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Modifications of local and regional bird diversity after a fire in the Monte Desert, Argentina

Modificaciones de la diversidad local y regional de aves después de un incendio en el desierto del Monte, Argentina

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ABSTRACT

A fire in the Monte Desert brought about an abrupt decrease in grass cover and the subsequent invasion by forbs. This led bird species that fed on seeds and buds on the ground to segregate spatially between burned and unburned sites (while there was food in the burned habitat). Owing to the disappearance of food resources from the burned sites, four bird guilds withdrew from those sites, while the generation of new resources led to the selection of the burned habitat by two guilds scarcely represented in the unburned area. These modifications in habitat use brought about a decrease in local bird diversity and an increase in regional bird diversity. The structural simplification of the habitat in burned sites may account for the decrease in local diversity, according to the theory of habitat selection. The increase in regional diversity may be a consequence of the complementary spatial distributions betwen burned and unburned areas of species belonging to different guilds (either stressed or favored by the disturbance). The intermediate disturbance hypothesis explains satisfactorily the increase in regional bird diversity after the fire.

Key words: Trophic guilds, stress tolerance, habitat preference, intermediate disturbance.

RESUMEN

Un incendio en el desierto del Monte provocó la brusca disminución de la cobertura de gramíneas y la invasión de hierbas anuales. Esto condujo a las especies de aves que comen semillas y brotes sobre el suelo a segregarse espacialmente entre sitios quemados y no quemados (mientras hubo alimentos en el hábitat quemado). La desaparición de recursos alimentarios provocó el abandono del hábitat quemado por parte de cuatro gremios de aves, mientras que la generación de nuevos recursos desembocó en la selección del hábitat quemado por dos gremios ausentes o muy escasos en el área no quemada. Estas modificaciones en el uso del hábitat provocaron una disminución de la diversidad local y un aumento de la diversidad regional de aves. La simplificación estructural del hábitat puede explicar la disminución de la diversidad local, de acuerdo a la teoría de selección del hábitat. El aumento de la diversidad regional pude ser una consecuencia de las distribuciones espaciales complementarias entre áreas quemadas y no quemadas de especies pertenecientes a gremios diferentes (estresados o beneficiados por la perturbación). La hipótesis de la perturbación intermedia explica satisfactoriamente el aumento de la diversidad regional de aves después del incendio.

Palabras claves: Gremios tróficos, tolerancia al estrés, preferencia de hábitat, perturbación intermedia.

INTRODUCTION

Disturbances such as fires, hurricanes, floods and vulcanism play a remarkable role in the organization of natural communities (Sousa 1984, Pickett & White 1985). Theoretical and empirical evidence indicates that some natural communities reach maximum local diversity (Connell 1975, 1978, Lubchenco 1978, Fox 1979, Huston 1979) and maximum regional diversity (Pickett 1976, Abugov 1982, Miller 1982) when subjected to disturbances of intermediate intensity or frequency. However, the hump-backed response of local diversity to natural disturbances is not a common phenomenon among terrestrial vertebrates (Fuentes & Jaksić 1988), and has not been observed in fires affecting bird and mammal assemblages in the chaparral of southern California (Wirtz 1984). However, an increase in regional bird diversity after moderately extensive fires has been reported by Walter (1988) in Mediterranean islands.

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Bird diversity is positively correlated with habitat structural complexity (MacArthur & MacArthur 1961, MacArthur *et al.* 1962, Recher 1969, MacArthur 1972, Wiens 1973, Tomoff 1974, Roth 1976). Explanations for this relationship emphasize the role of habitat complexity in promoting niche diversification, and thus diversity (Willson 1974, Roth 1976). A direct consequence of fires is the physiognomic and structural simplification of the habitat affected, which could bring about a decrease in the number of bird species able to exploit it, as well as an increase in the numerical dominance of those species favored by the opening of the habitat.

Both phenomena may cause a decrease in local bird diversity (within the burned habitat). On the other hand, if disturbances have taken part in the evolutionary history of communities, an increase in regional bird diversity (measured over burned and unburned habitats) is to be expected as a consequence of the enhanced complexity of the environmental mosaic caused by fire. The size of the patches generated by the disturbance and the synchronicity with which they occur (i.e., phases) could affect the regional diversity patterns (Sousa 1984).

Fires also modify food resource levels. Consequently, a similar response to fire is expected from those species within every trophic guild. Bird guilds should either avoid or prefer the burned patches, depending on whether their food resources decrease or increase. On the other hand, those species using resources not affected by fire should remain in the habitat, and their abundance should depend on their specific aptitudes for dealing with such resources in burned areas.

In this paper, changes in composition and abundance of bird species as a consequence of a fire are assessed. The influence of those modifications on local and regional bird diversity is studied as well.

MATERIAL AND METHODS

This study was carried out in the Man and the Biosphere Reserve of Ñacuñán (34°02'S, 67°58'W) in the Monte Desert, Mendoza Province, Argentina (Morello 1958). In January 1986 a fire, probably of natural origin, affected approximately 45 ha of the reserve. Inside this burned area, two 4-ha sites were established, where bird counts were carried out starting in October 1986 (burned sites A and B). Other four 4-ha sites, two of which were located approximately 1 km away from the burned area (unburned sites C and D), and two about 6 km away (unburned sites E and F), were used as controls.

Plant cover in these sites was estimated with the "point quadrat" method (Daget & Poissonet 1969). Foliage height diversity was estimated by counting the number of contacts with vegetation on a "point quadrat" stick, at 25 cm intervals. Foliage proportions recorded in each interval were the p_is in Shannon's formula (MacArthur & MacArthur 1961) (Table 1).

Bird censuses were carried out using strip transects (Burnham *et al.* 1980, Conner & Dickson 1980) in October and December of 1986, 1987, and of 1988. The transects, located in all six sites, were monitored several times during every sampling occasion (average = 8 times), after sunrise for no more than 4 h, and during the last 3 h of daylight.

Birds species were assigned to six trophic guilds (Capurro & Bucher 1982, 1986, Marone 1990): (1) Terrestrial-granivores: birds that feed on seeds and tender buds on the ground; (2) Tree-herbivores: they feed on leaves, buds or fruits mainly among the foliage; (3) Terrestrial-insectivores: they feed on arthropods mainly on the ground; (4) Tree-insectivores: they feed on arthropods from the bark or leaves, or from the foliage using short flights; (5) Aerial-insectivores: they chase insects using long flights, their prey being caught in the air or on the ground; (6) Birds of prey: they hunt for large prey or eat carrion.

Descriptive statistics for bird assemblages were calculated after Hill (1973) (also see Rotenberry 1978, Rotenberry & Wiens 1980). Bird diversity was measured according to $N2 = (\Sigma p_i^2)^{-1}$ where p_i is the proportion of the ith species in the sample.

TABLE 1

Characteristics of vegetation in burned and unburned sites. Cover of species or group of species is expressed as average percentage, calculated for 4 unburned and 2 burned sites.

Características de la vegetación en los sitios quemados y no quemados. La cobertura de las especies o grupos de especies está expresada como porcentaje promedio, calculado para 4 sitios no quemados y 2 sitios quemados.

Species or group of species	Unburned area		Burned area	
	% cover	± SD	% cover	± SD
Thorny tall shrubs and trees	11.40	7.90	0.40	0.07
Prosopis flexuosa	5.70	4.70	0.20	0.03
Geoffroea decorticans	4.00	3.20	0.10	0.03
Atamisquea emarginata	1.70	1.30	0.10	0.07
Condalia microphylla	1.20	0.50	0.00	0.00
Nonthorny tall shrubs	34.60	8.70	9.90	0.30
Larrea divaricata	12.70	9.20	3.50	0.80
Larrea cuneifolia	21.40	16.80	6.20	1.20
Atriplex lampa	1.00	0.50	0.20	0.07
Low shrubs (< 0.75 m tall)	15.30	8.60	1.40	0.70
Grasses	56.40	3.70	4.20	1.10
Forbs				
October 1986	3.20	1.60	33.00	3.10
December 1986	2.50	0.90	40.70	6.90
October 1987	2.80	0.50	24.40	3.50
December 1988	1.90	0.30	8.80	3.20
Foliage height diversity	2.17	0.15	1.04	0.12

Richness is expressed as the number of species present in the sample, and evenness was estimated through the ratio proposed by Hill (1973): $E = N2/N1$, where $Ni = \exp(-\Sigma\, pi \ln pi)$.

Local bird diversity was calculated in the burned area (burned sites A + B), in control I (unburned sites C + D), and in control II (unburned sites E + F). Regional bird diversity was calculated for unburned sites (C + D + E + F), and for combinations of burned and unburned sites in equal proportion (partially burned area I = burned A + B + unburned C + D; and partially burned area II = burned A + B + unburned E + F).

Determination of the statistical significance of the difference in guilds or species mean densities was carried out by using the non-parametric Kruskal-Wallis test (Sokal & Rohlf 1981).

RESULTS

Analysis of habitat preferences of trophic guilds

Terrestrial-insectivores were significantly more abundant in unburned sites on five of the six sampling occasions. So were tree-herbivores and tree-insectivores during all six sampling occasions. Terrestrial-granivores were significantly more abundant in unburned sites in two opportunities (December 1987 and October 1988), and showed no preference for burned or unburned sites during the remaining sampling occasions. Aerial-insectivores, instead, were significantly more abundant in burned sites on five of the six sampling occasions, and birds of prey showed higher densities in burned sites during all six opportunities (Table 2).

TABLE 2

Mean abundance of bird guilds (individuals per hectare) in 2 burned and 4 unburned sites, during six sampling occasions. The number of species of each guild observed in every sample is indicated in parentheses. Those densities which differ significantly betwen burned and unburned sites are indicated with asterisks.

Abundancia promedio de gremios de aves (individuos por hectárea) en 2 sitios quemados y 4 no quemados durante seis ocasiones de muestreo. Entre paréntesis se indica el número de especies de cada gremio observado en cada muestra. Con asteriscos se denotan aquellas densidades que difieren significativamente entre hábitats quemados y no quemados.

Trophic guilds	Oct. 86	Dec. 86	Oct. 87	Dec. 87	Oct. 88	Dec. 88
Terrestrial-granivores						
unburned	1.64 (6)	2.12 (6)	1.01 (6)	2.55 (6)	0.82 (6)	0.48 (4)
				***	*	
burned	1.97 (7)	3.25 (7)	1.81 (5)	0.50 (6)	0.31 (2)	0.50 (5)
Terrestrial-insectivores						
unburned	0.65 (2)	0.83 (2)	0.50 (2)	1.06 (2)	0.53 (2)	0.89 (3)
	*	*	***	***		***
burned	0.20 (1)	0.46 (2)	0.05 (1)	0.17 (3)	0.59 (2)	0.06 (1)
Tree-herbivores						
unburned	0.84 (5)	1.18 (5)	1.45 (3)	1.46 (4)	1.64 (4)	1.00 (5)
	***	***	***	***	***	***
burned	0.07 (1)	0.02 (1)	0.09 (1)	0.00	0.00	0.00
Tree-insectivores						
unburned	1.00 (10)	1.14 (10)	1.26 (9)	1.12 (9)	1.28 (8)	1.20 (8)
	***	***	***	***	***	***
burned	0.04 (2)	0.02 (1)	0.12 (2)	0.08 (3)	0.03 (3)	0.00
Aerial-insectivores						
unburned	0.05 (2)	0.13 (2)	0.05 (2)	0.07 (2)	0.09 (2)	0.39 (3)
	*	***		***	***	*
burned	0.11 (2)	0.67 (3)	0.05 (3)	0.94 (3)	0.72 (3)	0.94 (3)
Birds of prey						
unburned	0.00	0.00	0.00	0.00	0.00	0.00
	***	***	***	***	***	***
burned	0.19 (3)	0.25 (2)	0.51 (1)	0.75 (1)	0.59 (1)	0.53 (1)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Analysis of habitat preferences of terrestrial granivorous species

Out of the seven more abundant species, only two showed clear habitat preferences throughout the study: *Poospiza ornata* was always more abundant in unburned sites, and *Zenaida auriculata* showed significant preference for burned sites (Table 3). On the other hand, species of this guild appeared to be selective in habitat occupation at the beginning of the study, but this trend was reversed as time went by (Table 3).

Analysis of local bird species diversity

Mean diversity (N2), richness (S) and evenness (E) (n = 6 sampling occasions in all cases) and standard deviation for each of the three areas analyzed were: 1) Burned area: N2 = 5.12 ± 0.99, S = 13.30 ± 3.20, E = 0.75 ± 0.12; 2) Control I: N2 = 6.35 ± 1.35, S = 17.70 ± 2.70, E = 0.71 ± 0.07; 3) Control II: N2 = 8.65 ± 1.30, S = 21.50 ± 0.80, E = 0.70 ± 0.03. Bird diversity and richness were higher in unburned sites, while evenness was slightly higher in the burned site.

TABLE 3

Mean abundance of bird species (individuals per hectare) that feed on seeds and tender buds on the ground in burned and unburned sites. Significant differences in bird densities between habitats are indicated with asterisks.

Abundancia promedio de especies de aves (individuos por hectárea) que se alimentan de semillas y de brotes tiernos en el suelo, en los sitios quemados y no quemados. Las diferencias significativas en densidad de aves entre hábitats son indicadas mediante asteriscos.

Terrestrial-granivores	Oct. 86	Dec. 86	Oct. 87	Dec. 87	Oct. 88	Dec. 88
Poospiza ornata						
unburned	0.96	1.62	0.42	2.18	0.30	0.00
	***	*	***	***	**	
burned	0.04	0.87	0.03	0.19	0.00	0.00
Phrygilus carbonarius						
unburned	0.49	0.15	0.02	0.00	0.06	0.00
	**					
burned	0.12	0.08	0.00	0.00	0.00	0.06
Junco capensis						
unburned	0.07	0.13	0.19	0.14	0.25	0.31
burned	0.10	0.17	0.39	0.08	0.19	0.16
Zenaida auriculata						
unburned	0.00	0.00	0.00	0.00	0.00	0.00
	***	***	**	**		**
burned	0.64	1.96	0.05	0.08	0.00	0.19
Diuca diuca						
unburned	0.09	0.17	0.17	0.11	0.12	0.12
	***		*			
burned	0.70	0.06	1.19	0.06	0.00	0.03
Eudromia elegans						
unburned	0.03	0.02	0.17	0.04	0.06	0.01
	***	*				
burned	0.16	0.08	0.16	0.04	0.12	0.00
Columba maculosa						
unburned	0.00	0.02	0.04	0.02	0.02	0.03
	***					
burned	0.21	0.02	0.00	0.04	0.00	0.06

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Analysis of regional bird species diversity

Mean diversity (N2), richness (S) and evenness (E) (n = 6 sampling occasions in all cases) and standard deviation for each of the three areas analyzed were: 1) Unburned area: N2 = 7.90 ± 1.49, S = 23.30 ± 1.40, E = 0.68 ± 0.04; 2) Partially burned area I: N2 = 9.01 ± 1.85, S = 22.80 ± 3.80, E = 0.73 ± 0.09; 3) Partially burned area II: N2 = 11.27 ± 1.93, S = 26.20 ± 1.90, E = 0.75 ± 0.04. Bird diversity was higher in partially burned sites because bird assemblages generally showed higher richness and evenness in those sites.

DISCUSSION

Habitat preferences of trophic guilds

Habitat occupation by the six bird trophic guilds showed clear responses to the modification of resource levels brought about by fire.

Tree-herbivores and tree-insectivores abandoned the burned area (Table 2). The mean cover of trees and thorny tall shrubs in burned sites was 0.4%, and in unburned ones 11.4% (Table 1). More than 80% of birds belonging to these two guilds were recorded on those plant species during the breeding season (L. Marone, unpublished data). Selection of undisturbed habitats by these species seems to be the consequence of their intolerance to stress caused by the reduction of the substratum where they look for food.

Population density and number of species of aerial-insectivores increased in the burned sites (Table 2). These birds were favored by habitat opening because of their foraging mode: they use the "skeletons" of burned shrubs as watch-towers for sallying on arthropods in the air or on the gound. Visibility and maneuvering possibilities increased in burned sites for these species.

Birds of prey seemed to prefer burned sites throughout the sampling period (Table 2). Habitat opening may have also favored the hunting mode of these birds. Besides, the most abundant species in this guild was the Burrowing Owl, *Athene cunicularia*, which builds its nest in rodent burrows. After the fire, the area was invaded by the rodent *Lagostomus maximus* (Ojeda 1989), which builds extensive underground galleries. Several owl pairs nested in burrows deserted by these rodents.

Most terrestrial-insectivores seemed to prefer the unburned habitat (Table 2). This guild was formed by four species. One of them, the White-banded Mocking bird, *Mimus triurus*, represented 65% of the guild records. Although this species gets its food mainly on the ground, it defends territories by singing on trees (*Prosopis* sp., *Geoffroea* sp.). The need for perches to defend territories may have negatively affected the presence of this species in burned sites, and –because of their numerical overrepresentation– that of the guild in general.

Terrestrial-granivores did not occupy the environment in a consistent manner. Occupation of the burned area by this guild decreased as sampling progressed (Table 2). In Ñacuñán, this guild feeds mainly on seeds and tender grass buds. Grass cover in unburned sites was over 50%. In burned sites, instead, grass cover was reduced to less than 5% and has not recovered so far (Table 1). After the fire, there was an abrupt increase in forb cover (*Verbena* sp., *Sphaeralcea* sp., *Plantago* sp., *Heliotropium* sp.) due to an increase in water, light and nutrient availability. In December 1986, cover of these species in unburned sites was 2.5% and in burned ones 40.7% (Table 1). In the latter, terrestrial-granivores turned to feeding on the colonizing forbs.

Settlement of these plant species depends on rainfall. In the growing season (September through March) rainfall averages 286.5 mm in Ñacuñán (n = 17 years). During the seasons 1984-85 (392.6 mm), 1985-86 (328.2 mm), and 1986-87 (323.0 mm) that average was surpassed. On the other hand, the seasons 1987-88 (180.0 mm) and 1988-89 (150.2 mm) were well under the average. Forb cover in burned sites decreased abruptly starting in September 1987 (Table 1). Terrestrial-granivores deserted the burned habitat starting in December 1987 (Table 2). This guild also responded to the stress caused by food reduction by avoiding the burned area.

Habitat preferences of terrestrial-granivorous species

Unlike other trophic guilds, for which the fire immediate consequences were the disappearance of critical resources for birds and their abandonment of the burned area, terrestrial-granivores not only remained in the burned area but also became more abundant in it during 1986 and part of 1987 (Table 2). Total density of this guild during 1986 (adding up October and December samplings) was significantly higher in the burned area ($P < 0.05$).

In October 1986, four species clearly preferred the burned habitat dominated by forbs. Other two species, instead, preferred the unburned habitat, where grasses prevailed. Only one species (*Junco capensis*) showed no habitat preferences (Table 3). Although the habitat segregation pattern of granivores lost consistency with the passing of time, several granivorous species selected the burned habitat while there was food in it, probably due to their greater capability for dealing with the resources set free by the effect of the fire (forbs). When drought provoked forb cover to decrease, only *Zenaida auriculata*, a species traditionally associated with open and disturbed areas, stayed at the burned site. Changes in forb cover could have produced the temporal succession in patch use by granivorous species (Table 3).

Modifications of local and regional bird diversity

Local diversity of bird species decreased as a consequence of the fire. The decrease in number of bird species in the burned area was responsible for this diversity dive, and was a consequence of burned habitats being avoided by those guilds rich in species (e.g., tree-insectivores), and preferred by species-poor guilds (e.g., aerial-insectivores). On the other hand, evenness was higher in the burned area. This indicates that the resources set free by the fire were not monopolized by a few species, but rather exploited in a more equitable way than elsewhere in the reserve.

Species that were abundant in unburned sites (e.g., *Poospiza torquata* among tree-herbivores, *Serpophaga munda* among tree-herbivores, *Mimus triurus* among terrestrial-insectivores) were scarce or even absent in burned sites. In their place, however, no similar species were established, but species belonging to other trophic guilds favored by the fire. In five of the six guilds no compensatory replacements of potential competitors were observed at all.

A direct consequence of this was an increase in bird regional diversity after the fire. Burned and unburned sites combined proved to be more diverse than unburned sites of identical size. When combining unburned sites, only a few species were added (species richness increased slightly) and, as the same dominant species occurred in each site, evenness remained identical or decreased. On the other hand, when burned and unburned sites were combined, several species were added (either entire guilds –Table 2–, or species of the same guild with complementary spatial distributions, as in the case of granivorous species –Table 3–), and a compensatory effect of the abundance of dominant species in burned and unburned sites occurred, which brought about an increase in evenness.

In sum, bird local species diversity did not increase after the disturbance introduced by fire in the study area. This evidence concurs with Wirtz's observations in California (1984), and fits Fuentes & Jaksić's predictions (1988). Bird regional diversity did increase as a consequence of fire either due to the complementary distribution between burned and unburned patches of bird guilds that tracked existing resources in an opportunistic manner, or due to the complementary distributions of birds that shared those resources, but that showed different aptitudes for coping with them in burned and unburned sites. This latter evidence concurs with Connell's hypothesis (1978) that disturbances of intermediate intensity or frequency maintain highest species diversity in natural communities.

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APPENDIX 1

Species composition of each trophic guild. Species listed have been observed at least on one occasion in some of the sampling sites. Scientific names after Olrog (1978).

Composición específica de cada gremio trófico de aves. Las especies citadas han sido observadas por lo menos en una ocasión en alguno de los sitios de muestreo. La nomenclatura científica usada sigue a Olrog (1978).

Bird-guilds	Bird species belonging to each guild
Terrestrial-granivores	*Eudromia elegans* *Columba livia* *Columba maculosa* *Zenaida auriculata* *Sicalis luteola* *Diuca diuca* *Phrygilus carbonarius* *Junco capensis* *Poospiza ornata* *Carduelis magellanica*
Terrestrial-insectivores	*Rhinocrypta lanceolata* *Mimus triurus* *Sturnella superciliaris* *Pseudoseisura lophotes*
Tree-herbivores	*Cyanoliseus patagonus* *Myiopsitta monacha* *Phytotoma rutila* *Saltator aurantiirostris* *Poospiza torquata* *Saltatricula multicolor*
Bird-guilds	Bird species belonging to each guild
Tree-insectivores	*Coccyzus cinereus* *Colaptes melanolaimus* *Drymornis bridgesii* *Lepidocolaptes angustirostris* *Upucerthia certhioides* *Leptasthenura aegithaloides* *Synallaxis albescens* *Certhiaxis pyrrohophia* *Tripophaga* spp. *Troglodytes aedon* *Anairetes flavirostris* *Stigmatura budytoides* *Serpophaga munda* *Elaenia albiceps*
Aerial-insectivores	*Empidonomus aurantiotrocristatus* *Pyrocephalus rubinus* *Myiarchus tyrannulus* *Tyrannus melanocholicus* *Tyrannus savana* *Xolmis coronata*
Birds of prey	*Circus cinereus* *Polyborus chimango* *Spiziapteryx circumcinctus* *Athene cunicularia*