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Avian Community Response to Grazing Intensity on Monoculture and Mixed Florida Pastures

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Abstract

Monoculture and mixed pastures in Florida provide habitat for a variety of resident and migratory bird species. The objectives of this study were to investigate the effects of grazing on vegetation structure and bird species richness and abundance in grazed monoculture and mixed pastures. Study pasture units were subject to four cattle grazing intensities: 0 = nongrazed (control), 15 = low, 20 = medium, or 35 = high animal units (AU) per pasture unit (no cattle, 1.3, 1.0, and 0.6 ha · AU^{-1}, on monoculture pastures and no cattle, 2.1, 1.6, and 0.9 ha · AU^{-1}, on mixed pastures). Monoculture pastures displayed a greater decrease in spatial heterogeneity of the vegetative community in the presence of grazing than mixed pastures. An increase in grazing intensity led to declines in total avian species richness and abundance and species richness within short-distance migrant, neotropical migrant, and permanent resident guilds on monoculture pastures. Declines in total species richness and abundance and neotropical migrant guild species richness and abundance were observed on mixed pastures subject to increasing grazing intensity. However, species richness within short-distance migrant and urban guilds and abundance within the grassland guild increased on this pasture type in the presence of grazing. Loss of spatial heterogeneity typically results in a lack of suitable habitat for birds that occupy the extremes of the vegetation structure gradient. This can lead to a loss of species richness and abundance. For the majority of avian guilds, a low grazing intensity of 1.3 ha · AU^{-1} and 2.1 ha · AU^{-1} on monoculture and mixed pasture, respectively, is recommended to maintain abundance. However, these grazing intensities may result in declines in species richness. Ultimately, if a range of avian species are to be supported on monoculture and mixed pastures, spatial heterogeneity of plant structure and composition must be maintained.

Resumen

Monocultivos y potreros con mezclas de pastos en Florida, Estados Unidos proporcionan hábitat para una gran variedad de especies de aves locales y migratorias. Los objetivos de este estudio fueron el investigar los efectos de pastoreo en la estructura de la vegetación, riqueza y abundancia de las especies de aves en potreros con monocultivos y potreros con pastos mixtos. Los potreros utilizados para este estudio estuvieron sujetos a cuatro niveles de pastoreo: 0 = no pastoreo (control), 15 = bajo, 20 = medio, o 35 = alta, unidades animales (UA) por potrero (sin ganado, 1.3, 1.0 y 0. 6 hectáreas · AU^{-1} en potreros con monocultivos y sin ganado, 2.1, 1.6 y 0.9 hectáreas · AU^{-1} en potreros con pastos mixtos). Los potreros con monocultivos presentaron una mayor disminución en la heterogeneidad espacial de la comunidad vegetativa en la presencia del pastoreo que los potreros con mezclas de pastos. Un aumento en el nivel del pastoreo produjo la disminución en la riqueza y abundancia total de especies de aves y la riqueza de la abundancia de especies migratorias de corta distancia, migrantes neo-tropicales y asociaciones de residentes permanentes en los potreros con monocultivos. Se observaron disminuciones en la riqueza y abundancia total de especies así como la riqueza y la abundancia de las asociaciones de especies de aves migratorias neo-tropicales en potreros mixtos sujetos a un incremento en los niveles de pastoreo. Sin embargo, la riqueza de especies migratorias de corta distancia y asociaciones urbanas y abundancia en las asociaciones de aves del pastizal aumentaron en este tipo de potreros en presencia de pastoreo. La pérdida de la heterogeneidad espacial típicamente resulta en la deficiencia de un hábitat apropiado para aves que ocupan los gradientes extremos en la estructura de la vegetación. Esto puede ocasionar una perdida en la riqueza y abundancia de las especies. Para la mayoría de las asociaciones de aves, un nivel bajo de pastoreo de 1.3 y 2.16 hectáreas · AU^{-1} en monocultivos y potreros con mezcla de pastos respectivamente, se recomienda para mantener la abundancia. Sin embargo, estos niveles de pastoreo pueden provocar una disminución en la riqueza de las especies. Por último, si se quiere apoyar un amplio rango de especies de aves ya sea en monocultivos o con una mezcla de plantas, debe mantenerse tanto la heterogeneidad espacial de la estructura de la planta como su composición.

Key Words: abundance, avian–habitat relationships, biodiversity, guild, heterogeneity, migratory birds, vegetation structure

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INTRODUCTION

There are approximately 1.2 million ha of monoculture and mixed pasture in Florida, 78% of which occurs on private lands and is used primarily for cattle grazing. Monoculture pastures, also known as nonnative or improved pastures, are dominated by nonnative forage species and are usually comprised of former native pastures that have been cleared, tilled, and reseeded with improved forage types so that few native vegetative species remain. Mixed pastures, also known as seminative or semi-improved pastures, are comprised of a mixture of nonnative improved forage species interspersed with substantial quantities of native grasses and forbs. Mixed pasture conversion is less intense than for monoculture pastures, and management inputs (e.g., fertilizer, weed control) are lower (Florida Fish and Wildlife Commission [FWC] 2005).

Monoculture and mixed pastures are not a native part of Florida's landscape but, if grazed appropriately, have the potential to provide significant habitat for and be utilized by a diversity of wildlife species, including resident and migratory birds (Alsop 2002; Engstrom et al. 2005; FWC 2005). Many of these species, some of which are federally and/or state listed as endangered or threatened, have decreasing populations and are of conservation concern (FWC 2005).

Grazing livestock most typically affect avian communities indirectly through changes in vegetation composition, structure, and biomass and can cause decreases in spatial heterogeneity of the vegetative community (Brennan and Kuvlesky 2005; Coppedge et al. 2008; Derner et al. 2009). Reductions in spatial heterogeneity caused by grazing imply the loss of habitat diversity (Adler et al. 2001) and changes in food abundance and foraging conditions and breeding, thermal, and escape cover (Bock and Webb 1984; Vallentine 1990; Milchunas and Lauenroth 1993; Saab et al. 1995). Such changes have the potential to cause declines in avian species richness of grazed pastures, although avian abundance may be little affected, as species adapted to the grazed conditions often become highly abundant (Kantrud and Kologiski 1982). Therefore, avian community structure has the potential to be strongly influenced by the degree of structural heterogeneity in associated plant communities (Wiens 1974), with certain birds being attracted to habitats with specific vegetative attributes (Cody 1985).

The majority of research on the effects of grazing on plant communities and bird abundance and species richness has been conducted in the western United States. However, the transfer of results among environmentally divergent lands should be done cautiously. If management activities of benefit to birds associated with monoculture and mixed pastures are to be promoted in Florida, the impact grazing of these lands has on avian communities needs further investigation. The objectives of this study were 1) to compare avian species richness and abundance on monoculture and mixed pastures subject to four grazing intensities (nongrazed, low, medium, and high) and 2) to explore the role structural habitat attributes play in determining avian species richness and abundance on monoculture and mixed grazed pastures.

METHODS

Research was conducted at the MacArthur Agro-Ecology Research Station (MAERC), a 4 170-ha cattle ranch operated by Archbold Biological Station, located in Highlands County, south Florida (lat 27°09′N, long 81°12′W). One monoculture pasture and one mixed pasture study area were selected at MAERC. During 1996–1998, the 162-ha monoculture pasture study area was subdivided using fences into eight approximately 20-ha experimental pasture units used for summer grazing (May–October). These monoculture pasture units were composed almost entirely of bahiagrass (*Paspalum notatum* Flüggé) but included scattered wetlands, the majority of which were ditched and consisted of grasses, sedges, and miscellaneous wetland species (Werner et al. 1998). Wetland dominants included carpetgrass (*Axonopus furcatus* Flüggé Hitchc.), maidencane (*Panicum hemitomon* Schult.), soft rush (*Juncus effuses* L.), yellow-eyed grass (*Xyris* sp.), pickerelweed (*Pontederia cordata* L.), and sawgrass (*Cladium jamaicense* Crantz). A number of the monoculture pastures also contained small cabbage palm (*Sabal palmetto* [Walt.] Lodd. ex J. A. and J. H. Schultes) hammocks (Werner et al. 1998). During 1996–1998, the 260-ha mixed pasture study area was subdivided using fences into eight approximately 32-ha experimental pasture units used for winter grazing (November–April). These mixed pasture units were comprised of bahiagrass and a variety of native species, such as broomsedge (*Andropogon virginicus* L.) and bushy bluestem (*A. glomeratus* [Walt] B. S. P). The mixed pasture units were interspersed with seasonal wetlands, nearly all within 30 m of existing ditches, and comprised of grasses, sedges, and miscellaneous wetland species. Dominants in these wetlands included carpetgrass, maidencane, red top panicum (*P. rigidulum* Bosc ex Nees), hat pins (*Eriocaulum* sp.), yellow-eyed grass, and some pickerelweed and soft rush. Cabbage palm hammocks occurred in the western third of this mixed pasture unit array. Mixed pastures were not as intensively drained as monoculture pastures and were frequently flooded or saturated during the June–October rainy season (Werner et al. 1998). Swain et al. (2007) provide additional details on pastures. Forage production was higher on summer grazed monoculture pastures than on winter grazed mixed pastures. Therefore, to provide similar amounts of forage in both seasons and accommodate consistent grazing intensities, it was necessary for mixed pasture units to be larger than monoculture pasture units (Capece et al. 2007; McSorley and Tanner 2007).

In 1998, a grazing study was initiated on the monoculture and mixed pasture units. Pasture units were subject to four cattle grazing intensities: 0 = nongrazed (control), 15 = low, 20 = medium, or 35 = high animal units (AU) per pasture unit (no cattle, 1.3, 1.0, and 0.6 $\text{ha} \cdot \text{AU}^{-1}$, on monoculture pastures and no cattle, 2.1, 1.6, and 0.9 $\text{ha} \cdot \text{AU}^{-1}$, on mixed pastures). Stocking densities were selected based on input from the Florida Cattleman's Association and the University of Florida Institute of Food and Agricultural Sciences to reflect typical regional stocking densities, which average 1.42 $\text{ha} \cdot \text{AU}^{-1}$ (Gornak and Zhang 1999). Each grazing intensity was replicated twice for each pasture type and randomly assigned to the pasture units. The monoculture pasture units were summer grazed from May to October, and mixed pasture units were winter grazed from November to April each year. Cattle were introduced and grazing intensities initiated on mixed pasture units in October 1998 and on monoculture pasture units in May 1999. Monoculture pasture units were not grazed from October 1998 through April 1999. Prior to the initiation of study grazing treatments, cattle grazed the two pasture types during these same seasons at an average stocking density of approximately 1 $ha \cdot AU^{-1}$ and 1.6 $ha \cdot AU^{-1}$ on monoculture and mixed pastures, respectively.

Prescribed burning was conducted in all mixed pasture units during November–December 1998 and in all monoculture pastures units during February 1999 with similar affects observed across the study areas. All mixed pasture units were prescribed burned again in February 2002 and monoculture pastures in April 2002. All monoculture pasture units were mowed at a height of 35 cm for general weed control between September and November in 1998, 2000, and 2002. Dog fennel (*Eupatorium capillifolium* Lam.) in the monoculture pasture units was treated with a combination of dimethylamine salts of dicamba and 2,4-D (WEEDMASTER®) at 4.6 $L \cdot ha^{-1}$ plus 7.5 $mL \cdot L^{-1}$ of nonionic surfactant from May to July 2001, 2002, and 2003. More details on pasture management are provided in Swain et al. (2007).

Vegetation Sampling

Vegetation sampling was conducted quarterly during spring (March 15–April 15), summer (June 1–July 1), fall (October 1–November 1), and winter (January 1–February 1) for 4 yr (1999–2003). Vegetation sampling methods were similar to those described by Wiens (1969) and utilized a transect system. One 800-m line transect was established in each pasture and divided into four sampling units of equal length. Within each sampling unit, we randomly located four vegetation sampling subpoints on either side of the transect. Sampling was repeated in each of the transect sampling units for a total of 32 subpoints per transect.

At each subpoint, we visually estimated percent canopy coverage of grasses, forbs, litter, and bare ground to the nearest 5% within a 2.4-m^2 circular plot (Wiens 1969; Higgins et al. 2005). We measured vertical stem density in the center of each plot by recording the number of vegetation contacts with a pole at 10-cm-height intervals (Weins 1969). These data were used to calculate vertical stem density 0–30, 30–60, 60–90, and 90–120 cm aboveground (stems/30 cm). Litter depth to the nearest 10 cm was measured on the same pole.

Bird Surveys

The avian communities within pastures were sampled using strip transect methods. Two parallel, 50×800 m strips were positioned centrally in each of the 16 pasture units by marking the start and end points, as well as each 200-m interval, with 3-m-tall polyvinyl chloride pipe. Strip transects were separated by a 50-m buffer and ≥ 50 m from an adjacent pasture (Eberhardt 1978; Wiens and Rotenberry 1981; Gibbons et al. 1996; Bibby et al. 2000). Vegetation sampling and avian surveys were conducted concurrently. We sampled avian transects quarterly between 1999 and 2003, corresponding to presumed seasonal differences in avian habitat utilization: spring (March 15–April 15) and fall (October 1–November 1) migrations and breeding (June 1–July 1) and wintering (January 1–February 1) seasons. The June 1–July 1 breeding season selected for this study is the same as that used by the North American Breeding Bird Survey (Peterjohn and Sauer 1993). Each transect was sampled twice per season beginning at sunrise and ending no later than 3.5 h after sunrise. Sampling time per transect was 25–30 min. Sampling was not conducted during excessive wind, rain, fog, or periods of other unusual weather conditions (Gibbons et al. 1996; Bibby et al. 2000). Transects within the same pasture unit were not sampled on the same day to reduce the chance of counting the same bird twice (Wiens and Rotenberry 1981). We alternated sampling order each sampling period to reduce bias of counting the same transect at the same time of the morning. Only birds recorded within the 50-m strip boundaries were counted (Bibby et al. 2000). We counted flushed birds at the point they were first observed. We used careful observation, including recording of the location of flushed birds, to reduce the likelihood of double counting (Gregory et al. 2004). Average height of the herbaceous vegetation was approximately 75 cm and 150 cm in the summer and winter pasture arrays, respectively, allowing observers consistent sighting ability within the pasture types.

We divided counts of avian abundance and species richness into guilds prior to analyses. Eight guilds were utilized, each falling into one of two major categories based on breeding habitat or migrant status (Peterjohn and Sauer 1993). Grassland, wetland and open water, successional-scrub, woodland, and urban species guilds made up the breeding habitat category and short-distance migrant, neotropical migrant, and permanent resident species guilds the migrant status category. Not all species fell within a breeding habitat and migrant status guild. Within each category, guilds were independent and did not overlap in species composition (Table 1).

Analyses

We performed repeated-measures analyses using mixed model regressions, with season and time since introduction of grazing as repeated measures, followed by Fisher's protected least significant difference tests, to examine differences in vegetation attributes (mean, variance, and maximum percent coverage of grasses, forbs, bare ground, and litter; litter depth; and vertical stem density), total avian abundance and species richness, and avian abundance and species richness by guild among grazing intensities for monoculture and mixed pastures. We focused on grazing intensity effects rather than repeated-measures effects. Two- and three-way grazing intensity interactions were noted in the results if they occurred. Because three-way interactions are difficult to reliably interpret, they were not discussed further (Zar 1998; SYSTAT 2007).

On both monoculture and mixed pastures, multiple linear regression was used to examine which combination of vegetation attributes best described changes in avian abundance and species richness, both overall and by guild. To reduce multicollinearity problems, all predictor variables involved in pairwise correlations with $r \geq 0.7$ were subjected to a univariate, one-way analysis of variance with each dependent variable. For each pair of highly correlated predictor variables, the variable retained was the one with the greatest F value (Noon 1981; McGarigal et al. 2000). All regression models were fit using a forward stepwise procedure with tolerance = 0.001, F to enter = 0.15, and F to remove = 0.15. These values are considered appropriate for predictor variables that are relatively independent (SYSTAT 2007). Regression models

Table 1. Avian guild composition and seasonal abundance on monoculture and mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003.

			Abundance (no. of individuals)							
			Fall		Winter		Spring		Summer	
Guild[1]	Common name	Scientific name	Mono[2]	Mixed[3]	Mono	Mixed	Mono	Mixed	Mono	Mixed
WT	American bittern	*Botaurus lentiginosus*	6	9	1	1	0	0	0	0
WD, SD	American crow	*Corvus brachyrhynchos*	50	32	63	53	23	32	22	13
SS, SD	American goldfinch	*Carduelis tristis*	0	0	31	15	57	28	0	0
SD	American kestrel	*Falco sparverius*	16	11	14	20	21	12	0	0
UB, SD	American robin	*Turdus migratorius*	0	0	96	122	28	26	0	0
WT	Anhinga	*Anhinga anhinga*	0	1	2	0	0	0	0	0
WT, SD	Bald eagle	*Haliaeetus leucocphalus*	0	0	0	1	0	0	0	0
GR, SD	Barn owl	*Tyto alba*	0	1	0	0	0	0	0	0
NM	Barn swallow	*Hirundo rustica*	83	52	0	0	4	0	0	0
WD, RE	Barred owl	*Strix varia*	0	2	0	2	0	0	0	0
WT	Belted kingfisher	*Ceryle alcyon*	1	0	5	0	0	0	0	0
RE	Black vulture	*Coragyps atratus*	4	7	26	19	8	22	0	0
WT	Black-crowned night-heron	*Nycticorax nycticorax*	5	1	0	0	0	0	0	0
WT	Black-winged teal	*Anas discors*	1	0	0	0	0	0	0	0
UB, SD	Blue jay	*Cyanocitta cristata*	0	3	0	0	0	1	0	0
WD, NM	Blue-gray gnatcatcher	*Polioptila caerulea*	12	20	6	8	0	0	0	0
WT, RE	Boat-tailed grackle	*Quiscalus major*	130	191	28	30	36	12	30	36
GR, NM	Bobolink	*Dolichonyx garrulus*	64	40	0	0	0	0	0	0
SD	Brown-headed cowbird	*Molothrus ater*	0	0	2	0	0	0	0	1
GR, NM	Burrowing owl	*Athene cunicularia*	0	0	0	0	1	0	1	0
SS, RE	Carolina wren	*Thryothorus ludovicianus*	4	3	0	0	3	0	0	0
WT	Cattle egret	*Bubulcus ibis*	1 063	249	23	6	25	3	237	25
UB, SD	Common grackle	*Quiscalus quiscula*	5	287	0	4	14	7	34	19
SS, RE	Common ground dove	*Columbina passerine*	1	2	1	0	0	2	7	11
WT	Common moorhen	*Gallinula chloropus*	0	1	0	0	0	0	1	0
WT	Common snipe	*Gallinago gallinago*	146	27	147	88	26	20	0	26
SS, NM	Common yellowthroat	*Geothlypis trichas*	226	499	46	54	27	71	18	72
RE	Crested caracara	*Caracara cheriway*	7	5	5	5	5	15	1	4
WT	Double-crested cormorant	*Phalacrocorax auritus*	0	1	1	0	2	0	0	2
NM	Eastern kingbird	*Tyrannus tyrannus*	0	0	0	0	0	0	0	7
GR, SD	Eastern meadowlark	*Sturnella magna*	7 141	568	394	265	723	465	648	606
SD	Eastern phoebe	*Sayornis phoebe*	17	15	27	11	1	2	0	0
SS	Eastern towhee	*Pipilo erythrophthalmus*	0	1	0	0	0	0	0	0
UB, SD	European starling	*Sturnus vulgaris*	0	4	8	0	0	8	0	0
WT,	Glossy ibis	*Plegadis falcinellus*	3	1	37	8	0	0	0	0
GR, NM	Grasshopper sparrow	*Ammodramus savannarum*	0	1	0	5	2	19	0	0
SS, NM	Gray catbird	*Dumetella carolinensis*	1	4	0	0	0	0	0	0
WT	Great blue heron	*Ardea herodias*	3	2	3	7	3	1	0	3
WT	Great egret	*Ardea alba*	43	22	28	7	11	0	33	11
WT, NM	Greater yellowlegs	*Tringa melanoleuca*	3	0	3	3	19	18	0	19
WT	Green heron	*Butorides virescens*	4	0	0	0	1	0	3	1
SS, NM	House wren	*Troglodytes aedon*	3	28	5	37	5	18	0	0
SS, NM	Indigo bunting	*Passerina cyanea*	0	1	0	0	0	0	0	0
SD	Killdeer	*Charadrius vociferous*	6	0	16	18	12	9	0	4
WT	King rail	*Rallus elegans*	10	5	0	0	0	0	0	0
GR, SD	Le Conte's sparrow	*Ammodramus leconteii*	0	0	0	11	1	0	0	0
WT, NM	Least sandpiper	*Calidris minutilla*	3	0	0	0	0	3	0	0
WT, NM	Lesser yellowlegs	*Tringa flavipes*	2	0	0	0	0	0	0	0
WT	Little blue heron	*Egretta garzetta*	38	10	5	2	2	1	9	2
SD	Loggerhead shrike	*Lanius ludovicianus*	9	19	3	7	0	4	3	6
WT, SD	Marsh wren	*Cistothorus palustris*	9	25	1	1	0	0	0	0

Table 1. Continued.

Guild[1]	Common name	Scientific name	Abundance (no. of individuals) Fall Mono[2]	Fall Mixed[3]	Winter Mono	Winter Mixed	Spring Mono	Spring Mixed	Summer Mono	Summer Mixed
WD, NM	Merlin	*Falco columbarius*	2	0	0	0	0	0	0	0
WT	Mottled duck	*Anas fulvigula*	58	63	28	18	26	70	19	26
UB, SD	Mourning dove	*Zenaida macroura*	7	12	2	14	18	25	27	32
SS, RE	Northern bobwhite	*Colinus virginianus*	158	17	60	6	142	29	145	35
SS, RE	Northern cardinal	*Cardinalis cardinalis*	5	7	2	5	1	5	3	5
GR, SD	Northern harrier	*Circus cyaneus*	0	3	7	20	4	11	0	0
UB, RE	Northern mockingbird	*Mimus polyglottos*	4	18	10	3	2	16	6	8
WT, SD	Osprey	*Pandion haliaetus*	0	0	0	0	1	0	0	1
SS	Palm warbler	*Dendroica palmarum*	264	310	341	152	94	72	0	0
WD, RE	Pileated woodpecker	*Dryocopus pileatus*	0	1	0	1	0	1	0	0
WD, RE	Red-bellied woodpecker	*Melanerpes carolinus*	8	10	2	18	0	15	12	7
WD, SD	Red-shouldered hawk	*Buteo lineatus*	24	12	9	9	11	16	19	10
WT, SD	Red-winged blackbird	*Agelaius phoeniceus*	2 156	1 672	671	213	490	523	711	490
NM	Rough-winged swallow	*Stelgidopteryx serripennis*	0	0	0	0	0	0	2	0
WT	Sandhill crane	*Grus canandensis*	1	6	44	19	15	13	2	15
GR, SD	Savannah sparrow	*Passerculus sandwichensis*	126	142	359	654	423	393	1	0
GR, SD	Sedge wren	*Cistothorus plantensis*	32	232	152	301	93	192	0	0
WT,	Snowy egret	*Egretta thula*	3	1	10	1	1	0	0	0
NM	Solitary sandpiper	*Tringa solitaria*	0	0	2	0	0	0	0	0
SS, SD	Song sparrow	*Melospiza melodia*	0	0	0	0	2	0	0	0
WT	Sora	*Porzana carolina*	9	2	3	0	0	0	0	0
SD	Swamp sparrow	*Melospiza georgiana*	1	12	70	727	14	124	0	0
WD	Swallow-tailed kite	*Elanoides forficatus*	0	0	0	0	0	1	0	0
SD	Tree swallow	*Tachycineta bicolor*	68	144	631	379	349	198	0	0
WT	Tricolored heron	*Egretta tricolor*	14	1	4	0	0	0	0	0
SD	Turkey vulture	*Cathartes aura*	2	40	12	29	2	9	0	5
WT	Virginia rail	*Rallus limicola*	3	2	0	0	0	0	0	0
WT	White ibis	*Endocimus albus*	958	119	61	2	0	0	110	0
RE	White-tailed kite	*Elanus leucurus*	0	0	0	4	0	0	0	0
WT	Wood stork	*Mycteria americana*	71	23	19	11	3	2	0	3
WD	Yellow-rumped warbler	*Dendroica coronate*	0	0	2	15	0	2	0	0
WD	Yellow-throated warbler	*Dendroica dominica*	0	0	0	1	0	0	0	0

[1]Breeding habitat guilds: WT = wetland, GR = grassland, SS = successional-scrub, WD = woodland, and UB = urban; migrant status guilds: RE = resident, SM = short-distance migrant, and NM = neotropical migrant.
[2]Monoculture pasture.
[3]Mixed pasture.

were considered statistically and biologically significant at $R^2 \geq 0.3$ and $P \leq 0.1$. The relative importance of each variable in the best model was assessed by examining standardized regression coefficients (SC; i.e., variables with higher coefficients made greater individual contributions to the explanatory power of the model).

All data sets were rank transformed prior to analyses because of violations of normality and homogeneity of variance assumptions (Zar 1998; Conover 1999; SYSTAT 2007). Statistical significance was concluded at $P \leq 0.1$ for all tests. This value was used rather than the more conservative $P \leq 0.05$ to minimize the probability of making a type II error (Zar 1998). All statistical tests were performed using SYSTAT (2007) statistical software.

RESULTS

Vegetation

Monoculture Pasture. Variance of grass cover and litter depth were affected by grazing, decreasing as grazing intensity increased. Grazing also affected mean, variance, and maximum forb cover, mean and variance of litter cover, maximum vegetation height, mean litter depth, and mean, variance, and maximum stem density at 60–90 cm and 90–120 cm. All generally decreased in the presence of grazing compared to control pasture units, but effects at low, medium, and high grazing intensities were similar. Mean grass cover was also affected by grazing, increasing as grazing intensity increased (Table 2).

Table 2. Effects of grazing intensity on vegetation attributes of monoculture and mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003.

Pasture type	Vegetation attributes	Cattle grazing intensity[1,2]				P
		Control[3]	Low[4]	Medium[5]	High[6]	
Monoculture	Mean grass cover (%)	78.9 ± 1.7 a	90 ± 0.8 b	86.9 ± 1.1 b	90.0 ± 0.9 b	≤ 0.001
	Variance of grass cover (%)	734.7 ± 62.9 a	400.0 ± 42.1 b	533.8 ± 1.0 ac	482.0 ± 57.2 bc	0.003
	Mean forb cover (%)	38.0 ± 20.7 a	6.5 ± 0.6 b	9.0 ± 1.0 c	6.6 ± 0.9 b	≤ 0.001
	Variance of forb cover (%)	552.3 ± 63.3 a	226.2 ± 28.0 b	312.3 ± 36.2 b	285.7 ± 46.1 b	0.001
	Maximum forb cover (%)	85.9 ± 3.4 a	65.9 ± 4.4 b	74.0 ± 3.8 b	70.3 ± 4.0 b	0.003
	Maximum vegetation height (cm)	53.4 ± 6.4 a	30.4 ± 3.0 b	34.6 ± 5.6 b	30.8 ± 4.8 b	≤ 0.001
	Mean litter depth (cm)	3.3 ± 0.6 a	2.3 ± 0.5 bc	2.1 ± 0.4 b	2.3 ± 0.6 c	≤ 0.001
	Variance of litter depth (cm)	13.2 ± 4.3 a	4.4 ± 1.5 b	8.2 ± 5.8 c	3.2 ± 1.2 c	≤ 0.001
	Mean litter cover (%)	34.5 ± 5.2 a	31.2 ± 5.4 b	29.6 ± 5.3 b	24.8 ± 5.4 b	0.001
	Variance of litter cover (%)	343.0 ± 60.9 a	255.2 ± 48.6 bc	300.0 ± 69.4 b	177.0 ± 48.1 c	0.001
	Mean stem density 60–90 cm (stems · 30 cm^{-1})	0.2 ± 0.1 a	0.03 ± 0.01 b	0.04 ± 0.2 b	0.03 ± 0.01 ab	0.006
	Variance of stem density 60–90 cm (stems · 30 cm^{-1})	0.8 ± 0.3 a	0.1 ± 0.03 b	0.2 ± 0.1 b	0.1 ± 0.1 ab	0.007
	Maximum stem density 60–90 cm (stems · 30 cm^{-1})	3.4 ± 0.7 a	0.9 ± 0.3 b	1.0 ± 0.4 b	2.3 ± 1.2 ab	0.009
	Mean stem density 90–120 cm (stems · 30 cm^{-1})	0.1 ± 0.0a	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b	0.001
	Variance of stem density 90–120 cm (stems · 30 cm^{-1})	0.3 ± 0.1 a	0.0 ± 0.0 b	0.1 ± 0.0 b	0.1 ± 0.1 b	0.001
	Maximum stem density 90–120 cm (stems · 30 cm^{-1})	1.8 ± 0.5 a	0.4 ± 0.2 b	0.4 ± 0.2 b	0.7 ± 0.4 b	0.001
Mixed	Mean grass cover (%)	90.8 ± 10.4 a	85.7 ± 1.9 b	88.2 ± 2.4 ab	90.7 ± 2.2 ab	0.033
	Mean forb cover (%)	4.16 ± 0.5 a	7.8 ± 1.0 b	5.5 ± 0.7 abc	3.8 ± 0.6 ac	0.011
	Variance of forb cover (%)	111.5 ± 16.2 a	248.8 ± 38.1 b	157.9 ± 24.3 abc	99.2 ± 0.023 ac	0.023
	Maximum forb cover (%)	50.3 ± 4.7 ab	62.3 ± 4.9 a	57.9 ± 4.9 a	41.1 ± 5.2 b	0.043
	Mean vegetation height (cm)	23.5 ± 2.9 a	21.6 ± 2.8 ab	20.7 ± 2.5 b	19.3 ± 2.1 b	0.029
	Mean litter depth (cm)	4.0 ± 0.1 a	3.2 ± 0.7 ab	2.7 ± 0.5 ab	2.3 ± 0.4 b	0.020

[1]$n = 2$/grazing intensity.
[2]$\bar{x} \pm$ SE followed by different letters in the same row are significantly different ($P \leq 0.1$).
[3]Nongrazed.
[4]1.3 ha · animal unit (AU)$^{-1}$ on monoculture pasture and 2.1 ha · AU^{-1} on mixed pasture.
[5]1.0 ha · AU^{-1} on monoculture pasture and 1.6 ha · AU^{-1} on mixed pasture.
[6]0.6 ha · AU^{-1} on monoculture pasture and 0.9 ha · AU^{-1} on mixed pasture.

A grazing intensity × season interaction affected mean vegetation height, maximum litter depth, maximum litter cover, mean bare ground cover, variance in stem density at 0–30 cm, and mean, variance, and maximum stem density at 30–60 cm (Table 3). During the spring, maximum stem density at 30–60 cm and maximum litter depth decreased in the presence of grazing compared to control pasture units. Mean vegetation height and mean and variance of stem density at 30–60 cm typically decreased in the presence of grazing in winter and spring. Maximum litter cover decreased in the presence of grazing in all seasons. For all these vegetation attributes, effects at low, medium, and high grazing intensities were similar. In spring, variance of stem density at 0–30 cm decreased in the presence of grazing compared to control pasture units, with reductions similar at low and high and greatest at medium grazing intensities. Mean bare ground cover decreased at high grazing intensity compared to control pasture units in fall, winter, and summer. Depending on season, reductions in this variable were also observed at medium grazing intensity (Table 3). Mean, variance, and maximum stem density at 0–30 cm were affected by a grazing intensity × time interaction (Table 4). Decreases in mean stem density at 0–30 cm were typically observed at medium and high grazing intensities compared to control pasture units 1–4 yr after introduction of grazing. Similar decreases were seen in variance and maximum stem density at 0–30 cm but generally only immediately following and up to 1 yr after introduction of grazing (Table 4). Variance in vegetation height and bare ground cover were affected by a grazing intensity × season × time interaction ($P = 0.019$ and $P = 0.098$, respectively). Grazing alone and grazing intensity × time, grazing intensity × season, and grazing intensity × season × time interactions had no impact on maximum grass or bare ground cover ($P \geq 0.449$).

Mixed Pasture. Grazing affected mean and variance of forb cover, which increased at low grazing intensity compared to controls. In contrast, mean grass cover decreased at low grazing intensity. No clear trend in mean and variance of forb cover or

Table 3. Effects of a grazing intensity × season interaction on vegetation attributes of monoculture and mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003.

Pasture type	Vegetation attributes	Season	Cattle grazing intensity[1,2] Control[3]	Low[4]	Medium[5]	High[6]	P
Monoculture	Mean vegetation height (cm)	Fall	26.3 ± 4.4 a	19.6 ± 3.2 a	19.1 ± 3.9 a	17.6 ± 3.2 a	0.052
		Winter	14.0 ± 0.8 a	11.6 ± 0.3 a	10.4 ± 0.3 b	10.2 ± 0.2 b	
		Spring	15.0 ± 1.4 a	10.8 ± 0.6 b	10.9 ± 0.6 b	10.5 ± 0.4 b	
		Summer	24.4 ± 5.4 a	16.4 ± 3.3 a	14.7 ± 3.3 a	11.5 ± 2.2 a	
	Maximum litter depth (%)	Fall	12.9 ± 3.4 a	59.5 ± 10.7 a	18.6 ± 9.8 a	8.4 ± 3.4 a	0.084
		Winter	11.2 ± 4.0 a	11.3 ± 5.0 a	5.7 ± 1.4 a	5.7 ± 1.3 a	
		Spring	13.3 ± 3.7 a	4.8 ± 1.3 b	6.0 ± 1.4 b	4.3 ± 1.3 a	
		Summer	15.0 ± 8.1 a	5.4 ± 1.9 a	4.5 ± 1.8 a	6.3 ± 3.8 a	
	Maximum litter cover (%)	Fall	80.0 ± 6.7 a	59.5 ± 10.7 b	56.5 ± 11.5 a	46.0 ± 10.5 b	0.067
		Winter	84.2 ± 11.0 a	75.0 ± 13.1 b	71.7 ± 13.5 a	80.0 ± 11.3 b	
		Spring	73.6 ± 11.0 a	56.9 ± 12.3 b	61.9 ± 12.3 a	53.1 ± 9.5 b	
		Summer	72.0 ± 9.8 a	70.5 ± 8.0 b	69.0 ± 9.1 a	54.0 ± 8.7 b	
	Mean bare ground cover (%)	Fall	5.6 ± 1.4 a	3.12 ± 1.0 a	6.4 ± 1.3 b	5.3 ± 1.2 b	0.064
		Winter	2.7 ± 0.8 a	2.9 ± 1.0 a	3.1 ± 0.8 ab	3.4 ± 1.0 b	
		Spring	2.6 ± 0.9 a	2.6 ± 0.7 a	1.5 ± 0.3 a	2.0 ± 0.8 a	
		Summer	3.4 ± 2.1 a	4.4 ± 1.7 a	3.8 ± 1.0 a	2.5 ± 0.8 b	
	Variance of stem density 0–30 cm (stems · 30 cm^{-1})	Fall	102.7 ± 34.3 a	46.6 ± 6.9 a	51.7 ± 7.0 b	62.5 ± 22.6 ab	0.005
		Winter	68.1 ± 22.3 a	43.6 ± 9.0 a	29.0 ± 6.2 a	25.6 ± 7.3 a	
		Spring	71.6 ± 23.6 a	19.5 ± 3.1 b	18.6 ± 3.8 c	20.0 ± 2.7 bc	
		Summer	40.1 ± 11.5 a	23.1 ± 8.4 a	25.6 ± 8.4 a	19.5 ± 10.1 a	
	Mean stem density 30–60 cm (stems · 30 cm^{-1})	Fall	2.2 ± 0.6 a	1.2 ± 0.5 a	1.0 ± 0.4a	1.0 ± 0.4 a	0.015
		Winter	0.2 ± 0.1 a	0.0 ± 0.0 ab	0.0 ± 0.0 b	0.1 ± 0.1 ab	
		Spring	0.5 ± 0.2 a	0.0 ± 0.0 b	0.0 ± 0.0 b	0.1 ± 0.0 b	
		Summer	1.4 ± 0.1 a	1.0 ± 0.7 a	0.7 ± 0.4 a	0.4 ± 0.3 a	
	Variance of stem density 30–60 cm (stems · 30 cm^{-1})	Fall	15.2 ± 6.0 a	4.3 ± 1.8 a	4.4 ± 2.1 a	4.1 ± 1.8 a	0.031
		Winter	0.7 ± 0.2 a	0.1 ± 0.1 ab	0.0 ± 0.0 b	0.7 ± 0.6 ab	
		Spring	2.5 ± 1.3 a	0.0 ± 0.0 b	0.2 ± 0.1 b	0.2 ± 0.1 b	
		Summer	4.5 ± 2.3 a	3.9 ± 3.1 a	3.0 ± 2.0 a	1.5 ± 1.1 a	
	Maximum stem density 30–60 cm (stems · 30 cm^{-1})	Fall	15.6 ± 4.2 a	8.2 ± 2.0 a	8.6 ± 2.4 a	8.1 ± 1.6 a	0.052
		Winter	4.5 ± 1.0 a	2.0 ± 1.0 a	0.3 ± 0.2 a	3.7 ± 2.2	
		Spring	7.6 ± 2.6 a	0.4 ± 0.3 ab	1.6 ± 1.0 b	2.4 ± 0.9 ab	
		Summer	26.6 ± 19.4 a	4.0 ± 2.2 a	4.4 ± 2.4 a	2.8 ± 1.5 a	
Mixed	Mean vegetation density 0–30 cm	Fall	18.9 ± 3.4 a	15.7 ± 2.1 a	18.7 ± 2.8 a	18.9 ± 2.7 b	0.012
		Winter	15.0 ± 2.5 a	13.5 ± 2.4 a	10.1 ± 2.1 a	9.9 ± 2.2 a	
		Spring	13.5 ± 2.1 a	8.0 ± 1.5 a	9.9 ± 2.0 a	8.1 ± 1.5 a	
		Summer	9.6 ± 1.3 a	8.0 ± 1.0 a	8.8 ± 1.0 a	8.4 ± 1.5 b	

[1] $n = 2$/grazing intensity × season.
[2] $\bar{x}$ ± SE followed by different letters in the same row are significantly different ($P \leq 0.1$).
[3] Nongrazed.
[4] 1.3 ha · animal unit $(AU)^{-1}$ on monoculture pasture and 2.1 ha · AU^{-1} on mixed pasture.
[5] 1.0 ha · AU^{-1} on monoculture pasture and 1.6 ha · AU^{-1} on mixed pasture.
[6] 0.6 ha · AU^{-1} on monoculture pasture and 0.9 ha · AU^{-1} on mixed pasture.

mean grass cover was observed with further increases in grazing intensity. Mean litter depth and vegetation height were affected by grazing. Mean litter depth decreased at high grazing intensity, and mean vegetation height decreased at medium and high grazing intensities when compared to control pasture units. Grazing affected maximum forb cover, but no clear trend was observed with increasing grazing intensity (Table 2).

Mean stem density at 0–30 cm was affected by a grazing intensity × season interaction, decreasing at high grazing intensity in fall and summer (Table 3). This vegetation attribute was also affected by a grazing intensity × time interaction, with decreases observed 2 yr, 3 yr, and 5 yr after introduction of grazing at high and sometimes medium and low grazing intensities compared to control pasture units (Table 4). Grazing intensity alone and grazing intensity × time, grazing intensity × season, and grazing intensity × season × time interactions had no impact on variance and maximum grass cover; variance and maximum vegetation height; variance and maximum litter depth; mean, variance, and maximum litter cover; mean, variance, and maximum bare ground cover; variance and

Table 4. Effects of a grazing intensity × time interaction on vegetation attributes of monoculture and mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003.

Pasture type	Vegetation attributes	Time[1]	Cattle grazing intensity[2,3]				P
			Control[4]	Low[5]	Medium[6]	High[7]	
Monoculture	Mean stem density 0–30 cm (stems · 30 cm^{-1})	0	22.3 ± 5.4 a	10.8 ± 3.4 a	10.3 ± 4.0 a	9.9 ± 4.6 a	≤ 0.001
		1	13.5 ± 1.6 a	8.9 ± 1.0 abc	7.2 ± 0.7 b	40.3 ± 7.2 c	
		2	7.4 ± 1.8 a	5.9 ± 1.6 a	5.0 ± 1.4 a	4.4 ± 1.3 b	
		3	11.0 ± 1.9 a	8.9 ± 1.4 ab	8.0 ± 1.2 b	7.0 ± 1.3 c	
		4	11.6 ± 0.4 a	12.0 ± 1.0 a	14.5 ± 1.5 b	11.9 ± 1.0 a	
	Variance of stem density 0–30 cm (stems · 30 cm^{-1})	0	179.5 ± 74.2 a	47.1 ± 22.7 b	43.1 ± 23.9 b	84.0 ± 61.4 b	0.005
		1	97.7 ± 20.7 a	49.1 ± 8.5 ab	40.3 ± 7.2 a	40.3 ± 7.2 b	
		2	28.4 ± 7.7 a	20.6 ± 6.3 a	15.5 ± 5.1 a	13.9 ± 4.6 a	
		3	54.6 ± 15.0 a	27.1 ± 3.2 a	28.5 ± 4.6 a	20.7 ± 4.0 a	
		4	40.8 ± 9.6 a	25.3 ± 5.1 a	41.4 ± 8.8 a	33.5 ± 5.9 a	
	Maximum stem density 0–30 cm (stems · 30 cm^{-1})	0	45.5 ± 5.1 a	26.3 ± 7.7 b	23.5 ± 9.5 b	26.5 ± 12.5 b	0.013
		1	38.5 ± 3.7 ab	27.4 ± 2.5 ab	40.3 ± 7.2 a	26.0 ± 3.0 b	
		2	19.3 ± 4.4 a	16.9 ± 4.2 a	28.125 ± 14.0 a	12.8 ± 3.3 a	
		3	35.4 ± 8.4 a	24.0 ± 1.6 a	24.3 ± 2.5 a	20.8 ± 2.4 a	
		4	32.8 ± 6.0 a	23.5 ± 2.4 a	33.5 ± 3.1 b	27.7 ± 2.5 a	
Mixed	Mean stem density 0–30 cm (stems · 30 cm^{-1})	0	45.0 ± 0.0 a	4.9 ± 0.0 b	38.8 ± 0.0 a	42.4 ± 0.0 a	≤ 0.001
		1	15.5 ± 3.7 a	15.2 ± 3.3 a	14.7 ± 4.0 a	13.1 ± 3.3 a	
		2	15.3 ± 2.8 a	12.8 ± 3.1 ab	14.6 ± 2.3 b	14.4 ± 1.9 b	
		3	13.6 ± 0.9 a	9.3 ± 2.4 b	9.4 ± 1.0 b	8.2 ± 1.0 b	
		4	11.9 ± 2.4 a	9.3 ± 2.4 a	9.4 ± 2.2 a	8.1 ± 2.5 a	
		5	11.2 ± 2.8 a	10.3 ± 1.2 a	10.1 ± 1.0 a	11.4 ± 1.3 b	

[1]Time since introduction of grazing (years).
[2]$n = 2$/grazing intensity × time.
[3]$\bar{x} \pm$ SE followed by different letters in the same row are significantly different ($P \leq 0.1$).
[4]Nongrazed.
[5]1.3 ha · animal unit (AU)$^{-1}$ on monoculture pasture and 2.1 ha · AU^{-1} on mixed pasture.
[6]1.0 ha · AU^{-1} on monoculture pasture and 1.6 ha · AU^{-1} on mixed pasture.
[7]0.6 ha · AU^{-1} on monoculture pasture and 0.9 ha · AU^{-1} on mixed pasture.

maximum stem density at 0–30 cm; or mean, variance, and maximum stem density at 30–60 cm, 60–90 cm, and 90–120 cm ($P \geq 0.127$).

Avian Abundance and Species Richness

Monoculture Pasture. Sixty-nine bird species were observed on monoculture pasture units (Table 1). Grazing affected wetland guild abundance ($P = 0.075$), which decreased at low and medium grazing intensities and increased at high grazing intensity compared to control pasture units. Short-distance migrant ($P = 0.028$) and permanent resident ($P \leq 0.001$) guilds were also affected by grazing, exhibiting decreases in abundance at low and high grazing intensities. However, at medium grazing intensity, abundance within these guilds was similar to that observed on control pasture units. Grazing affected neotropical migrant guild abundance ($P \leq 0.001$), which decreased at low, medium, and high grazing intensities. Declines were similar at low and medium grazing intensities and greatest at high grazing intensity (Fig. 1).

Total species richness was affected by grazing ($P \leq 0.001$), decreasing in the presence of grazing compared to control pasture units. Reductions were similar at low and high grazing intensities and greatest at medium grazing intensity. Grazing also affected short-distance migrant ($P = 0.001$) and permanent resident ($P \leq 0.001$) guild species richness, which decreased in the presence of grazing. Declines were similar at low and medium grazing intensities and greatest at high grazing intensity. Species richness within successional scrub ($P \leq 0.001$) and neotropical migrant ($P \leq 0.001$) guilds was affected by grazing. Both decreased in the presence of grazing compared to control pasture units, but reductions at low, medium, and high grazing intensities were similar (Fig. 2).

A grazing intensity × season interaction affected grassland ($P = 0.002$) and woodland ($P = 0.055$) guild abundance and woodland species richness ($P = 0.086$). In the fall, grassland guild abundance increased in the presence of grazing compared to control pasture units. However, increases at low, medium, and high grazing intensities were similar. Woodland guild abundance and species richness decreased in the fall at low grazing intensity, but no differences were observed between control pasture units and those subject to medium and high grazing intensities (Fig. 3).

Abundance within successional-scrub ($P = 0.053$) and woodland ($P = 0.074$) guilds was affected by a grazing intensity × time interaction. Successional-scrub guild abundance decreased in the presence of grazing compared to control pasture units 3–4 yr after the introduction of grazing. However, reductions at low, medium, and high grazing intensities were similar. Woodland guild abundance decreased at low grazing intensity

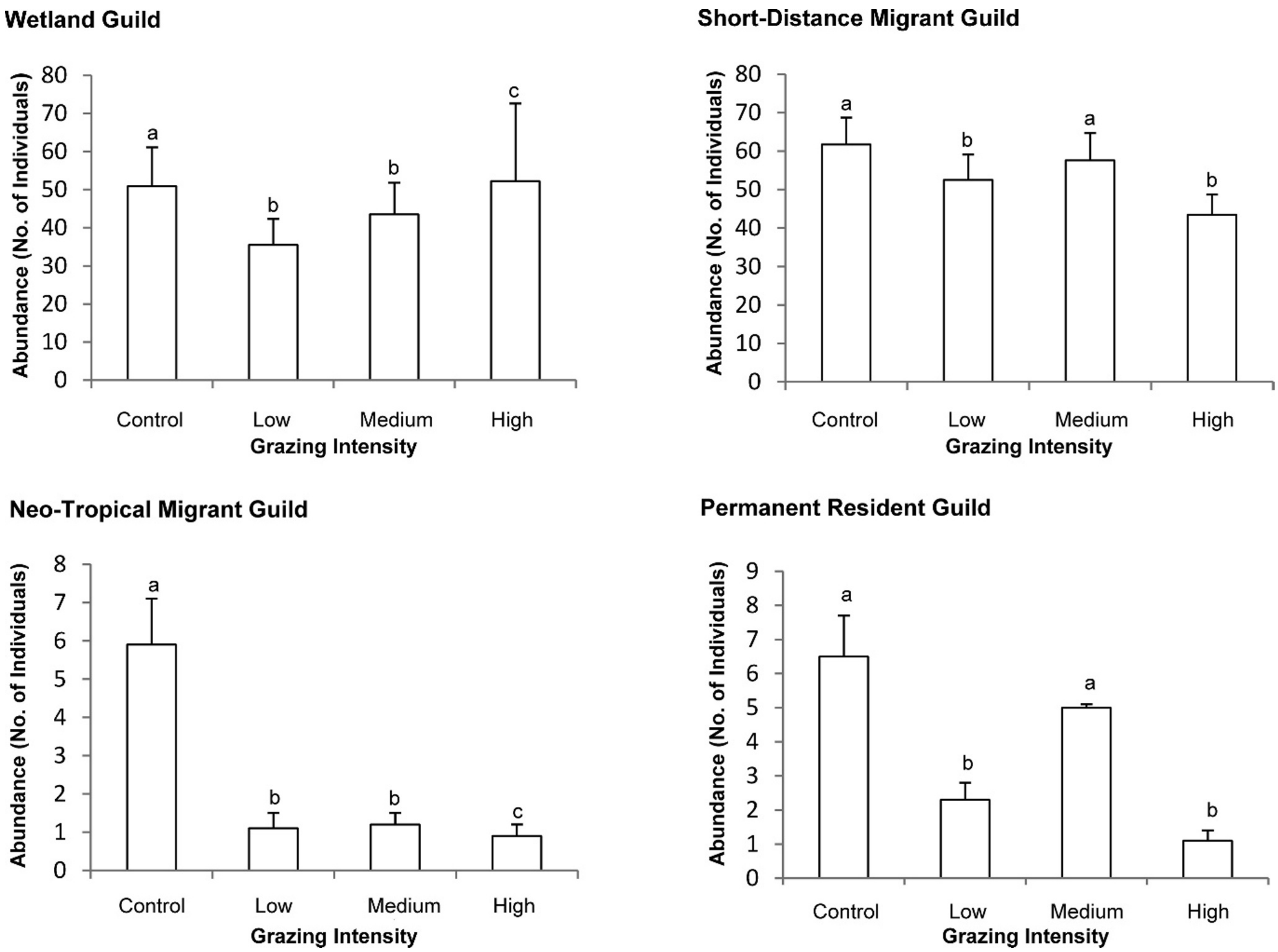

Figure 1. Effects of grazing intensity on avian abundance by guild in monoculture pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 1.3 ha · animal unit $(AU)^{-1}$, medium = 1.0 ha · AU^{-1}, and high = 0.6 ha · AU^{-1}.

2 yr after the introduction of grazing. However, abundance at medium and high grazing intensities was similar to that observed on control pasture units (Fig. 4). Grazing intensity alone and grazing intensity × time, grazing intensity × season, and grazing intensity × season × time interactions had no effect on total avian abundance, urban guild abundance, and wetland, grassland, and urban guild species richness ($P \geq 0.209$).

Mixed Pasture. Seventy-eight bird species were observed on mixed pasture units (Table 1). Grazing affected total avian abundance ($P = 0.017$), which decreased at medium and high grazing intensities. At low grazing intensity, total avian abundance was similar to that observed on control pasture units. Within the grassland guild, abundance was also affected by grazing ($P = 0.045$), increasing at low and medium grazing intensities ($P = 0.045$). However, at high grazing intensity, abundance was similar to that observed on control pastures units. Grazing affected urban ($P = 0.046$) and neotropical migrant ($P = 0.002$) guild abundance. For both guilds, abundance decreased at high grazing intensity, but no differences were observed between control pastures and those subject to low and medium grazing intensities. Successional scrub abundance was affected by grazing ($P = 0.013$). However, no clear trend in abundance was observed with increasing grazing intensity. Short-distance migrant guild abundance was affected by grazing ($P = 0.071$) but was similar at low, medium, and high grazing intensities to that observed on control pasture units (Fig. 5).

Grazing affected successional-scrub guild richness ($P = 0.009$), which decreased at high grazing intensity. However, no differences in richness were observed between control pastures and those subject to low and medium grazing intensities. Neotropical migrant guild abundance was affected by grazing ($P = 0.070$), decreasing at medium and high grazing intensities. However, at low grazing intensity, abundance was similar to that observed on control pasture units. Grazing affected urban species richness ($P = 0.027$), which increased at high and low grazing intensities. No differences in urban species richness were observed between control pasture units and those subject to medium grazing intensity. Species richness within the short-distance migrant guild was affected by grazing intensity ($P = 0.015$). However, no clear trend was observed as grazing increased (Fig. 6).

A grazing intensity × season interaction affected woodland ($P = 0.048$) and permanent resident ($P = 0.055$) guild abundance. In fall, within the woodland guild, abundance increased

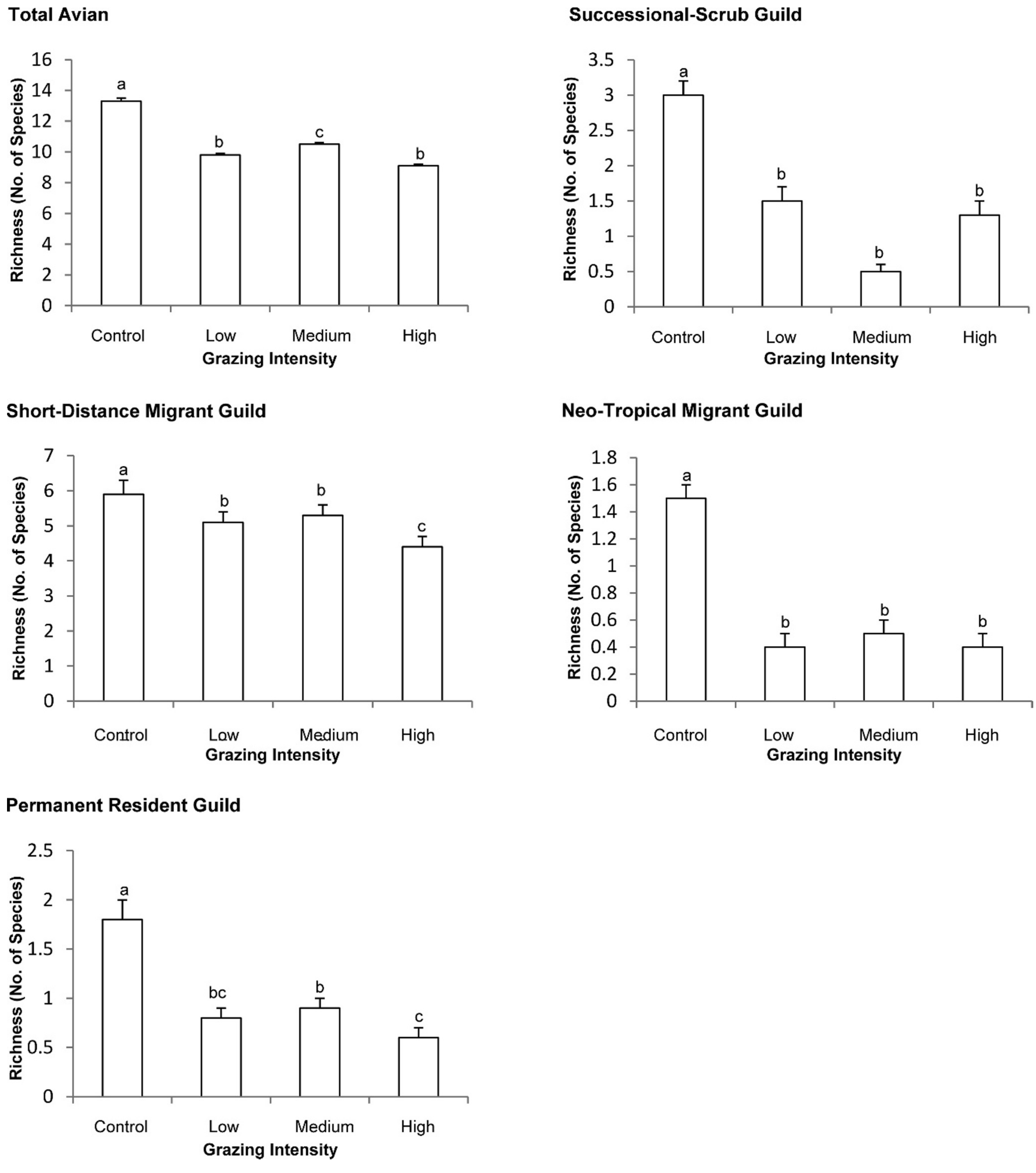

Figure 2. Effects of grazing intensity on total avian species richness and avian species richness by guild in monoculture pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 1.3 ha · animal unit (AU)$^{-1}$, medium = 1.0 ha · AU^{-1}, and high = 0.6 ha · AU^{-1}.

at medium grazing intensity but was similar to control pasture units at low and high grazing intensities. In all seasons, abundance within the permanent resident guild was similar on control pasture units and those subject to low, medium, and high grazing intensities. Total avian species richness ($P = 0.075$) and species richness within the woodland guild ($P = 0.028$) were also affected by a grazing intensity × season interaction. However, in all seasons, total species richness was similar on control pasture units and those subject to low, medium, and high grazing intensities. In fall, species richness within the woodland guild increased at medium grazing intensity but was similar to control pastures at low and high grazing intensities. Woodland guild richness also increased in spring at high grazing intensity but was similar on control

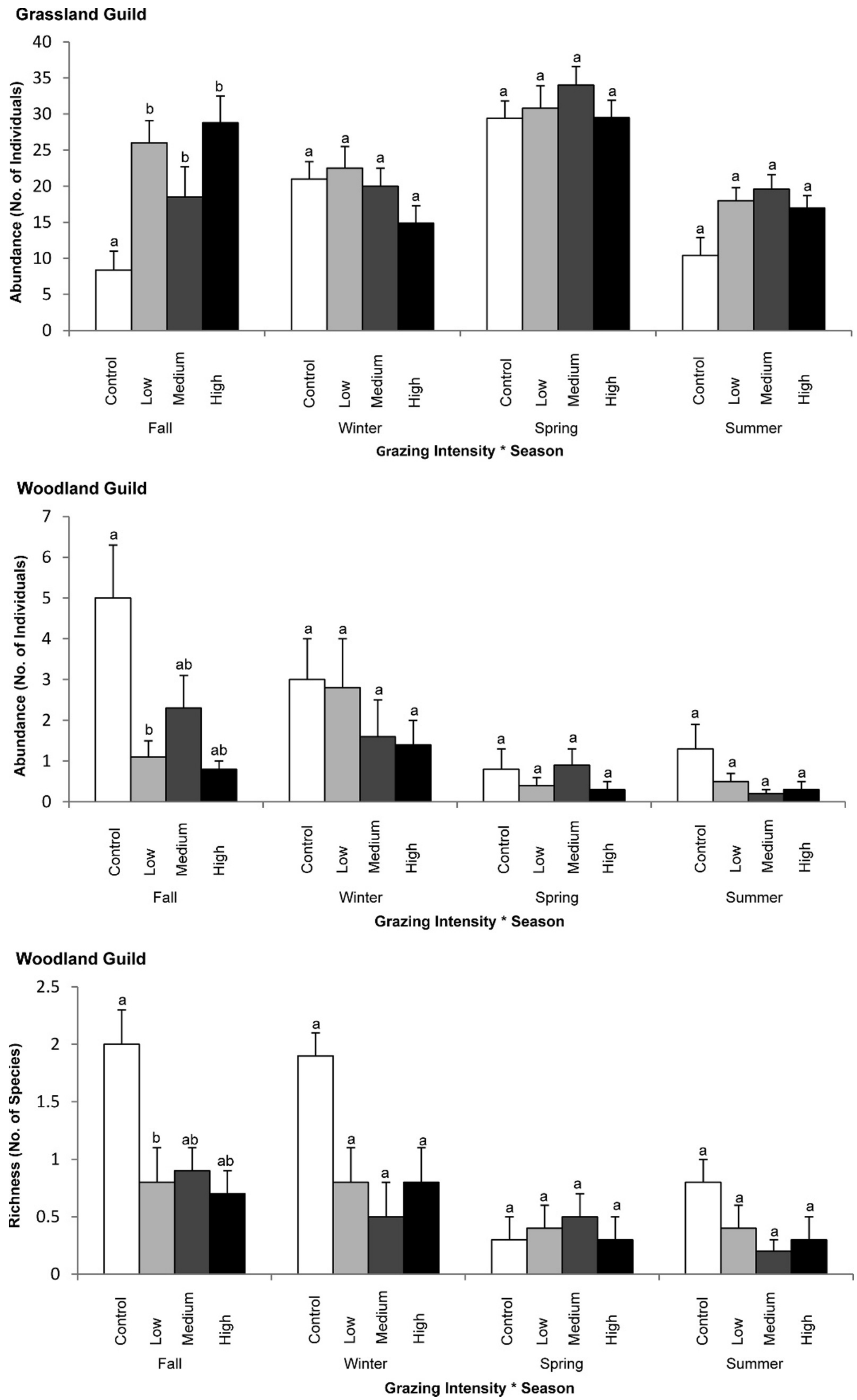

Figure 3. Effects of a grazing intensity × season interaction on avian abundance and species richness by guild in monoculture pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 1.3 ha · animal unit $(AU)^{-1}$, medium = 1.0 ha · AU^{-1}, and high = 0.6 ha · AU^{-1}.

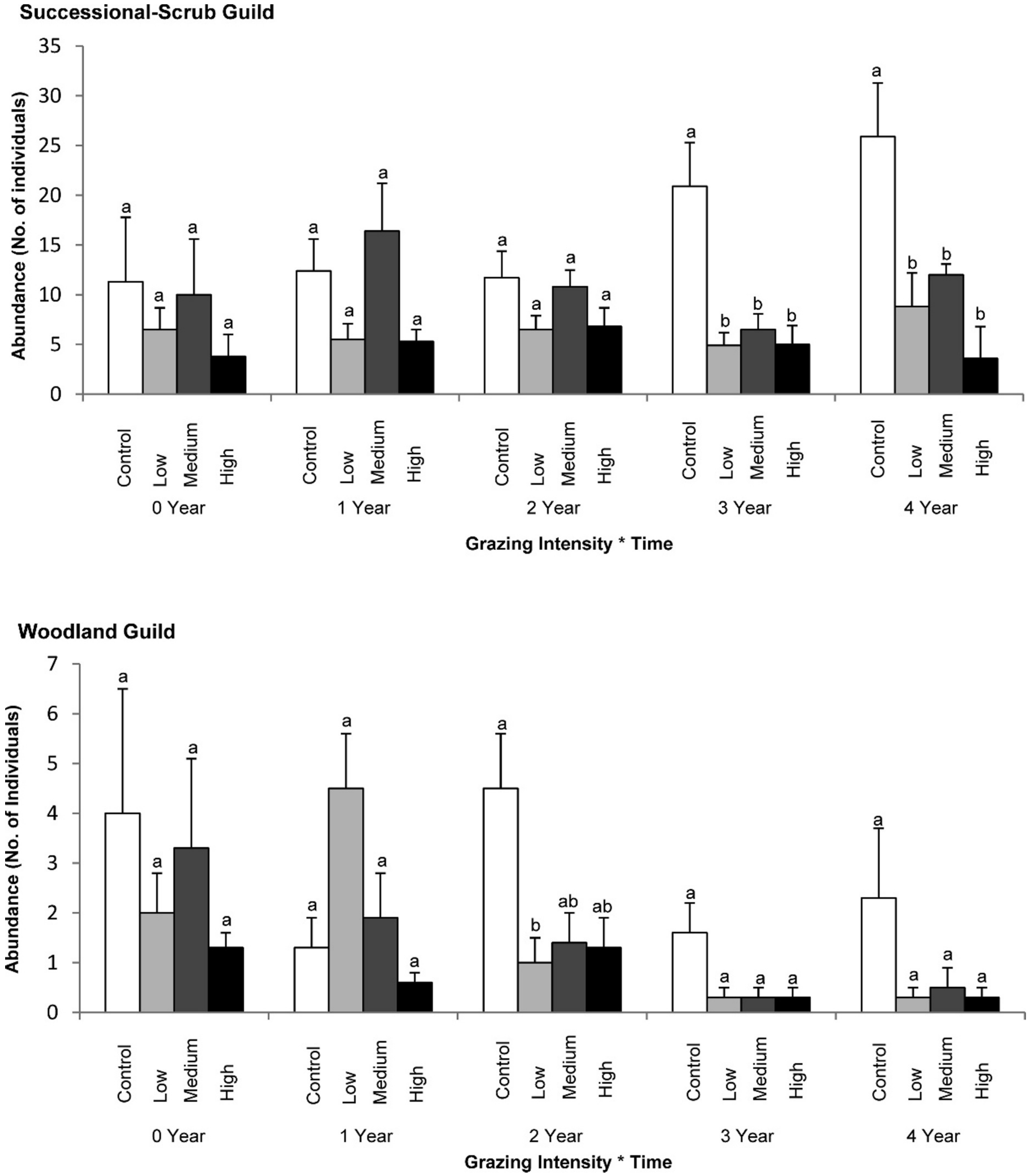

Figure 4. Effects of a grazing intensity × time interaction on avian abundance by guild in monoculture pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 1.3 ha · animal unit (AU)$^{-1}$, medium = 1.0 ha · AU^{-1}, and high = 0.6 ha · AU^{-1}.

pasture units and those subject to low and medium grazing intensities (Fig. 7).

Total species richness was affected by a grazing intensity × time interaction ($P = 0.092$). However, richness was similar at low, medium, and high grazing intensities compared to controls at all times following introduction of grazing (Fig. 8). Grassland guild species richness was affected by a grazing intensity × season × time interaction ($P = 0.087$). Grazing intensity alone and grazing intensity × time, grazing intensity × season, and grazing intensity × season × time interactions had no effect on wetland guild abundance and wetland and permanent resident guild abundance and species richness ($P \geq 0.124$).

Avian–Habitat Relationships

Monoculture Pasture. Vegetation attributes that best predicted wetland guild abundance were mean vegetation height

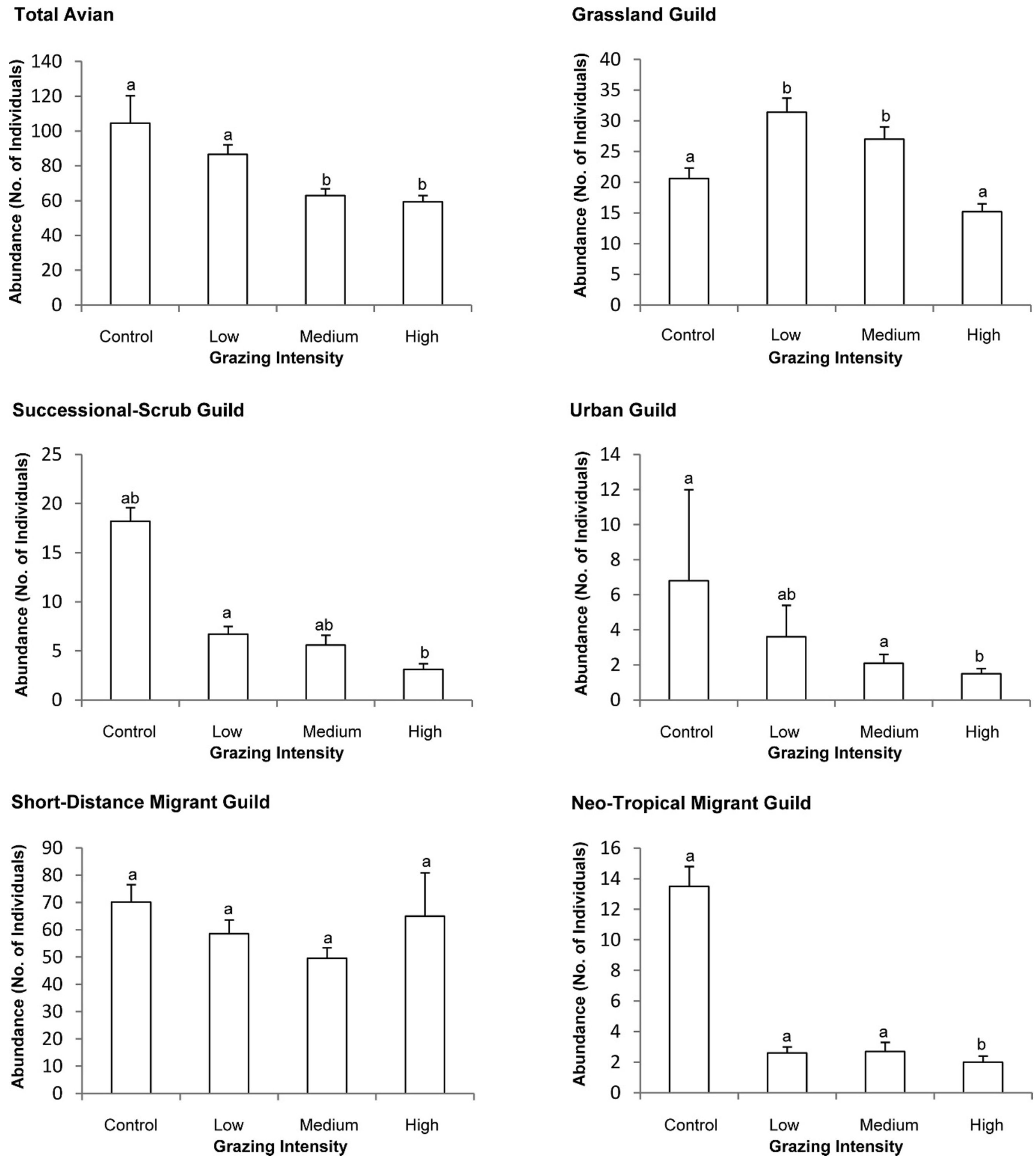

Figure 5. Effects of grazing intensity on total avian abundance and avian abundance by guild in mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 2.1 ha · animal unit $(AU)^{-1}$, medium = 1.6 ha · AU^{-1}, and high = 0.9 ha · AU^{-1}.

(SC = 0.425), minimum bare ground cover (SC = 0.262), variance of litter depth (SC = −0.182), and variance of stem density at 0–30 cm (SC = 0.161; $R^2 = 0.387$, $P \leq 0.001$). Mean vegetation height (SC = 0.358), variance of stem density at 0–30 cm (SC = 0.231), variance of litter depth (SC = 0.153), and mean forb cover (SC = 0.143; $R^2 = 0.368$, $P \leq 0.001$) were the vegetation attributes that best explained neotropical migrant guild abundance.

Vegetation attributes that best predicted species richness within the wetland guild were mean stem density 0–30 cm (SC = 0.631), maximum stem density at 60–90 cm (SC = −0.330), mean bare ground cover (SC = 0.282), mean

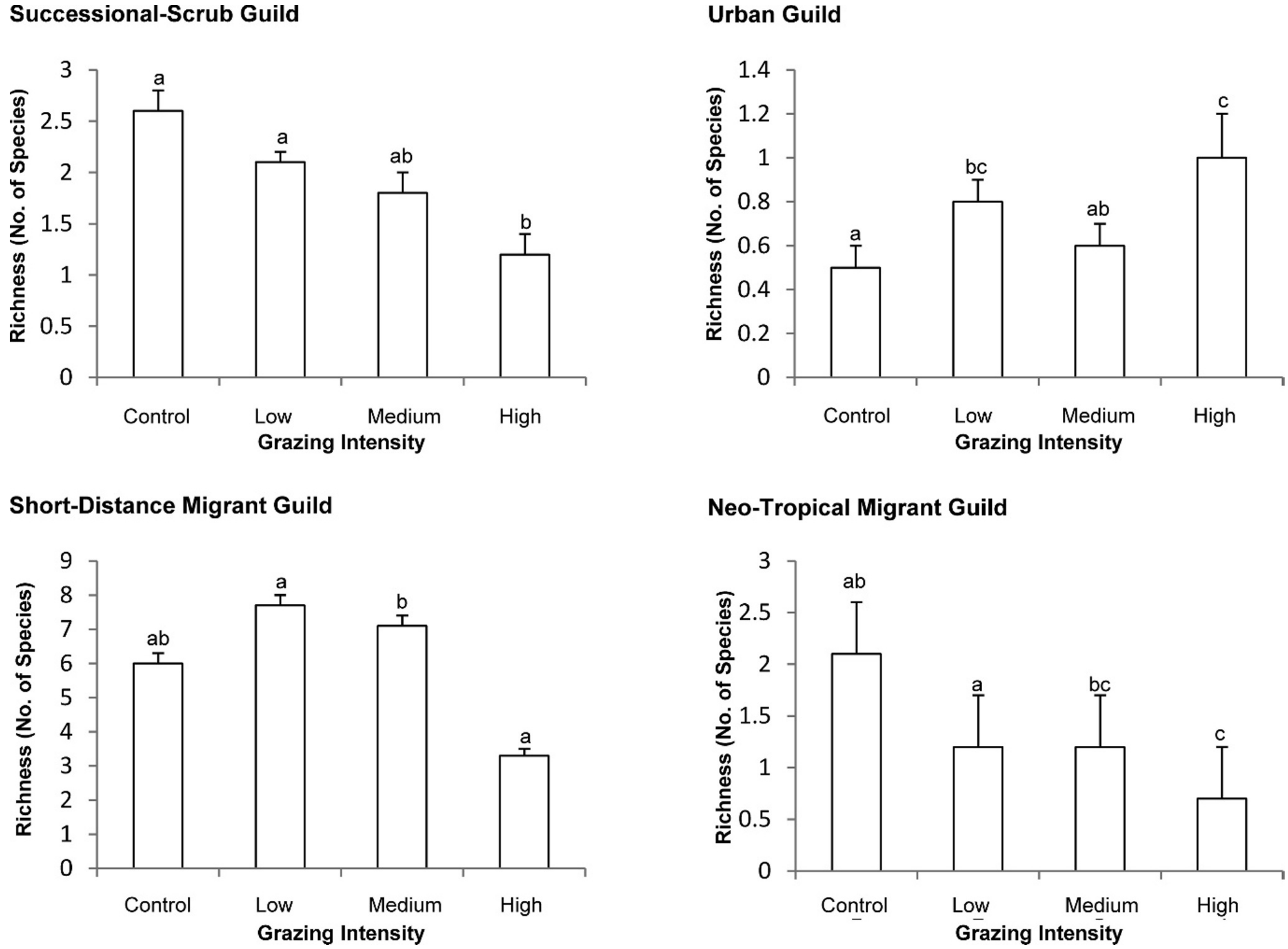

Figure 6. Effects of grazing intensity on avian species richness by guild in mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 2.1 ha · animal unit (AU)$^{-1}$, medium = 1.6 ha · AU^{-1}, and high = 0.9 ha · AU^{-1}.

litter cover (SC = −0.201), maximum stem density at 0–30 cm (SC = −0.197), and mean stem density at 90–120 cm (SC = 0.166; $R^2 = 0.358$, $P \leq 0.001$). The combined effects of variance of stem density at 0–30 cm (SC = 0.641), maximum stem density at 0–30 cm (SC = −0.558), mean vegetation height (SC = −0.558), mean litter depth (SC = 0.476), mean stem density at 0–30 cm (SC = 0.329), mean litter cover (SC = −0.327), and variance of grass cover (SC = 0.166; $R^2 = 0.359$, $P \leq 0.001$) best predicted grassland guild species richness. Variance of litter depth (SC = 0.354), variance of vegetation height (SC = 0.333), maximum litter cover (SC = −0.218), and mean forb cover (SC = 0.175; $R^2 = 0.308$, $P \leq 0.001$) were the vegetation attributes that best explained succesional-scrub guild species richness. Vegetation attributes that best predicted short distance migrant guild species richness were mean litter depth (SC = 0.422), variance of stem density at 0–30 cm (SC = 0.404), mean vegetation height (SC = −0.366), mean litter cover (SC = −0.334), maximum forb cover (SC = 0.278), and maximum vegetation height (−0.268; $R^2 = 0.326$, $P \leq 0.001$). Mean vegetation height (SC = 0.458), maximum litter depth (SC = 0.185), and mean forb cover (SC = 0.138; $R^2 = 0.324$, $P \leq 0.001$) were the vegetation attributes that best explained neotropical migrant guild species richness.

Mixed Pasture. Vegetation attributes that best explained successional-scrub guild abundance were maximum stem density at 90–120 cm (SC = 0.413), mean grass cover (SC = −0.403), variance of litter depth (SC = 0.373), mean litter cover (SC = −0.365), variance of grass cover (SC = −0.223), and maximum grass cover (SC = 0.118; $R^2 = 0.452$, $P \leq 0.001$). Vegetation attributes that best predicted neotropical migrant guild abundance were maximum litter depth (SC = 0.385), variance of vegetation density at 60–90 cm, mean litter cover (SC = −0.275), variance of forb cover (SC = 0.102), and maximum grass cover (SC = 0.097; $R^2 = 0.475$, $P \leq 0.001$). Neotropical migrant guild species richness was best explained by maximum litter depth (SC = 0.320), maximum stem density at 90–120 cm (SC = 0.301), variance of grass cover (SC = 0.196), and maximum litter cover (SC = −0.149; $R^2 = 0.306$, $P \leq 0.001$).

DISCUSSION

Vegetation

Monoculture Pasture. The only vegetation attribute that increased as grazing intensity increased on monoculture pasture was mean grass cover. The dominant grass in monoculture pastures was the improved species bahiagrass. Persistence of monoculture pastures and improved grasses, when subject to grazing, is a crucial factor in their sustainability. Bahiagrass is capable of forming a highly persistent sward that tolerates severe defoliation (Beaty et al. 1977; Stanley et al. 1977; Hirata 1993, 2000; Hirata and Pakiding 2001) and, when grown in regions with warm summers and cool winters, often shows large seasonal variations in herbage mass under grazing (Pakiding and Hirata 2002).

Eighteen of the other vegetation attributes examined exhibited some degree of decline in the presence of grazing. A decrease in the variance of a considerable number of vegetation attributes in the presence of grazing suggests a loss of spatial heterogeneity. Grazing can result in decreased spatial heterogeneity through reductions in plant biomass and cover and changes in structural conditions (e.g., plant density and height and litter cover and depth; Vallentine 1990; Milchunas and Lauenroth 1993; Fuhlendorf and Engle 2001; Derner et al. 2009).

Current grazing practices often neglect to recognize the importance of maintaining spatial heterogeneity in plant structure and composition to biodiversity conservation. Livestock have typically been managed for uniform use of vegetation or "management to the middle" with extremes in vegetations structure (e.g., low-sparse and high-dense) absent (Derner et al. 2009). However, if used appropriately, grazing offers a potentially important tool for conservation management because of its influence on habitat structure and composition (Collins et al 1998; Adler et al. 2001). It has recently been proposed that livestock have the potential to be used as ecosystem engineers, altering the heterogeneity of vegetation (Derner et al. 2009). Herbivores naturally exhibit preference for the consumption of certain plants over others (Van Soest 1996). If stocking rates are appropriate and pastures of a sufficient size, this results in differential patterns of use of individual plant species across a pasture (Launchbaugh and Howery 2005). Typically, declines in heterogeneity are observed only at very low or very high intensities of grazing as, respectively, livestock remove almost none or all of the vegetation. At medium grazing intensity, heterogeneity is maintained or increased as livestock selectively alter and remove a greater proportion of the vegetation in certain areas compared to others (Ausden 2007; Derner et al. 2009). We did not observe such a trend on monoculture pasture during this study, and further investigation is needed to understand grazing intensity, pasture sizes, and other livestock management activities that might permit maintenance of spatial heterogeneity in vegetation structure and composition on monoculture pastures in Florida. Possible methods proposed for enhancing spatial heterogeneity at the pasture scale include the strategic placement of supplemental feed, implementation of patch burns, and manipulation of water sources to alter vegetation structure in certain locations across the pasture area (Derner et al. 2009).

Mixed Pasture. Far fewer vegetation attributes were affected by grazing on mixed than monoculture pastures and then often only at low or high grazing intensities. Only three vegetation attributes (mean grass cover, mean litter depth, and mean vegetation height) exhibited decreases based on grazing intensity alone on this pasture type. Mean and variance of forb cover increased at low grazing intensities. Other studies have shown that moderate livestock grazing can result in increased forb cover, abundance, and species richness. These changes, as in this study, are often concomitant with decreases in vegetation height and litter depth (Talbot et al. 1939; Fensham et al. 1991; McNaughton 1993; Hayes and Holl 2003).

No vegetation attributes exhibited a decline in variance on mixed pasture as a result of grazing, suggesting that spatial heterogeneity of plant structure and composition may have been better maintained than on monoculture pastures. Grazing of native pasture systems tends to reduce their heterogeneity by favoring the most productive and palatable forage species for domestic cattle (Fuhlendorf and Engle 2001). On mixed pasture, such changes may have been observed at higher grazing intensities and over a longer time period. However, they may not have occurred during the relatively short duration of this study as a result of interannual and seasonal fluctuations in vegetation composition and quality and spatial and temporal patterns in diet selection observed in more complex vegetation (Ash and Smith 1996). Certainly, many of the native bunch grasses present on mixed pasture, such as broomsedge bluestem, chalky bluestem (*Andropogon cappilipes*), and little bluestem (*Schizachyrium scoparium* [Michx.] Nash var. *stoloniferum* [Nash] Wipff), can grow to considerable heights compared to bahiagrass. During the winter, when this pasture type was grazed, these grasses become largely dormant, leaving dry, rank vegetation aboveground. This vegetation is largely unpalatable to and not grazed by livestock. These taller grasses, in combination with shrubs and lower-growing and newly sprouting grasses and forbs, may help maintain structural variability in this habitat (E. V. Willcox, personal observation, February 2008).

Avian Abundance and Species Richness

Monoculture Pasture. Although grazing had no impact on total avian abundance on monoculture pastures, total species richness decreased as grazing intensity increased. Heavy grazing can reduce overall species richness in grassland ecosystems (Kantrud 1981; Kantrud and Kologiski 1982) as spatial heterogeneity in the plant community is reduced (Derner et al. 2009). Reductions in spatial heterogeneity caused by grazing imply the loss of habitat diversity (Adler et al. 2001) and can influence the suitability and availability of food and cover resources for a variety of avian species (Saab et al. 1995; Brennan and Kuvalesky 2005; Coppedge et al. 2008; Derner et al. 2009). It has been proposed that declines in grassland birds may, in part, be associated with grazing-driven reductions in vegetation heterogeneity that minimize the heavily disturbed and undisturbed plant communities that different species require (Brennan and Kuvlesky 2005). Despite declines in species richness, total avian abundance is often little affected. Although some species are negatively affected by grazing, others respond positively (Saab et al. 1995). Species adapted to the grazed conditions become highly abundant, resulting in little change in the total number of birds present (Kantrud and Kologiski 1982).

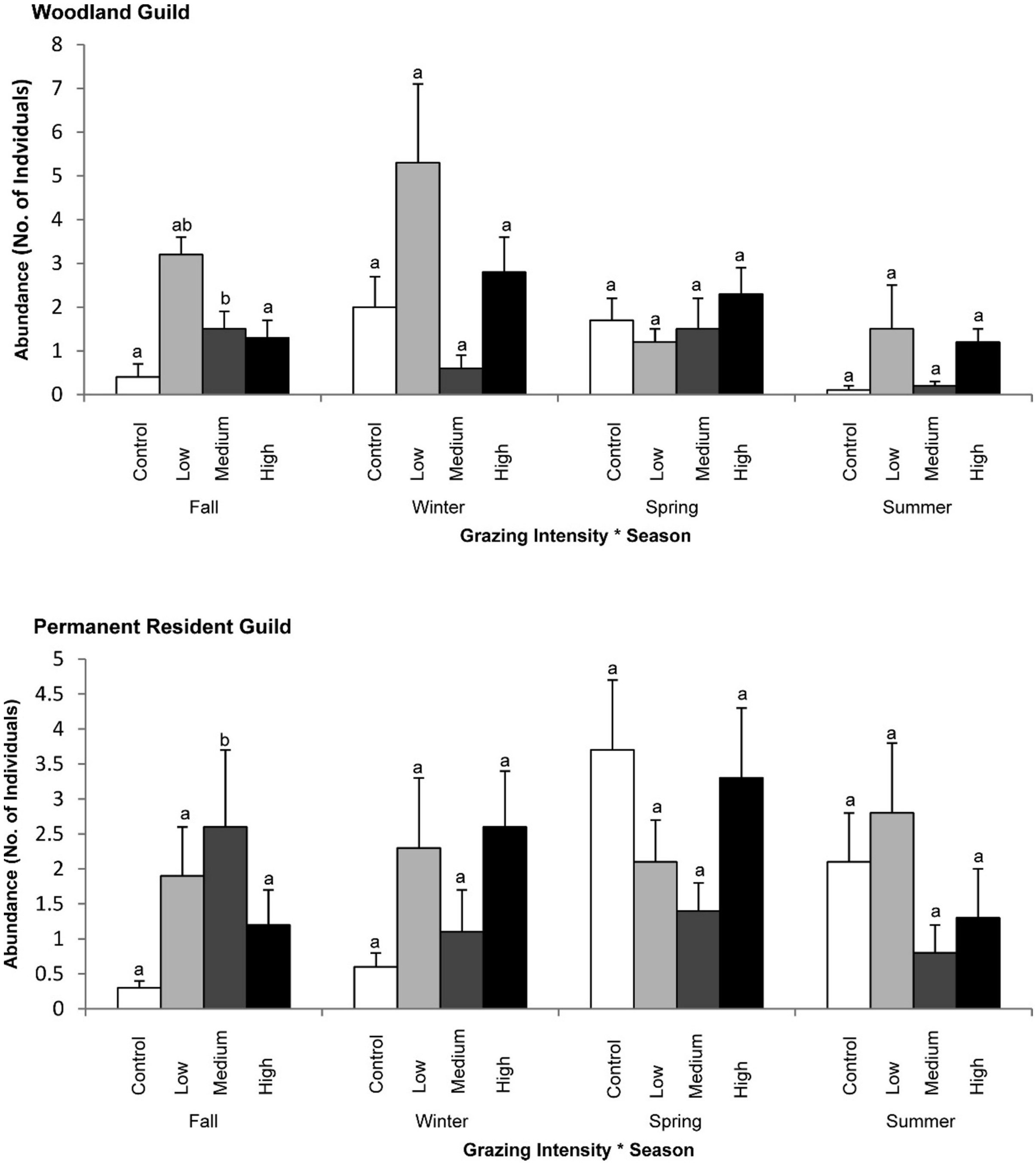

Figure 7. Effects of a grazing intensity × season interaction on total avian species richness and avian abundance and species richness by guild in mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 2.1 ha · animal unit $(AU)^{-1}$, medium = 1.6 ha · AU^{-1}, and high = 0.9 ha · AU^{-1}.

On monoculture pastures, grazing proved detrimental to many of the avian guilds examined, negatively affecting species richness and abundance. Most notably affected were short-distance migrant, neotropical migrant, and permanent resident guilds, all of which exhibited a decrease in species richness with increasing grazing intensity. In addition, these guilds also exhibited decreases in abundance as grazing intensity increased. ''Management to the middle'' places emphasis on the homogeneous use of vegetation by grazers. The results of this study indicated grazing of monoculture pasture led to a trend of decreasing heterogeneity for a variety of habitat attributes. Loss of heterogeneity typically results in a lack of suitable habitat for birds that occupy the extremes of the vegetation structure gradient (e.g., low-sparse and high-dense vegetation), many of which are in these guilds (Kantrud and Kologiski 1982; Bollinger and Gavin 1992; Wilkins and Swank 1992; Saab et al. 1995; Guzy and Ritchison 1999; Derner et al. 2009). This results in loss of species richness and, if remaining guild members do not increase in number, decreases in abundance. The use of livestock as ecosystem engineers at the pasture scale

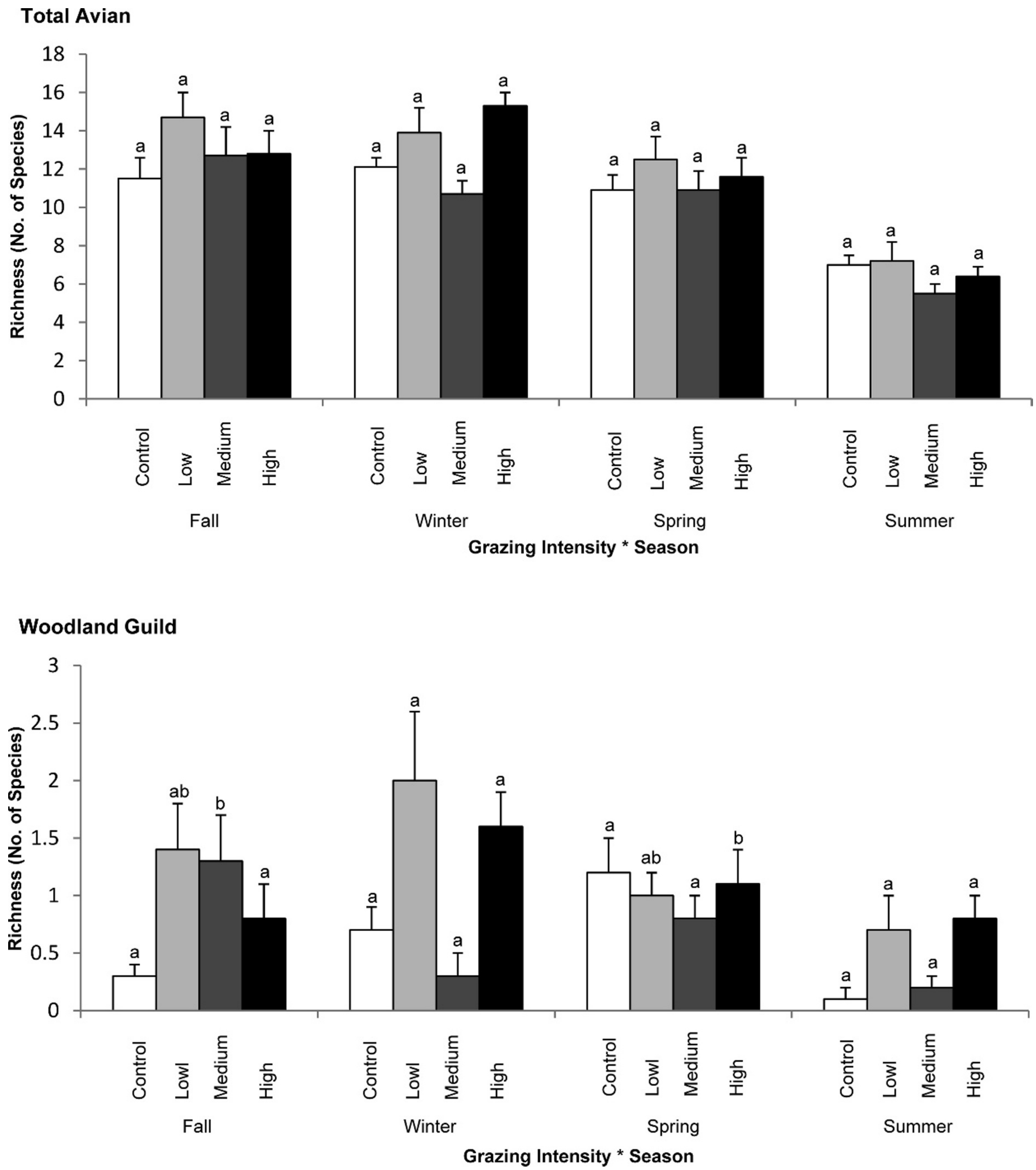

Figure 7. Continued.

has the potential to alter and maintain vegetation structure, particularly at the extremes of the structure gradient. Grazing management of this type would permit the creation and maintenance of a variety of habitat types and bird species (Derner et al. 2009).

Wetland guild abundance increased with increasing grazing intensity. At high grazing intensity, abundance within this guild was higher than in control pastures. Studies have shown that waterfowl are tolerant of light to medium grazing, although optimal habitat conditions probably occur in the absence of grazing (Kirsch 1969; Kruse and Bowen 1996). On monoculture pasture, the successional scrub guild did not exhibit declines in abundance until 3–4 yr and the woodland guild until 2 yr after the introduction of grazing. This suggests that the birds within these guilds were sensitive to the vegetation effects and decreased heterogeneity of monoculture pasture habitats only after prolonged, high-intensity grazing. High adult breeding-site fidelity is typical for many migratory birds. These species will often return yearly to the same areas to nest despite declining habitat conditions. After failing to reproduce successfully for a number of years, they may make the decision to move to new breeding habitats (Haas 1998; Hoover 2003) or

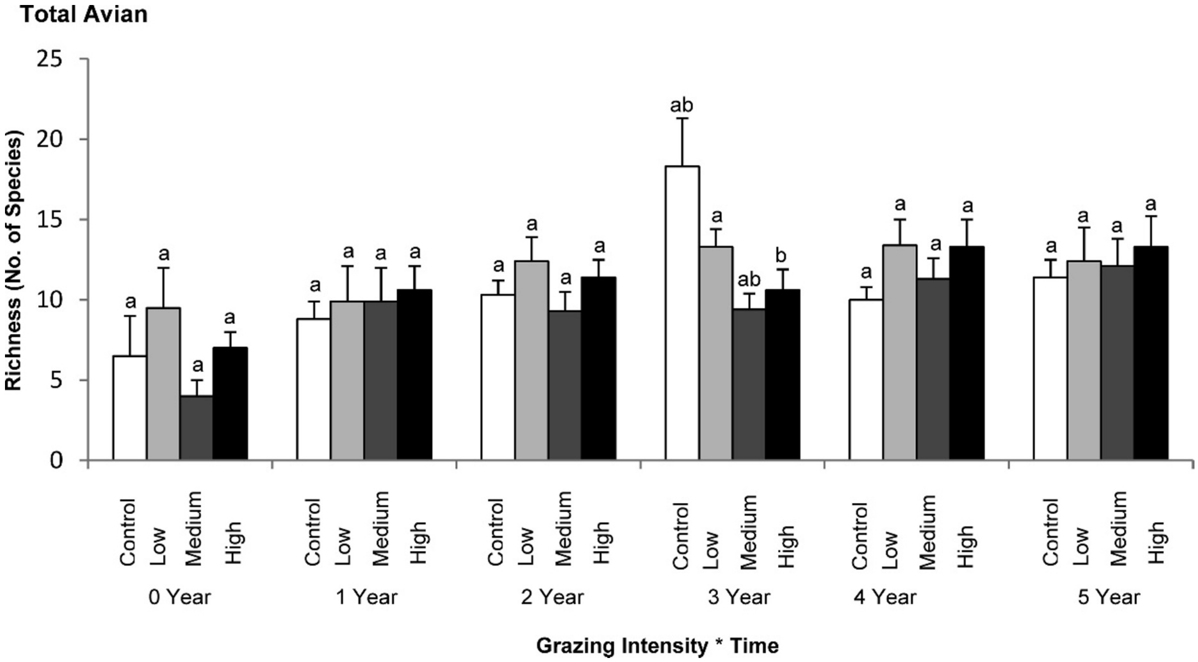

Figure 8. Effects of a grazing intensity × time interaction on total avian species richness in mixed pastures at MacArthur Agro-Ecology Research Station, Highlands County, Florida, 1999–2003. Bars represent $\bar{x} \pm 1$ SE. Bars topped by different letters are significantly different ($P \leq 0.1$). Grazing intensities: control = nongrazed, low = 2.1 ha · animal unit (AU)$^{-1}$, medium = 1.6 ha · AU^{-1}, and high = 0.9 ha · AU^{-1}.

die, resulting in declines in avian abundance (Greenwood 1980; Greenwood and Harvey 1982; Beheler et al. 2003; Ortega et al. 2006). However, it should be noted that pasture management strives to reduce woody plant dominance, so declines in shrub-associated species are to be expected.

Attributes that were most often identified as positively related to avian abundance and richness within guilds on monoculture pasture were mean vegetation height and cover of forbs and variance of litter depth and stem density 0–30 cm aboveground. All these attributes exhibited declines of some degree in the presence of grazing, with some declines being seasonal and others affected by time since introduction of grazing. All these attributes may be important to a variety of bird species because of their role in providing food and cover resources. Cover of forbs, litter, and bare ground are likely to affect seed and invertebrate food availability. Vegetation height and stem density may influence the type and availability of cover present (Saab et al. 1995).

Mixed Pasture. Total avian abundance decreased at medium and high grazing intensities, but total species richness was not affected until 3 yr after introduction of grazing, at which point declines were observed at high grazing intensity. Grazing of mixed pastures had a detrimental effect on species richness and abundance within some avian guilds. However, in this pasture type, the number of guilds negatively affected by grazing was fewer than in monoculture pastures. In addition, in mixed pastures, we observed negative impacts on species richness and abundance only at high grazing intensity, compared to monoculture pastures where detrimental effects were frequently observed at low and medium grazing intensities. Species richness and abundance within successional-scrub and neotropical migrant guilds decreased only at high grazing intensity. Few vegetation attributes on mixed pasture were affected by grazing and typically only at high grazing intensity. Short-distance migrant and urban guild species richness increased over that of control pastures at medium and high grazing intensities, respectively. Grassland guild abundance increased at low and medium grazing intensities. Members of the grassland guild are of particular concern because of recent population declines (Brennan and Kuvalesky 2005). It has been suggested that their decline may be associated with grazing-driven reductions in vegetation heterogeneity and the suitability and availability of food and cover resources (Saab et al. 1995; Brennan and Kuvalesky 2005; Coppedge et al. 2008; Derner et al. 2009). However, spatial heterogeneity in plant structure and composition was largely maintained on mixed pastures throughout the study. This likely resulted in a diversity of food and cover resources that helped maintain and increase avian abundance within the grassland guild and species richness within the short-distance migrant and urban guilds (Saab et al. 1995; Coppedge et al. 2008; Derner et al. 2009). This study suggests that, on mixed pastures, management and conservation of species within the grassland guild may be compatible with low to medium grazing intensities and that livestock have the potential to serve as ecosystem engineers for members of this and other guilds (Derner et al. 2009).

Attributes that were most often identified as positively related to avian abundance and richness on mixed pasture were mean and maximum grass cover and maximum litter depth and vegetation density 90–120 cm aboveground. Mean grass cover was the only one of these attributes to decrease in the presence of grazing and may be important to birds as a food and cover resource. Within many guilds, abundance declined as maximum litter depth increased. Therefore, methods that reduce litter present on the ground may benefit many species.

IMPLICATIONS

On monoculture and mixed pasture, increasing grazing intensity resulted in changes in a variety of vegetation attributes. There was a trend toward increasing homogeneity of plant structure and composition as grazing intensity increased, particularly on monoculture pasture, and, depending on guild, this resulted in increases or decreases in abundance and richness within particular avian guilds. If the management and conservation of certain avian guilds is a priority, grazing intensity should be tailored to fit their needs. On monoculture and mixed pasture, the minimization of grazing intensity would be advantageous and likely result in increased abundance and species richness of many guilds. Based on the results of this study, a grazing intensity of 1.3 ha $\cdot$ AU^{-1} and 2.1 ha $\cdot$ AU^{-1} on monoculture and mixed pasture, respectively, is recommended. However, some decline in species richness may still be expected. Ultimately, if habitat diversity is to be maximized and a range of avian species supported on monoculture and mixed pastures, the goal should be to maintain spatial heterogeneity in plant structure and composition, potentially using livestock as ecosystem engineers.

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