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Endangered species management requires a new look at the benefit of fire: The Cape Sable seaside sparrow in the Everglades ecosystem

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ABSTRACT

Although disturbance processes play important roles in maintaining habitat heterogeneity, the potential effects of such processes on rare or endangered species is virtually unknown and difficult to test. We use an unplanned fire, which burned half of a long-term study plot, as a natural experiment to test the effects of fire on the federally endangered Cape Sable seaside sparrow in Everglades National Park. By implementing a before-after-control-impact study design we determine the mechanistic link between fire and demography of this endangered sparrow. Our results show that while the sparrow tolerates fire, neither sparrow density nor nesting success are enhanced by fire, which runs contrary to the current paradigm in which sparrows are expected to benefit and therefore require fire for persistence. Our results caution against the assumption that occupancy of disturbance-prone habitat automatically suggests dependence on disturbance. Land managers must prevent large and frequent fires from burning occupied sparrow habitat to best manage for the species. Moreover, it is imperative that more studies focus on the effects of disturbance processes on rare and endangered species in order to prevent further loss of biodiversity.

1. Introduction

Disturbance often plays an important role in maintaining habitat heterogeneity (Askins, 2002; Brawn et al., 2001; Pickett and White, 1986; Sousa, 1984). In many cases this heterogeneity must be sustained for select species to persist (Madden et al., 1999; Tucker et al., 2006), whether being directly responsible for the substrate required by an organism for survival or the creation of multiple habitat types that satisfy the diverse needs of a particular organism (Law and Dickman, 1998; Moran-lopez et al., 2006). However, when the species of concern is threatened with extinction even natural disturbance events must be viewed with caution. Such populations are by definition low in numbers and often restricted to small areas of suitable habitat. Thus, disturbance events may drive the population to extinction even if the event is precipitated by natural causes and despite the fact that the disturbance may be required to maintain or create suitable habitat (Jakalaniemi et al., 2006). For this reason there is a critical need to understand how species threatened with extinction respond to disturbance events so that these events can be managed (as much as feasible) to ensure recovery. Despite this need there are remarkably few studies that follow the effects of disturbance on any species in natural environments, much less

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endangered vertebrates (Whelan, 1995). Here we provide information on the demographic response of an endangered bird, the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*), to an unplanned fire that swept through its habitat within the Florida Everglades ecosystem. Our results illustrate the complexity of managing an endangered species within dynamic ecosystems, and the value of testing the assumption that such species rely on disturbances events for their long-term persistence.

The Cape Sable seaside sparrow has been protected under the United States Federal Endangered Species Act since the act's inception in 1973. This non-migratory subspecies is geographically restricted to six subpopulations, almost all of which are located within the borders of Everglades National Park (ENP) and Big Cypress National Preserve of South Florida, USA (Fig. 1). The sparrow lives exclusively in short hydroperiod (<7 months of standing water) freshwater marl prairie. This ecotype, although extensive, is not contiguous sparrow habitat. Slight decreases in elevation allows for the formation of marsh, whereas slight increases in elevation allows for the emergence of pines and upland hardwoods. Work by Jenkins et al. (2003a,b) showed that the sparrows avoid habitat within 40 m of emergent pine or hardwood vegetation. Likewise, sparrows avoid habitat that is too wet, as it does not provide the necessary structure for nesting or foraging (Lockwood et al., 2001). Therefore, sparrow habitat is limited to a subset of the total marl prairie community, that which is free of emergent vegetation and has a drydown period during the peak breeding season from early March through May.

Overlain across this landscape is the effect of fire (Lockwood et al., 2003). There are multiple feedbacks between water flows, vegetation, soil type and fire in the Everglades that creates a complex temporal and spatial burn pattern (DeAngelis and White, 1994; Lockwood et al., 2003). In their fire history analysis of the Everglades from 1948 through 1992, Gunderson and Snyder (1994) outlined temporal fire patterns for the entire ecosystem. They found that fires consumed large areas (annual geometric mean >93 km^2) of the Everglades about every 10 to 15 years, and these large fires were followed by years of significantly smaller total area

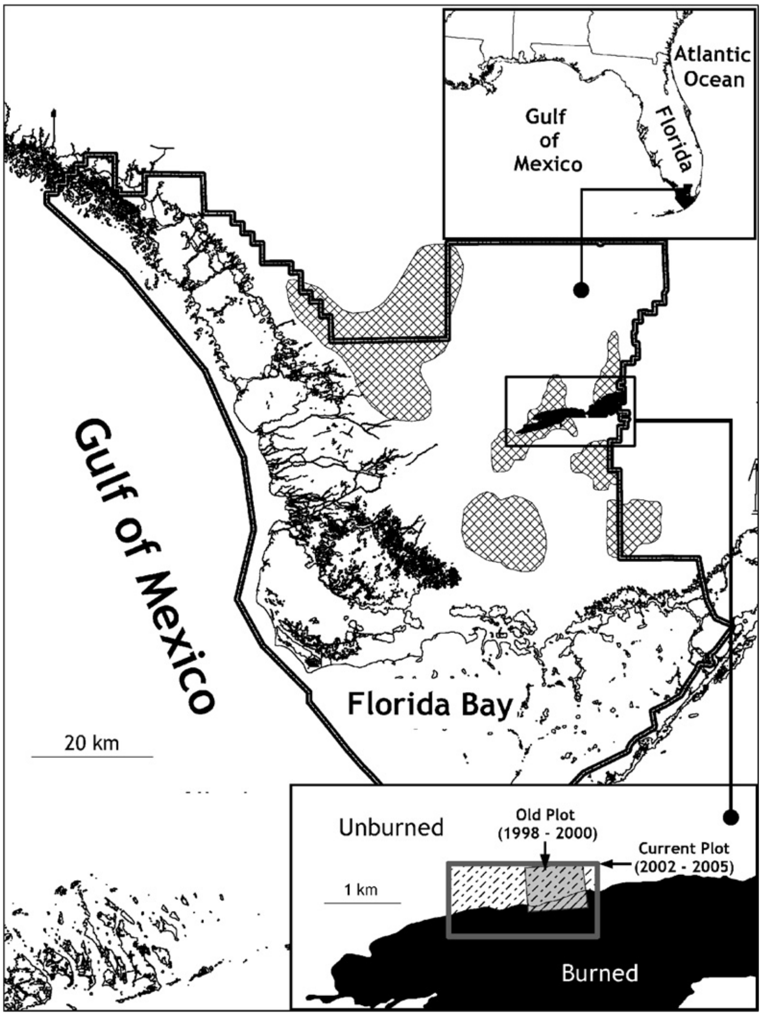

Fig. 1 – Map showing South Florida coastline with Everglades National Park boundary. Cross-hatched areas represent extent of Cape Sable seaside sparrow habitat. The Lopez fire (solid black) is shown originating from the eastern boundary of the park, and extending westward, bisecting a subpopulation of the sparrows. Inset: Detail of the Lopez fire (solid black) and our 2 km × 1 km study plot (hatched rectangle).

burned. Most natural fires occurred during wet season thunderstorms typical of June and July, however, very large fires occurred during May when the conditions were still relatively dry, and intensified in El Nino years (Beckage et al., 2003; Gunderson and Snyder, 1994).

This naturally variable fire return interval is further complicated by the effects of incendiary fires (i.e. arson and escaped agricultural burns) and fire management practices. Everglades National Park, and other land-holding public agencies, actively pursue the use of fire as a management tool for maintaining early successional plant communities and controlling invasive plant species. Additionally, incendiary fires result in the wildland-urban interface burning both more often, and more out of season, than what is considered natural (Lockwood et al., 2003). Each of these human-derived sources of fire in the ecosystem has a spatial and temporal signature that is distinct from more natural fires. Prescribed burns tend to produce more frequent and smaller fires than those ignited by lightening, whereas incendiary fires burn a significantly larger (>2x) area and greater frequency than natural fires due to their concentration during the driest months (Gunderson and Snyder, 1994).

We know from previous work that fire removes all standing vegetation within sparrow habitat making it unsuitable for some period of time and creates a complex burn pattern that may contribute to the spatial segmentation of the sparrow population (Werner, 1975; Taylor, 1983). However, it is not clear how long the effects of fire last, whether fire is needed to 're-set' the habitat so it remains suitable for sparrows over the long-term, or how sparrow dispersal dynamics interplay with the spatial extent of fires to influence subpopulation recovery or metapopulation persistence.

In Fig. 2, we outline three possible scenarios of how fire may impact Cape Sable seaside sparrow populations based on our understanding of the species and previous work (Pimm et al., 2002; Taylor, 1983; Werner, 1975). In all three cases, we expect the dependent variable (i.e. some measure of sparrow population size or demography) to be reduced immediately following fire and persist in a reduced state for at least one breeding season. Scenario A, where habitat is enhanced by fire, most closely represents the current paradigm of sparrow habitat management, based on work by Werner (1975) and Taylor (1983). Both studies substituted space-for-time in correlating sparrow density to habitat quality using habitat of a known burn history. Werner (1975) concluded that sparrow density peaked in the third year and declined to zero in 6 years after fire. Taylor (1983) found similar results but extended the duration of suitable habitat to 10 years and contributed the difference to environmental factors such as soil depth. The result of this work has been a recommendation for marl prairie to be burned on a 6–10 year rotation to maintain suitability for the sparrow. In scenario B, the case where fire has no lasting effect, the demographic features of the burned site return to levels indistinguishable from the control. Finally, if fire has a lasting negative effect (C), we expect demographic rates within the burned site to persist at levels significantly below the control. We compare our results from below to these competing models thereby deducing which scenario predominates for Cape Sable seaside sparrows.

2. Methods

On May 8, 2001 a human-ignited fire (hereafter the Lopez fire) began at the eastern boundary of Everglades National Park (Fig. 1). Over the course of 15 days the Lopez fire burned 3410 ha until controlled on May 23, 2001. Given the dry conditions at the time, the fire consumed the great majority of vegetation in its path, leaving little in the way of an unburned vegetation mosaic. The Lopez fire represents an early season fire event that would not be characteristic of an average fire season. However, the Lopez fire does fall well within the range of fires over the period of record provided by Gunderson and Snyder (1994) and such fires may be expected to occur more frequently given the altered water flow regime currently affecting the northeastern portion of Everglades National Park (Lockwood et al., 2003).

The path of the fire included the southern portion of subpopulation E of the Cape Sable seaside sparrow, including the

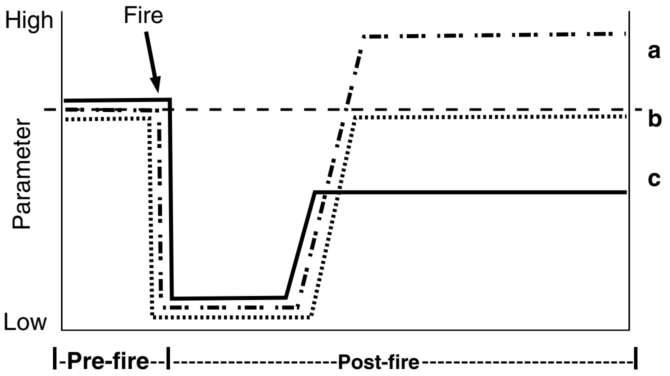

Fig. 2 – Three theoretical scenarios of the effect of fire on *Ammodramus maritimus mirabilis*. The horizontal dashed line represents the control plot, where no change is occurring. After fire, each scenario is predicted to show a drop in a measured parameter, which in our case would be either sparrow density or nesting success. This condition is expected to continue for some period of time, at which point the burned habitat will show either a measurable degradation due to fire (c), no effect of fire (b), or enhancement by fire (a). Our time scale is based on previous research by Pimm et al. (2002) and work by Werner (1975) and Taylor (1983).

southern edge of a 4-year old study plot originally designed to document demographic parameters of this population (Fig. 1). We extended this plot to be 2 km by 1 km (200 ha; see Fig. 1 inset) and it contained 60% (120 ha) unburned habitat (hereafter referred to as the control plot) and 40% (80 ha) burned habitat (hereafter referred to as the burned plot). This situation permitted us to utilize a before-after-control-impact (BACI) design, which allows more precise inferences on the effect of fire on sparrow demography (Manly, 2001).

2.1. *Sparrow density*

In order to document changes in sparrow density due to the fire, we established 15 permanent point count locations distributed systematically across the entire study plot. The number of sparrows seen or heard within a 200 m radius was recorded over a 5-min interval during each visit. Each point was surveyed eight times each breeding season (late March–early July) from 2002 to 2005. The time of day of counts was held constant at between 0700 and 0900, although the order in which point counts were visited was varied to correct for any unforeseen time-dependent variance. Our survey points, being located at 400 m intervals across the site, therefore ensured near complete coverage of the plot. Our study design did not allow us to estimate detection probability and therefore our comparisons below are between relative density.

Using ArcGIS (ESRI, 2005) we classified each point count location as either burned, edge or control by placing a buffer of 200 m diameter around each point and superimposing the buffered points on the perimeter of the fire scar. All points with a buffer >75% in either the burned or control plot were assigned accordingly, whereas any point with a buffer of 25–75% burned was classified as edge. This resulted in a final distribution of eight points in the unburned area, three points on the edge of burned and unburned, and four in the burned area. Because we return to the same point count stations each year, and the Cape Sable seaside sparrow shows significant site fidelity (Pimm et al., 2002) we cannot assume that our point counts are independent of each other between years. Therefore, we used a repeated measures multivariate analysis of variance, or MANOVA (SAS for Windows v.9), to analyze our point count data with burned, edge, and control as our treatment levels and year as our repeated measure factor. To determine the polarity of any detected differences, we performed a comparison of least square means with the standard Bonferroni correction for multiple comparisons. A post hoc comparison of means between the 2002 and 2004 points in the control plot was used to test for significance of observed differences between the 2 years.

2.2. *Dispersal*

Since 1998, we have color banded 383 Cape Sable seaside sparrows within our study plot, 156 of these were banded as adults and the remainder as first year juveniles (i.e. hatched during the breeding season in which they were banded). Color bands allow us to identify individuals and confirm their survival and breeding location without the need to recapture them. Because we marked adult and juvenile sparrows with color bands since 1998, we can document which individuals survived the fire and the origin of individuals that recolonized the burned area. We began looking for banded individuals 1-month post-fire and have since surveyed the burned plot annually to see if individuals from the control plot recruit to this site. Because we systematically search outside of our study plot for banded birds, all unmarked individuals that recruit to the plot are assumed to have dispersed from locations further than 200 m. Based on daily point count, nest surveys and territory mapping, we estimate we annually color banded 95% of the adult male sparrows, 55% of adult female sparrows, and 62% of nestling sparrows residing on our study.

2.3. *Daily probability of nest survival*

A key demographic parameter that indicates the likelihood of Cape Sable seaside sparrow population persistence is nesting success (Lockwood et al., 2001). Thus, we estimated daily probability of nest survival and how this probability was affected by fire. Nests were located by observing parental behavior, and were marked and monitored until fledging or failure. If nests were found empty, the area was observed for signs of fledged young, including parental activity away from the nest and the sound of fledgling–parent communication. We used the Logistic Mayfield method for calculating daily probability of nest survival with 95% confidence limits (Aebischer, 1999; Hazler, 2004). Logistic Mayfield is an extension of the traditional Mayfield method (Mayfield, 1975) which treats each day of nest observation (exposure day) as a binomial trial. The daily probability of survival can be raised to a power equal to the number of days in the nesting cycle (in our case that number is 25; Lockwood et al., 1997) to generate the total probability of a nest surviving the nest cycle. Because we have data on 21 nests prior to the Lopez fire ($n = 7$ in the burned plot, $n = 14$ in the control) we first calculated the daily probability of nest survival for these two groups to test for site-specific differences prior to the fire, as well as to provide a baseline with which to compare the post-fire data. We then calculated the daily probability of nest survival for the control and burned plot from 2002 to 2005 inclusive.

2.4. *Vegetation composition and structure*

If fire has a positive effect on sparrow density and nesting success, the mechanism likely lies within the vegetation dynamics initiated by the physical removal of vegetation and deposition of minerals post-fire. From previous work we know that vegetation structure plays a large role in determining where Cape Sable seaside sparrows place their nests and how successful these nests are (Pimm et al., 2002). Thus, in June 2001 (i.e. 1-month post-fire) we established one vegetation transect per treatment (control, burned) across our study plot. Each transect ran the length (east–west) of the plot. We systematically placed two 1 m^2 quadrats every 200 m along these lines and thus collected 22 vegetation samples along each east–west transect. The transects were sampled annually in June beginning in 2001 (1-month post-fire) and continuing to 2004. The variables measured included percentage cover of each live plant species, as well as the percentage cover of all dead vegetation (not separated by species) and bare ground. Structural variables included the height of the tallest grass, the height and number of sawgrass (*Cladium jamaicensis*) seedheads, and the effective height of ground cover. All vegetation variables have been collected and analyzed prior to this study and found to be important elements of sparrow habitat (Pimm et al., 2002).

For analysis of compositional data we used the multivariate software Primer-E®, and initially calculated the full Bray-Curtis species similarity matrix for all samples as compared to all others regardless of time since fire. We then used this matrix as the basis for constructing a compositional similarity graph using non-metric multidimensional scaling (NMDS) (Clarke and Warwick, 1994). The sample sites are the species compositions of each transect (burned or control) divided into four 'time since fire' categories; 1-month post-fire, 1-year post-fire, 2-years post-fire, and 3-years post-fire. Thus, in producing an NMDS plot, we are evaluating how the composition of the burned and control transects have changed since the time of the fire. The 22 positions of the points in the NMDS space can illustrate the extent to which the vegetation composition of the burned transect has recovered as measured by its similarity to the control transect. In addition, because the control transect has been measured across four successive years, we gain an understanding of the degree to which vegetation composition naturally varies from year to year within sparrow habitat.

Clarke and Warwick (1994) present a Monte Carlo procedure for evaluating whether or not groups of samples are statistically different in respect to their relative similarities. This test, called analysis of similarity (ANOSIM), mimics the procedures for a standard univariate ANOVA. In the context of this paper, ANOSIM calculates the average of all rank similarities among samples within one time transect (r_w), and the average of rank similarities arising from all sample comparisons made between transects (r_b). A test statistic, R, is then calculated as, $R = \frac{r_b - r_w}{1/2M}$, where $M = \frac{n(n-1)}{2}$ and n is the total number of samples (Clarke and Warwick, 1994). The test statistic R will thus vary between +1 and -1, and will take the value of +1 when all the samples on one transect at one a time period are more similar to each other than any of the samples from different time periods and burn histories, with the reverse being true if R equals -1. We conducted 10,000 random permutations to produce a distribution of R-values for comparison to the overall, or global, observed R-value.

For analysis of structural variables we used principal components analysis (PCA) (Reyment et al., 1984). Sample quadrats were again grouped by transect (burned, control) and further divided by time since fire (1-month, 1-year, 2-years, 3-years). The first two principal components were retained as they accounted for the majority of the observed variance between sample quadrats (66%). We used repeated measures MANOVA (SAS for Windows v.9) for each principal component score (PC1 and PC2) associated with the 22 samples, and a comparison of least square means to determine at what point the difference between the control and impact transects became non-significant.

3. Results

3.1. *Sparrow density*

After the Lopez fire, Cape Sable seaside sparrows were absent from the burned plot for the remainder of 2001, as well as for the 2002 and 2003 breeding seasons. Sparrows did, however, establish territories up to the edge of the burn and they occasionally ventured into the burned areas for unknown reasons (Table 1). The results of our MANOVA on sparrow counts indicate no significant effect of year alone, but a significant effect of the interaction between year and fire (Wilk's $\lambda = 0.1638$, $F = 4.90$, df = 6, 20, $P = 0.0031$). The comparison of least squares indicates that in 2002 the burned and control plots were significantly different ($P = 0.0029$), as would be expected given the virtual exclusion of sparrows from the burned plot in the first year post-fire. A similar pattern was evident in 2003 ($P = 0.0191$), with an additional difference between the points located entirely in the burned plot and those classified as edge ($P = 0.05$). Again, sparrows still did not establish territories within the burned habitat, which explains the observed differences in count numbers between the burned and unburned plots. In 2004 and 2005 however, we saw no statistically significant differences between burned and unburned plots in count numbers. Thus, by 2004 the burned plot had reached a density indistinguishable from the control.

3.2. *Dispersal*

Based on the results of Lockwood et al. (2001), Cape Sable seaside sparrows have nearly a 70% probability of surviving from 1 year to the next and an 85% probability of being recaptured or resighted assuming they did survive. Thus it is notable that none of the 32 individuals caught and color banded in the burned plot prior to the fire has been seen or caught again since the fire. The fate of these individuals is unknown, although, we do know they did not move to nearby adjacent unburned habitat as we did not find them in our control plot. The birds we have documented colonizing the burned plot colonized from within the unburned control plot, and from

Table 1 – Mean values (±SD) of the total number Cape Sable seaside sparrows detected at point count locations, Everglades National Park, 2002–2005

Treatment	*n*	2002 Average	2003 Average	2004 Average	2005 Average
Burned	4	0.72(0.40)	0.65(0.47)	1.44(0.77)	2.06(1.41)
Edge	3	1.79(1.01)	2.17(0.88)	1.29(0.52)	2.13(0.38)
Unburned	8	3.03(0.97)	2.09(0.74)	1.63(0.80)	2.38(0.98)

Sparrow density was lower for 2 years following fire in the burned area, returning by 2004 to a level consistent with the unburned area.

Table 2 – Overall nest survival probabilities for Cape Sable seaside sparrows based on daily survival estimates and calculated using the Logistic Mayfield Method (Hazler, 2004)

Treatment	Pre-fire	2002	2003	2004	2005
Nest survival probability for CSSS					
Burned	0.414 (*n* = 7)	No nests (0)	No nests (0)	0.407 (*n* = 14)	0.265 (*n* = 25)
Unburned	0.364 (*n* = 14)	0.137 (*n* = 25)	0.325 (*n* = 29)	0.313 (*n* = 26)	0.461 (*n* = 41)

The overall nest survival probability represents the probability that a single nest will survive from the beginning of egg-laying until the fledging of the last nestling. The value is derived by raising the daily nest survival probability to the average number of days in the nesting cycle (25). After two seasons of exclusion from the burned plot, the 2004 and 2005 survival probabilities for those birds that recolonized the area was indistinguishable from pre-fire levels.

unburned areas outside our plot boundaries. In 2004, five adults (four males and one female) that previously occupied the unburned plot in 2003 established territories in the burned plot, representing 26% of the total 2004 breeding population in the burned plot. Also, three birds banded as nestlings in the unburned plot during the 2003 season established territories in the burned plot in 2004. In 2005, three adults (two males and one female) that previously occupied the unburned plot in 2004 established territories in the burned plot, representing 18% of the total 2005 breeding population in the burned plot. Of the 43 birds banded as nestlings in 2004 across all areas (burned and unburned), three returned to their respective plots, and one that had been banded in the unburned plot established its territory within the burned plot. Also in 2005, three pairs of sparrows alternated nesting sites between the burned and unburned plots throughout the breeding season.

3.3. *Nesting success*

Between 2002 and 2005, we found and monitored 160 nests, 113 in the unburned plot and 47 in the burned plot. Our analysis of those nests monitored before the fire, in both the unburned and burned plot, indicate that the locations were statistically indistinguishable (Fig. 3). The overall daily nest survival probabilities within the control plot remained relatively constant over the 3 years post-fire; the exception being a drop from 36% prior to the fire, to 14% in 2002 (Table 2). The 2002 breeding season was a high water year and we know that peaks in water flows led to sharp drops in nest success (Pimm et al., 2002). Sparrows began breeding in the burned plot in 2004. The 2004 and 2005 daily probabilities of nest survival for nests placed in burned habitat are indistinguishable from those placed in unburned habitat (Fig. 3).

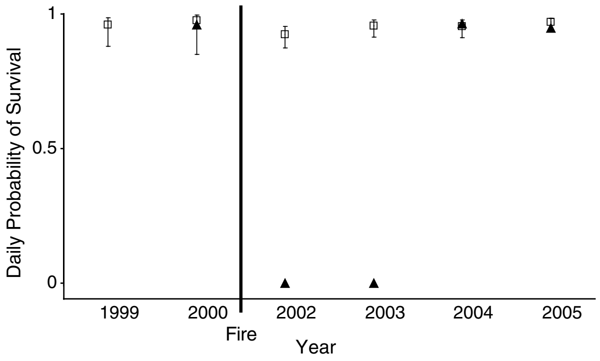

Fig. 3 – The daily probability of survival for nests of *Ammodramus maritimus mirabilis* calculated for each year in both the unburned area (solid line with open squares) and burned plot (dashed line with solid triangles) (μ ± 95% CI).

3.4. *Vegetation composition and structure*

Vegetation composition is clearly influenced by fire, but shows signs of significant recovery 2 years after the fire (Fig. 4). The global *R*-value for the ANOSIM was 0.142, which indicates that there is some degree of separation between years or treatment. Accordingly, none of the random permutations of the data yielded a global *R*-value larger than the observed, thus indicating that the transects show statistically different compositions through time or across space, or both ($P = 0.001$). Pairwise comparisons between transects at each time interval since the fire illustrate where this difference arises (Table 3). Sample quadrats within the burn transect show a difference in composition between the year of the fire (B0) and the first and 3-year post-fire (B1 and B3). This indicates that the fire substantially altered species composition immediately post-burn. However, since the first year after the fire, composition has not changed. The lowest recorded *R*-value for comparisons between the burned and control transects occurs when the samples are compared 2-years post-burn ($R = 0.083$). This *R*-value falls within the range of those obtained for comparisons across years but within the control transect.

According to the resulting eigenvalue loadings, the first Principal Component (PC1) represents a measure of vegetation height, specifically that of sawgrass (*Cladium jamaicense*), and the second Principal Component (PC2) represents a measure of overall vegetation cover and the amount of exposed bare ground (Table 4). Fig. 5 illustrates that the fire substantially decreased overall vegetation height, removed sawgrass seedheads, and exposed more bare ground. The MANOVA results for PC1 indicated a significant effect of year since burn (Wilk's $\lambda = 0.274$, $F = 15.9$, df = 3.18, $P = <0.0001$), and the interaction between year and treatment (Wilk's $\lambda = 0.392$, $F = 9.32$, df = 3.18, $P = 0.0006$). The comparison of least square means indicated a significant difference the first month after fire ($P = <0.0001$) as well as the first year after fire ($P = 0.023$) but no difference in subsequent years. Thus we see evidence of vegetation recovery in each successive year; however not

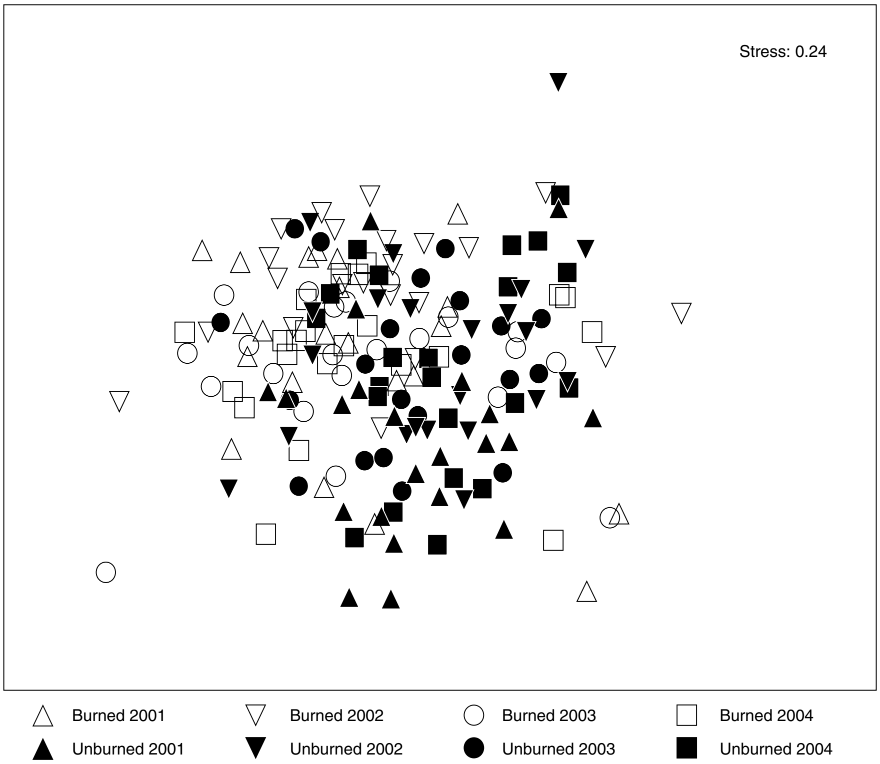

Fig. 4 – Non-metric multi dimensional scaling (NMDS) ordination for *Ammodramus maritimus mirabilis* habitat composition. Each symbol represents a single plot. Data are divided by treatment and time since fire; 1 month (triangles), 1 year (inverted triangles), 2 years (circles) and 3 years (squares). Open symbols represent vegetation plots in the burned treatment (*n* = 22) and solid symbols represent those in the control (*n* = 22). This ordination indicates very little compositional different between treatments and time-since fire, supporting the idea that composition recovers quickly following fire.

until the third year do we see recovery to the extent that the number and height of sawgrass seadheads becomes indistinguishable between the burned and control plots. The results for PC2 similarly indicated a significant effect of year since burn (Wilk's $\lambda = 0.383$, $F = 9.68$, df = 3.18, $P = 0.0005$), and the interaction between year and treatment (Wilk's $\lambda = 0.532$, $F = 5.28$, df = 3.18, $P = 0.0087$). The comparison of least square means for PC2 indicated a significant difference only in the first month after fire ($P = <0.0001$) but not afterward. Over the succeeding 2 years post-fire, the increased accumulation of both live and dead biomass shifted toward values typical for the control transect, regardless of year measured.

4. Discussion

Our study is unique in that the Cape Sable seaside sparrow is dependent on sub-tropical wet grasslands that are typical of the Everglades ecosystem but are rare worldwide. It has often been assumed that these wet grasslands behave as do temperate and Mediterranean grasslands in that they will suffer woody plant encroachment in the absence of fire (Beckage et al., 2003; Egler, 1952). Based on this idea, it has been postulated that the Cape Sable seaside sparrow requires fire to persist in this landscape as its habitat will quickly succeed into an unsuitable state without fire (Taylor, 1983; Werner, 1975). We directly tested the latter assumption, and in the process we shed new light on the applicability of grassland management paradigms to the marl prairies of the Florida Everglades and similar wet grasslands (e.g., Pantanal).

Individual sparrows are apparently driven far from burned habitat, or perish due to the fire. Certainly any nests that are active at the time of a fire are lost, as are most recent fledglings, given that they are relatively weak flyers (Werner, 1975). Sparrow habitat that has burned will remain unsuitable for sparrow breeding for at least 2 years after the fire largely because the vegetation structure necessary for sparrow breeding does not recover for 2 years. However, unburned habitat, even if it directly abuts burned spaces, will support sparrow densities and nesting success indicative of unburned habitat. When the burned habitat does recover it is very similar in species composition and vegetation structure to unburned places and the habitat shows no signs of being 'enhanced' based on our observation that sparrows re-occupy burned areas at densities indistinguishable from unburned areas. Recolonizing individuals will experience nest success probabilities that are indistinguishable from unburned habitat and equivalent to pre-fire habitat. The individuals that recolonize the burned site likely come from nearby unburned habitat, and these individuals may be relocating breeding adults or first-year breeders. There is no evidence from this study that dispersal distances are so limited that a spatial pattern of time to recovery is apparent. However, this result may be restricted to fires that burn relatively small areas of sparrow habitat or to situations where a source population

Table 3 – Pairwise analysis of similarity (ANOSIM) results for vegetation species composition (live only) between burned (B) and unburned (U) transects, 1-month (0), 1-year (1), 2-years (2), and 3-years (3) post-fire

	Comparison	Observed R-value
Control plots through years		
	U0,U1	0.103
	U0,U2	0.179
	U0,U3	0.154
	U1,U2	0
	U1,U3	0.038
	U2,U3	0.002
Burned plots through years		
	B0,B1	**0.17**
	B0,B2	0.092
	B0,B3	**0.217**
	B0,B2	0.058
	B1,B3	0.064
	B2,B3	0.044
Burned to unburned through years		
B0	B0,U0	**0.311**
	B0,U1	**0.273**
	B0,U2	**0.188**
	B0,U3	**0.305**
B1	B1,U0	**0.314**
	B1,U1	**0.182**
	B1,U2	**0.206**
	B1,U3	**0.156**
B2	B2,U0	**0.138**
	B2,U1	**0.117**
	B2,U2	0.083
	B2,U3	**0.13**
B3	B3,U0	0.154
	B3,U1	0.229
	B3,U2	0.169
	B3,U3	0.102

Results are from Monte Carlo simulation of 10,000 permutations. Bold numbers indicate significant differences.

Table 4 – Eigenvector loadings for principal component analysis

Variable	PC 1	PC 2
Max height of *Cladium jamaicense* Seedheads	**−0.429**	**−0.33**
Max height of vegetation	**−0.393**	0.061
Is max height *C. jamaicense* seedhead? N = 0, Y = 1	**−0.384**	**−0.378**
Density of seedheads/plot	**−0.381**	**−0.362**
Dead cover	−0.311	**0.353**
Effective height (cm)	−0.306	0.217
Soil depth (max)	−0.055	0.273
Soil depth (min)	0.022	0.307
Live:dead biomass	0.289	−0.313
Bare ground	0.302	**−0.418**

Values above 0.35 were deemed important and used in describing each Principal Component axes. Principal Component 1 (PC1) represents a measure of *Cladium jamaicense* seedhead height and seedhead density. Principal Component 2 (PC2) represents the amount of exposed bare ground, and amount of standing dead cover.

is within a few kilometers of the fire-affected places (we further consider these spatial effects below).

These results strongly support our scenario B, in which sparrow demography is immediately reduced after the fire, remains low for only a few breeding seasons following the fire, and returns to a level indistinguishable from unburned areas relatively quickly. This conclusion contradicts past studies and the prevailing wisdom that suggested Scenario A as the guiding model of Everglades marl prairie management for Cape Sable seaside sparrow recovery (Taylor, 1983; Werner, 1975). The notion that Cape Sable seaside sparrows do not require fire for their long-term persistence and that marl prairie grasslands do not readily succeed to an unsuitable state for sparrows, or are not 'enhanced' by fire, is supported by noting that sparrow density in our unburned control plot remained relatively stable over the course of this study. The control plot has not been burned since 1994, which is over 11 years of fire-free time.

These findings have several implications concerning the role of fire in Cape Sable seaside sparrow recovery efforts. Over the past 25 years the Cape Sable seaside sparrow has been reduced from 6600 individuals (1981) to fewer than 2500 individuals (2002) (Pimm et al., 2002). One of the sparrow subpopulations is feared to be extirpated, and two others are at such low densities that they are considered near extirpation (Pimm et al., 2002). In our study, which takes place in the center of one of the densest subpopulations, fire has removed sparrows from the burned area for 2 years. It is not clear how such an impact affects longer-term persistence of the subspecies. However, it clearly cannot help. The degree of harm caused by the Lopez fire was likely limited by the fire's relatively small spatial extent, and by the fact that there was occupied sparrow habitat surrounding the fire scar. In cases where the fire is large, or it occurs within a subpopulation that is near extirpation, greater harm will occur because it is more likely to precipitate the loss of a spatially distinct subpopulation. Furthermore, the Lopez fire was a typical early wet season fire in the sense that plant mortality was restricted to primarily above-ground components of the vegetation. The intensity and seasonality of fire will have a profound effect on the regeneration of suitable sparrow habitat. For example, a hot, dry fire which consumes all above-ground and below-ground vegetation may result in a longer return interval with unpredictable species composition. This same scenario followed by a high-water period has resulted in the conversion of marl prairie to marsh vegetation which may or may not revert to marl prairie depending on site hydrology (Pimm et al., 2002).

Our results argue for careful consideration of how fire extent and frequency are managed when fires occur, or are set, within occupied sparrow habitat. In cases where fuel reduction is necessary for reasons other than the protection of the sparrow, a fire management plan which allows frequent, large fires to burn sparrow habitat will undoubtedly have a negative impact on the species. Instead, a plan which maximizes the time between large fires to at least 10 years and then restricts all fires from burning within very small subpopulations will have the best chance of providing refuge to displaced sparrows, as well as reduce the risk of a single fire event driving a subpopulation to extirpation. This recommendation is a conservative approach that allows for small sparrow subpopula-

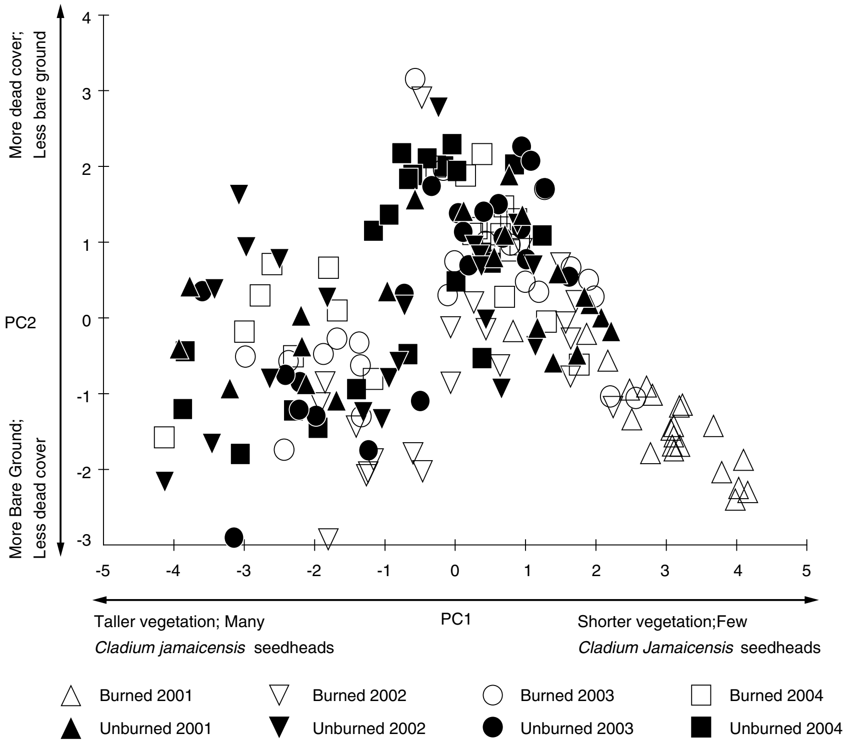

Fig. 5 – Principal component analysis (PCA) for *Ammodramus maritimus mirabilis* habitat structure. As above, each symbol represents a single plot. Data are divided by treatment and time since fire; 1 month (triangles), 1 year (inverted triangles), 2 years (circles) and 3 years (squares). Open symbols represent vegetation plots in the burned treatment (*n* = 22) and solid symbols represent those in the control (*n* = 22). Segregation is evident after the first month post-fire, characterized by shorter vegetation, fewer *Cladium jamaicense* seedheads, more bare ground, and less dead cover. In each successive time period, the burned plots increase convergence toward the control, but are noticeably slower on the PC1 axis than on the PC2, as bare ground is recovered sooner that vegetation height.

tions to recover in the absence of fire. What is now needed is a landscape-level understanding of how fire, and the interplay between hydrology and fire, affects sparrow meta-population persistence. If a landscape-level occupancy analysis supports our results on the plot-level scale, we will feel much more confident in setting a more precise and less conservative fire frequency to best manage the sparrow while still meeting the needs of the greater Everglades ecosystem.

Our findings lend considerable credence to the idea that more empirical studies must be completed to elucidate the effect of disturbance on the demography of endangered species. To assume that because an organism resides in a disturbance-prone ecosystem it therefore must benefit from such events, is to oversimplify the relationship and could very well lead to mismanagement. Instead, by understanding the impact that disturbance has on species of particular concern, we can better decide when and where to allow disturbances to occur in order to maximize benefits to all members of the ecosystem. We do not see the management for the sparrow as conflicting with the management of other species of concern or the Everglades ecosystem as a whole. In fact, the sensitivity of the species to both hydrological patterns (Curnutt et al., 2000; Curnutt et al., 1998; Lockwood et al., 1997) and fire suggests to us that the species may be acting as a ‘canary in the coalmine’ for the multi-billion dollar restoration plan currently in progress.

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