsh, these cover types remain one of the most used habitats in the Immokalee Rise and critical habitats for 105 species. Because of habitat loss, however, it is not surprising that 65% of the species that are rare in the region use pineland or marsh. Changes in the amount and configuration of pineland and wetlands are most likely to impact wide-ranging species, interior species with minimum contiguous area requirements and, as distances between pineland and marsh increase, species that use both cover types.

Florida panther and black bears (*Ursus americanus floridanus*) depend upon large contiguous areas of forest for quality habitat. Connecting these areas with wide dispersal corridors enhances their value as large mammal habitat. Models of Florida panther habitat within this study area by Pearlstine et al. (1995) show that the amount of potential habitat for panthers has decreased from ca. 1900 to 1989 and that under continued citrus development panther habitat will continue to decline. The authors suggested that in 1989, the Okaloacoochee Slough still provided a corridor for panthers traveling between the northern and southern habitats in the region, although the slough itself does not provide very suitable habitat. With anticipated development of additional citrus removing the remaining pineland habitats to the north, even that landscape connection may be broken, restricting panthers to the forested swamps to the south.

Black bears are another wide-ranging species to use the shrinking matrix of habitats available in this region. They have similar habitat requirements (Maehr et al., 1988; Mykytka and Pelton, 1989), but smaller home ranges (Brody and Pelton, 1989; Maehr, 1992) than the Florida panther. Habitat restrictions as a result of fragmentation should be similar for the two species.

Based on previous studies, we can hypothesize that diversity of native species in fragments will decrease and that community structure within patches will be influenced both by patch size and by the cover types surrounding the patch. Studies of fragmentation on avian species report decreased diversity (Freemark and Merriam, 1986; Dunning et al., 1995; McIntyre, 1995) as patches decreased in size and became more isolated. Webb (1989) found the same relationship with invertebrate diversity.

Webb (1989) and Hagan et al. (1996) showed that the structure and composition of the vegetation surrounding the habitat patches influenced invertebrate and avian diversity, respectively. For small mammals, Stout and Corey (1990) also reported on the importance of the surrounding landscape in influencing species richness. For example, Schieck et al. (1995) found no relationship between patch size and bird species abundance or richness and concluded that there may be less contrast between the logged landscape surrounding their old-growth montane forest patches than there is between forest patches in many previous studies surrounding by agricultural development or urbanization.

Fragmentation also may influence community structure by impacting species' dispersal. Hagan et al. (1996) found that fragmentation may initially lead to increased bird densities as a result of displaced individuals packing into remaining habitat and lead to decreased pairing success for some species. Thaxton and Hingtgen (1996) attribute significantly greater dispersal distances and mortality rates of Florida scrub-jays (*Aphelocoma coerulescens*) in suburban areas than in preserves to habitat fragmentation.

Dispersal for species that use more than one habitat in the landscape can be interrupted by increased distances between these habitats. The elimination of habitat linkages that provide essential elements for species survival could drastically restructure communities (Cole, 1987; Burdick et al., 1989). More than 35% of the species in the Immokalee Rise region have habitat components in both pineland and marsh. A typical direct terrestrial/aquatic linkage occurs when a species resides and feeds in one of these two habitats and breeds in the other. Examples include aquatic turtles which reside in wetlands and open water areas, but require adjacent uplands for nesting, and amphibians which are a cornerstone of the vertebrate food chain. Larval and aquatic life stages of amphibians are important prey items for wading birds and many terrestrial predators (Burton and Likens, 1975; Kushlan, 1976, 1979). Amphibians also are an important route for the transport of nutrients out of wetlands (Wassersug, 1975). Some amphibians disperse for distances of 2 km from a wetland, extending the role of small isolated wetlands in nutrient and energy cycling far beyond their borders (Breden, 1987; Moler and Franz, 1987). The integrity of this terrestrial/aquatic linkage is threatened as the intact mosaic of upland and wetland habitat is fragmented and distances wildlife must travel between the two habitats increases.

Although there was a very real loss of pineland and marsh area between 1973 and 1989, the difference in fragmentation of the area is exaggerated because of an interpreter bias to record more detail in the 1989 image than was recorded in the 1973 image. The problem of inconsistent interpretation between different map products is common in GIS analysis. The analyst needs to be particularly wary of comparisons of spatial databases from different sources. Although that was not the case here, the different date imagery may have been interpreted by different individuals or at different times. Although the numbers reported would change if interpretation had been more consistent, the trend structuring the landscape and reflected by the metrics overwhelms any variation in interpretation.

In addition to decreased patch sizes, patch size variability was greatly reduced. In ca. 1900, many small patches were present as well as large contiguous areas. Variability in available patch sizes in the landscape provided potential habitat for a wider diversity of wildlife species.

Regional planning to protect habitat in the Immokalee Rise must be shaped by the reality of working with small remnant patches. Restoration of missing land covers and opportunities for creating linkages should be considered (Harris and Scheck, 1991). Conservation efforts should consider the pineland and marsh matrix together in the landscape rather than concentrating on one or the other community. Management of the remaining habitat in this area also will require recognition that controlling the external influences in the landscape surrounding the habitat patches is just as important as preserving the patches themselves (Janzen, 1986).

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References

Behr, R.H., 1989. Report presented by Florida Department of Citrus, to the Gulf Coast Growers Association, Labelle, FL.

Brandt, L.A., Powell, D., Mazzotti, F.J., 1995. Vertebrate species habitat relationships for the Immokalee Rise area. Bulletin 303, Florida Cooperative Extension Service, Institute of Food and Agricultural Services, University of Florida, Gainesville, FL.

Breden, F., 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo Woodhousei Fowleri*. Copeia 1987, 386–395.

Brody, A.J., Pelton, M.R., 1989. Effects of roads on black bear movements in western North Carolina. Wildlife Soc. Bull. 17, 5–10.

Burdick, D.M., Cushman, D., Hamilton, R., Gosselink, J.G., 1989. Faunal changes and bottomland hardwood forest loss in the Tensas Watershed Louisiana USA. Conservation Biol. 3, 282–292.

Burton, T.M., Likens, G.E., 1975. Salamander populations and biomass in the Hubbard Brook Forest, New Hampshire. Copeia 1975, 541–546.

Cole, G.F., 1987. Changes in interacting species with disturbance. Environ. Manage. 11, 257–264.

Conner, R.N., Rudolph, D.C., 1991. Forest habitat loss, fragmentation and Red-cockaded Woodpecker populations. Wilson Bull. 103, 446–457.

Drew, R.D., Schomer, N.S., 1984. An Ecological Characterization of the Caloosahatchee River/Big Cypress Watershed. US Fish and Wildlife Service, FWS/OBS-82/58.2, Washington, DC.

Dunning, J.B., Borgella, R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. Conservation Biol. 9, 542–550.

Fahrig, L., Merriam, G., 1994. Habitat patch connectivity and population survival. Ecology 66, 1762–1768.

Freemark, K.E., Merriam, H.G., 1986. Importance of area and habitat heterogeneity on bird assemblages in temperate forest fragments. Biol. Conservation 36, 115–141.

Hagan, J.M., Haegen, W.M.V., McKinley, P.S., 1996. The early development of forest fragmentation effects on birds. Conservation Biol. 10, 188–202.

Haila, Y., Hanski, I., 1984. Methodology for studying the effect of fragmentation on land birds. Ann. Zool. Fennica 21, 393–397.

Harper, R.M., 1905. 'Hammock', 'hommock' or 'hummock'?. Science 22, 400–402.

Harris, L.D., 1988. Edge effects and conservation of biotic diversity. Conservation Biol. 2, 330–332.

Harris, L.D., Scheck, J., 1991. From implications to applications: the dispersal corridor principle applied to conservation of biological diversity. In: Saunders, D.A., Hobbs, R.A. (Eds.), Nature Conservation 2: the Role of Corridors. Surrey Betty and Sons, Chipping Norton, Australia, pp. 189–220.

Janzen, D.H., 1986. The eternal external threat. In: Soule, M.E. (Ed.), Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, pp. 286–303.

Kushlan, J.A., 1976. Wading bird predation in a seasonally flooded pond. Auk 93, 464–476.

Kushlan, J.A., 1979. Feeding ecology and prey selection in the White Ibis. Condor 81, 376–389.

Lovejoy, T.E., Bierregaard, R.O., Brown, K.S., Emmons, L.H., van der Voort, M.E., 1984. Ecosystem decay of Amazon forest fragments. In: Niteki, M.H. (Ed.), Extinctions. University of Chicago Press, Chicago, IL, pp. 295–325.

Lovejoy, T.E., Bierregaard, R.O., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S., Powell, A.H., Schubart, H.O.R., Hays, M.B., 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soule, M.E. (Ed.), Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, pp. 257–285.

Mader, H.J., 1984. Animal habitat isolation by roads and agricultural fields. Biol. Conservation 29, 81–96.

Maehr, D.S., 1992. Florida Black Bear. In: Humphrey, S.R. (Ed.), Rare and Endangered Biota of Florida. University Press of Florida, Gainesville, FL, pp. 265–275.

Maehr, D.S., Layne, H.N., Land, E.D., McCown, J.W., Roof, J., 1988. Long distance movements of a Florida black bear. Florida Field Naturalist 16, 1–6.

Mazzotti, F.J., Brandt, L.A., Pearlstine, L.G., Kitchens, W.M., Obreza, T.A., Depkin, F.C., Morris, N.E., Arnold, C.E., 1992. An evaluation of the regional effects of new citrus development in the ecological integrity of wildlife resources in southwest Florida. Final Report. South Florida Water Management District, West Palm Beach, FL.

McGarigal, K., Marks, B., 1995. Fragstats: Spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. US Department of Agriculture, Forest Service, Portland, OR.

McIntyre, N.E., 1995. Effects of forest patch size of avian diversity. Landscape Ecology 10, 85–99.

Moler, P.E., Franz, R., 1987. Wildlife values of small isolated wetlands in the southern coastal plain. Proceedings of the third southeastern nongame and endangered wildlife symposium. Georgia Department of Natural Resources, pp. 234–238.

Murphy, D.D., 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. Conservation Biol. 3, 82–84.

Mykytka, J.M., Pelton, M.R., 1989. Management strategies for Florida black bear based on home range habitat composition. Int. Conf. Bear Res. Manage. 8, 161–167.

Pearlstine, L.G., Brandt, L.A., Kitchens, W.M., Mazzotti, F.J., 1995. Impacts of citrus development on habitats of southwest Florida. Conservation Biol. 9, 1020–1032.

Saunders, D.A., de Rebeeira, C.P., 1991. Values of corridors to avian populations in a fragmented landscape. In: Saunders, D.A., Hobbs, R.J. (Eds.), Nature Conservation 2: the Role of Corridors. Surrey Betty and Sons, Chipping Norton, Australia, pp. 221–244.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biol. 5, 18–32.

Schieck, J., Lertzman, K., Nyberg, B., Page, R., 1995. Effects of patch size on birds in old-growth montane forests. Conservation Biol. 9, 1072–1084.

Simberloff, D., 1993. How forest fragmentation hurts species and what to do about it. In: Covington, W., Debano, L. (Technical coordinators), Sustainable Ecological Systems: Implementing an Ecological Approach to Land Management. US Department of Agriculture, Forest Service, General Technical Report RM-247, pp. 85–90

Stout, I.J., Corey, D.T., 1990. Patch-corridor effects on faunal assemblages of long-leaf pine-turkey oak sandhill communities. Florida Scientist 54 (Supplement 1), 36.

Thaxton, J.E., Hingtgen, T.M., 1996. Effects of suburbanization and habitat fragmentation on Florida scrub-jay dispersal. Florida Field Naturalist 24, 25–37.

Verner, J., 1986. Predicting effects of habitat patchiness and fragmentation—the researcher's viewpoint. In: Verner, J., Morrison, M.L., Ralph, C.J. (Eds.), Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison, WI, pp. 327–329.

Wassersug, R.J., 1975. The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. Am. Zool. 15, 405–417.

Webb, N.R., 1989. Studies of the invertebrate fauna of fragmented heathland in Dorset, UK, and the implications for conservation. Biol. Conservation 47, 153–165.

Wilcove, D.S., McLellan, C.H., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soule, M.E. (Ed.), Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, pp. 237–256.

Yahner, R.H., 1988. Changes in wildlife communities near edges. Conservation Biol. 2, 333–339.

Yoakum, J., Dasmann, W., 1971. Habitat manipulations practices. In: Giles, R. (Ed.), Wildlife Management Techniques, 3rd edn. The Wildlife Society, Washington, DC, pp. 173–231.