Effects of fire management on the richness and abundance of central North American grassland land snail faunas

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Abstract

Effects of fire management on the richness and abundance of central North American grassland land snail faunas.— The land snail faunas from 72 upland and lowland grassland sites from central North America were analyzed. Sixteen of these had been exposed to fire management within the last 15 years, while the remainder had not. A total of 91,074 individuals in 72 different species were observed. Richness was reduced by approximately 30% on burned sites, while abundance was reduced by 50–90%. One–way ANOVA of all sites (using management type as the independent variable), a full 2–way ANOVA (using management and grassland type) of all sites, and a 2–way ANOVA limited to 26 sites paired according to their habitat type and geographic location, demonstrated in all cases a highly significant (up to $p < 0.0005$) reduction in richness and abundance on fire managed sites. Contingency table analysis of individual species demonstrated that 44% experienced a significant reduction in abundance on fire-managed sites. Only six species positively responded to fire. Comparisons of fire response to the general ecological preferences of these species demonstrated that fully 72% of turf–specialists were negatively impacted by fire, while 67% of duff–specialists demonstrated no significant response. These differences were highly significant ($p = 0.0006$). Thus, frequent use of fire management represents a significant threat to the health and diversity of North American grassland land snail communities. Protecting this fauna will require the preservation of site organic litter layers, which will require the increase of fire return intervals to 15+ years in conjunction with use of more diversified methods to remove woody and invasive plants.

Key words: Land snail, Biodiversity, Conservation, Fire management, Grassland, North America.

Resumen

Efectos de la gestión con fuego sobre la riqueza y abundancia de la fauna de caracoles terrestres de las praderas de América del Norte.— Se analiza la fauna de caracoles terrestres de 72 praderas en mesetas y llanuras de la región central de América del Norte. En 16 de ellas se habían efectuado intervenciones de incendio controlado durante los últimos 15 años, mientras en el resto no. Se observaron un total de 91.074 individuos de 72 especies diferentes. La riqueza en especies estaba reducida en un 30% en las áreas quemadas, mientras que la abundancia de individuos estaba reducida en un 50–90%. Un ANOVA unidireccional de todas las áreas (usando como variable independiente el tipo de intervención), un ANOVA bidireccional completo (usando el tipo de intervención y el tipo de pradera) en todas las áreas y un ANOVA bidireccional limitado a 26 áreas agrupadas según su tipo de hábitat y localización geográfica, demostró en todos los casos una reducción altamente significativa de la riqueza y de la abundancia (hasta $p < 0,0005$) en áreas sometidas a incendio. Un análisis individual de las especies mediante tablas de contingencia demostró que el 44% experimentaron una reducción significativa de su abundancia en las áreas quemadas. Sólo seis especies respondieron positivamente al fuego. Comparando la respuesta al fuego con las preferencias ecológicas generales de estas especies se demostró que al menos el 72% de las especialistas que viven en sustrato herbáceo fueron afectadas negativamente por el fuego mientras que el 67% de las que viven en sustrato húmico no demostraron ninguna respuesta significativa. Estas diferencias fueron altamente significativas ($p = 0,0006$). Así pues, el uso frecuente del fuego representa una amenaza significativa para la salud y diversidad de las comunidades de caracoles terrestres de las praderas de América del Norte. La protección de esta fauna requerirá la preservación de las capas de materia orgánica y la ampliación de los intervalos entre las actuaciones de quema a periodos superiores a 15 años, así como el uso de métodos más diversos para eliminar las plantas leñosas e invasivas.

Palabras clave: Caracol terrestre, Biodiversidad, Conservación, Gestión con fuego, Praderas, América del Norte.

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Introduction

Fire has long been implicated in the maintenance of central North American grassland communities (WEAVER, 1954; CURTIS, 1959). Numerous native plant species respond to fire by increasing their growth and reproductive rates (EHRENREICH & AIKMAN, 1963; KUCERA & KOELLING, 1964; TOWNE & OWENSBY, 1984). One of the most direct effects of prairie fire is the removal of the soil mulch layer, which has been implicated in the 'stagnation' of prairie plant communities through the delay of initial spring growth, thinning of grass stem density, and prevention of herbaceous understory development (WEAVER & ROWLAND, 1952; KUCERA & KOELLING, 1964). Fire is also thought to limit invasion of woody and exotic plants into native prairie habitats (e.g., PAULY, 1985; ROOSA, 1984). For these reasons, prescribed fire has become the management tool of choice by prairie conservation groups throughout the midwestern USA (COLLINS & WALLACE, 1990).

However, an increasing body of research suggests that fire is not universally beneficial all prairie biota. Fire depresses growth and reproductive rates of native C_3 prairie plants (DIX, 1960; HADLEY, 1970; HILL & PLATT, 1975), which make up at least 50% of the native flora north of 44° N (STOWE & TEERI, 1978; SIMS, 1988). Fire has also been implicated in the loss and/or reduction of numerous native prairie invertebrate species including Lepidoptera, Homoptera, Hymenoptera, and Araneae (SWENGEL, 1996, 1998; HARPER et al., 2000). The effects of such practices on prairie soil biodiversity are largely undocumented. Combustion of mulch through repeated fire episodes will remove the detritusphere, one of the most important reservoirs for soil biodiversity (COLEMAN & CROSSLEY, 1996). HARPER et al. (2000) documented significant reductions in Collembola following Illinois prairie fires. As the soil fauna represents one of the largest species pools in terrestrial ecosystems (BEHAN–PELLETIER & NEWTON, 1999), the potential impacts of such processes on total site biodiversity may be large.

Although not as hyper–diverse as bacteria, fungi, nematodes, and arthropods, molluscs still represent one of the more important components of soil biodiversity (RUSSELL–HUNTER, 1983). Almost 600 species are known from eastern North America (HUBRICHT, 1985), with up to 21 taxa co-occurring within 400 cm^2 microhabitats (NEKOLA & SMITH, 1999). Most of these taxa represent generalist detritivores that live in and on dead organic material (BURCH & PEARCE, 1990)

As almost 90% of snails occur within 5 cm of the soil surface (HAWKINS et al., 1998), protection of this fauna will likely be tied to the fate of mulch layers. Disturbances such as logging, recreational or urban development, or bedrock and soil removal cause dramatic changes in woodland snail communities with duff soil surfaces (NEKOLA, in press a). The impact of fire, and associated detritusphere removal, on snail communities is unclear. Fire has been suggested to negatively influence the faunas of Aegean islands (WELTER–SCHULTES & WILLIAMS, 1999), Queensland fens (STANISIC 1996), and Tasmanian woodlands (REGAN et al., 2001). However, FREST & JOHANNES (1995) state that molluscs are able to survive natural fires in northwestern North America, and THELER (1997) argued that xeric prairie faunas in Wisconsin owe their existence to frequent fires that keep grassland areas treeless. Unfortunately, no data was presented by these various authors to validate such conflicting statements.

To evaluate this issue, the richness and abundance of land snails was quantitatively compared between unburned and recently (< 15 year) burned sites in the midwestern USA, including 13 pairs of sites which possess similar habitats and are spatiall proximate. From these, the following questions will be considered: 1. Is there a significant difference in land snail community richness between burned and unburned grasslands? 2. Is there a significant difference in land snail abundance between burned and unburned grasslands? 3. What species show positive, negative, or no response to fire? What ecological factors (if any) may help explain these responses?

Materials and methods

Study Sites

Seventy two grassland sites were surveyed between May 1996–November 2001 for terrestrial molluscs across a 850 km extent of central North America (fig. 1, table 1). Sites are generally centered on northwestern Minnesota and northeastern Iowa. Forty–two occur in Minnesota, 25 in Iowa, and 5 in Wisconsin. Thirty–two sites represent upland habitats (including tallgrass prairie, sand prairie, and bedrock glades), while the remaining 40 are lowland sites (including wet prairie, sedge meadow, and fens). Previous use of fire management on sites was assessed by either observing carbonized woody plant stems or other debris on the ground surface, or through interviews with site managers or other knowledgeable individuals. No use of fire management was noted from 56 sites (88% of total), while 16 (22%) had been subjected to some amount of prescribed burning. Eleven of these burned sites occur in Minnesota, while the remaining five occur in Iowa. The latitude–longitude location of each site was determined using either USGS 7.5 minute topographic maps or a hand–held GPS.

Field Methods

Documentation of terrestrial gastropod faunas from each site was accomplished by hand collection of larger shells and litter sampling for smaller taxa within 100–1,000 m^2 areas that contained examples of all major microhabitats and were thus representative of the larger site. The actual grain size employed was determined by the minimum size necessary to emcompass all microhabitats. Soil litter sampling was primary used as it provides the most complete assessment of grassland faunas (Oggier et al., 1998). A single site sample consisted of a composite of individual soil litter subsamples of approximately 200 ml collected from appropriate microhabitats. As suggested by Emberton et al. (1996), litter collections were made at places of high micromollusc density, with a constant volume (approximately 4 liters) being gathered from each site. Sampling was generally comprised of: 1. Small blocks (ca. 125 cm^3) of turf; 2. Loose soil and leaf litter accumulations under or adjacent to shrubs, cobbles, boulders, and/or hummocks; and 3. Other microsites supporting relatively thick mulch layers.

Laboratory procedures

Samples were slowly and completely dried in either a low–temperature soil oven (ca. 80–95°C) or in full sun in a greenhouse. Dried samples were then soaked in water for 3–24 hours, and subjected to careful but vigorous water disaggregation through a standard sieve series (ASTME 3/8" (9.5 mm), #10 (2.0 mm), #20 (0.85), and #40 (0.425 mm) mesh screens). Sieved sample fractions were then dried and passed again through the same sieve series. These dry, resorted fractions were hand picked against a neutral-brown background. All shells and shell fragments were removed.

All identifiable shells from each site were assigned to species (or subspecies) using the author's reference collection and the Hubricht Collection at the Field Museum of Natural History (FMNH), with the total number of shells per species per site being recorded. The total number of unassignable, immature individuals was also counted from each site. All specimens have been catalogued and are housed in the author's collection at the University of Wisconsin–Green Bay. Nomenclature generally follows that of Hubricht (1985), with updates and corrections by Frest (1990, 1991) and Nekola (in press b). The general ecological preferences (turf specialist, duff–specialist or generalist) of each species is based upon analyses presented in Nekola (in press a).

Statistical procedures

Differences in species richness and total shell abundance between burned and unburned grassland sites were analyzed via ANOVA. Initially, 1–way ANOVAs were preformed on the entire dataset. However, the effect of fire may be obscured in this analysis due to confounding effects of habitat type and geographic location. To help control for this, two additional sets of ANOVAs were conducted. First, full 2–way ANOVAs were calculated for all sites using grassland type (upland vs. lowland) and management history (burned vs. unburned) as the independent variables. Second, 13 pairs of sites representing closely similar habitats within the same geographic region, but differing in their fire management history, were selected. These site pairs are (first site is burned, second is unburned): Malmberg Prairie vs. Sandpiper Prairie; Pankratz Mesic Prairie vs. Radium NE; Pankratz Low Prairie vs. Bjornson WMA; Pankratz Fen vs. Faith South; Marcoux WMA vs. Cyr Creek; East Park WMA vs. Goose Lake; Felton Fen 1 vs. Ogema West; Waubun SE vs. Eastlund Lake; Chicog vs. Tansen; Beemis Creek vs. Hampton East; Fayette vs. Decorah Glade; Baty Glade vs. Canton Glade; Brayton–Horsley vs. Stapleton Church. A 2–way ANOVA without interaction was then calculated for these sites, with site pair identity and management type representing independent variables.

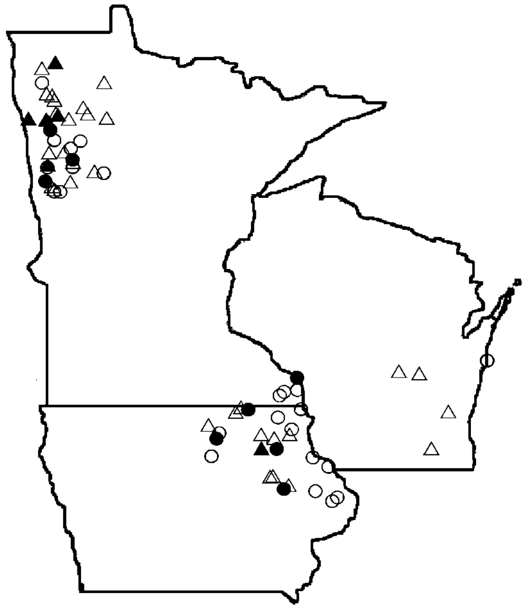


Fig. 1. Map of study region, showing location of surveyed grassland sites: ○ Unburned upland; ● Burned upland; △ Unburned lowland; ▲ Burned lowland.

Fig. 1. Mapa del área de estudio que muestra la localización de las praderas estudiadas: ○ Meseta no quemada; ● Meseta quemada; △ Llanura no quemada; ▲ Llanura quemada.

Table 1. Location, grassland type, management, species richness and total number of collected individuals from sample sites: GT. Grassland type; M. Management; R. Richness; I. Individuals.

Tabla 1. Localización, tipo de pradera, gestión, riqueza de especies y número total de individuos recogidos en cada área de estudio: GT. Tipo de pradera; M. Gestión; R. Riqueza; I. Individuos.

State / County / Site Name	Location	GT	M	R	I
Iowa					
Allamakee County					
Fish Farm Mounds	91°17'12" W – 43°27'13" N	Upland	Unburned	21	632
Williams Creek 3	91°29'1" W – 43°8'1" N	Upland	Unburned	23	2,708
Bremer County					
Brayton–Horsley Fen	92°6'29" W – 42°48'36" N	Lowland	Burned	16	627
Buchanan County					
Rowley Fen	91°51'7" W – 42°22'27" N	Lowland	Unburned	16	3,217
Rowley North Fen	91°51'3" W – 42°22'35" N	Lowland	Unburned	17	3,231
Rowley West Fen	91°54'40" W – 42°22'15" N	Lowland	Unburned	22	2,250
Cerro Gordo County					
Buffalo Slough	93°11'11" W – 43°10'36" N	Lowland	Unburned	19	4,770
Chickasaw County					
Stapelton Church Fen	92°6'14" W – 43°1'35" N	Lowland	Unburned	18	1,065
Clayton County					
Postville Fen	91°33'59" W – 43°2'3" N	Lowland	Unburned	12	252
Turkey River Mounds	91°2'11" W – 42°42'46" N	Upland	Unburned	22	870
Clinton County					
Maquoketa South	90°39'5" W – 42°1'12" N	Upland	Unburned	12	310
Dubuque County					
Roosevelt Road	90°44'30" W – 42°32'55" N	Upland	Unburned	18	375
Fayette County					
Fayette	91°47'28" W – 42°50'11" N	Upland	Burned	13	254
Turner Creek 1 Fen	91°52'11" W – 42°58'15" N	Lowland	Unburned	16	1,071
Floyd County					
Beemis Creek	93°1'18" W – 42°59'39" N	Upland	Burned	8	192
Juniper Hill	92°59'2" W – 43°3'10" N	Upland	Unburned	12	206
Franklin County					
Hampton East	93°8'13" W – 42°43'42" N	Upland	Unburned	15	381
Howard County					
Hayden Prairie	92°23'4" W – 43°26'30" N	Upland	Burned	12	132
Staff Creek Fen	92°30'34" W – 43°26'41" N	Lowland	Unburned	15	1,599
Jackson County					
Hamilton Glade	90°34'9" W – 42°4'23" N	Upland	Unburned	15	340
Jones County					
Canton Glade	90°59'52" W – 42°10'46" N	Upland	Unburned	19	446
Linn County					
Baty Glade	91°39'14" W – 42°11'44" N	Upland	Burned	16	345
Paris Fen	91°35'42" W – 42°13'40" N	Lowland	Unburned	12	1,254

Table 1. (Cont.)

State / County / Site Name	Location	GT	M	R	I
Mitchell County					
Stone School Fen	92°38'11" W – 43°22'49" N	Lowland	Unburned	18	2,926
Winneshiek County					
Decorah Glade	91°46'11" W – 43°18'55" N	Upland	Unburned	18	605
Minnesota					
Becker County					
Audubon South Fen	95°58'47" W – 46°49'58" N	Lowland	Unburned	15	1,816
Callaway North	95°55'22" W – 47°3'57" N	Upland	Unburned	19	362
Greenwater Lake Fen	95°29'59" W – 46°59'20" N	Lowland	Unburned	20	2,132
Ogema West Fen	95°55'59" W – 47°6'32" N	Lowland	Unburned	16	5,001
Straight Lake	95°18'40" W – 46°58'40" N	Upland	Unburned	13	281
Beltrami County					
Fourtown Fen	95°18'21" W – 48°15'56" N	Lowland	Unburned	14	1,403
Clay County					
Barnesville WMA	96°17'34" W –46°43'5" N	Upland	Unburned	11	469
Barnesville WMA Fen	96°17'38" W – 46°43'9" N	Lowland	Unburned	13	436
Bjornson WMA	96°21'24" W – 46°45'44" N	Lowland	Unburned	14	436
Bluestem Prairie	96°28'45" W – 46°51'18" N	Upland	Burned	15	371
Felton Prairie 1 Fen	96°26'21" W – 47°3'51" N	Lowland	Burned	15	2,370
Felton Prairie 2 Fen	96°26'20" W – 47°4'0" N	Lowland	Unburned	14	3,131
Felton Prairie	96°26'1" W – 47°3'34" N	Upland	Unburned	5	63
Tansen	96°11'17" W – 46°42'14" N	Upland	Unburned	10	146
Clearwater County					
Bagley Lake Fen	95°14'35" W – 47°45'41" N	Lowland	Unburned	9	126
Filmore County					
Vesta Creek	91°45'0" W – 43°40'5" N	Upland	Unburned	21	1,151
Houston County					
Twin Pines Farm	91°22'45" W – 43°44'48" N	Upland	Unburned	24	591
Yucatan Twp.	91°38'28" W – 43°43'23" N	Upland	Unburned	20	765
Mahnomen County					
Eastlund Lake	95°47'5" W – 47°26'41" N	Upland	Unburned	13	490
Mahnomen North	95°58'8" W – 47°21'27" N	Upland	Unburned	18	806
Waubun SE	95°54'55" W – 47°9'57" N	Lowland	Unburned	18	2,915
Waubun SE	95°55'4" W – 47°10'5" N	Upland	Burned	8	220
Marshall County					
East Park WMA	96°16'44" W – 48°31'57" N	Lowland	Burned	14	735
Florian WMA	96°33'21" W – 48°26'33" N	Lowland	Unburned	17	3,923
Radium NE	96°32'38" W – 48°16'49" N	Upland	Unburned	12	493
Norman County					
Faith South	96°5'12" W – 47°15'42" N	Lowland	Unburned	16	3,047
Prairie Smoke Dunes	96°18'22" W – 47°27'44" N	Upland	Unburned	3	19
Sandpiper Prairie	96°24'22" W – 47°14'43" N	Lowland	Unburned	12	1,261

Table 1. (Cont.)

State / County / Site Name	Location	GT	M	R	I
Pennington County					
Goose Lake	96°27'44" W – 48°5'37" N	Lowland	Unburned	17	996
Higenbotham WMA	96°17'41" W – 48° 0'22" N	Lowland	Unburned	22	1,114
Sanders Fen	96°21'9" W – 48°3'52" N	Lowland	Unburned	15	2,218
Polk County					
Chicog Prairie	96°23'14" W – 47°35'53" N	Upland	Burned	2	153
Erskine North	96°0'3" W – 47°44'17" N	Lowland	Unburned	19	741
Gulley Fen	95°37'22" W – 47°48'13" N	Lowland	Unburned	19	2,032
Malmberg Prairie	96°49'25" W – 47°43'52" N	Lowland	Burned	7	563
Pankratz Prairie	96°26'37" W – 47°43'23" N	Lowland	Burned	12	314
Pankratz Prairie	96°26'31" W – 47°43'23" N	Upland	Burned	11	159
Pankratz Prairie	96°26'48" W – 47°43'9" N	Lowland	Burned	7	190
Red Lake County					
Crane WMA	95°42'49" W – 47°53'27" N	Lowland	Unburned	15	425
Cyr Creek	96°16'12" W – 47°48'10" N	Lowland	Unburned	22	1,845
Marcoux WMA	96°13'27" W – 47°47'55" N	Lowland	Burned	12	688
Winona County					
Great River Bluffs	91°23'28" W – 43°56'53" N	Upland	Burned	19	788
Wisconsin					
Green Lake County					
Berlin Fen	88°54'20" W – 43°57'47" N	Lowland	Unburned	20	3,454
Manitowoc County					
Point Beach St. Forest	87°30'40" W – 44°11'52" N	Upland	Unburned	4	6
Walworth County					
Bluff Creek Fen	88°40'54" W – 42°48'2" N	Lowland	Unburned	20	1,106
Washington County					
Allenton Fen	88°18'25" W – 43°22'42" N	Lowland	Unburned	20	2,858
Waushara County					
Bass Lake Fen	89°16'59" W – 44°0'16" N	Lowland	Unburned	19	1,466

The central tendencies in these various relationships were graphically represented via box plots. In box plots, the central line represents the median of the sample, the margins of the box represent the interquartile distances, and the fences represent 1.5 times the interquartile distances. For data having a Gaussian distribution, approximately 99.3% of the data will fall inside of the fences (Velleman & Hoaglin, 1981). Outliers falling outside of the fences are shown with asterisks.

The average number of individuals per species per site was determined for burned uplands, unburned uplands, burned lowlands, and unburned lowlands. The average proportion of each species in the total community for each site was calculated for each management/habitat type. These proportions were placed in rank order, and plotted vs. log–transformed frequency to create dominance–diversity curves (Whittaker, 1975).

The response of individual species to fire was analyzed through log–linear modelling, as predicted values in the associated contingency table were sparse (< 5) in more than one–fifth of cells (Zar, 1984). The total number of individuals within all burned or unburned sites was compared to a null expectation of equal occurrence

Table 2. List of encountered species, with their average abundances from burned and unburned sites. *P*–values are based on log-likelihood ratio tests, with the two–tailed significance threshold being lowered to $p = 0.000347$ to account for the 72 tested species. General ecological preferences are based on NEKOLA (in press a). Turf–specialists represent those species demonstrating at least a $p < 0.05$ preference to sites with a friable upper A soil horizon supporting few living plant roots. Turf specialists represent those species demonstrating at least a $p < 0.05$ preference to sites with an upper A soil horizon that is bound together with living plant roots. Species without preferences were too infrequently encountered by NEKOLA (in press a) to be statistically assigned: AvU. Average unburned; Abb. Abundance burned; Ecp. Ecological preference (T. Turf; D. Duff; G. Generalist.)

Tabla 2. Lista de especies detectadas, con sus abundancias medias en áreas quemadas y no quemadas. Los valores de P *se basan en tests de cociente de probabilidad logarítmica, con el umbral de significación de doble cola reducido hasta* $p = 0{,}000247$ *para las 72 especies estudiadas. Las preferencias ecológicas generales se basan en* NEKOLA *(in press a). Las especies que viven en sustrato herbáceo presentan una preferencia de al menos* $p < 0{,}05$ *por las zonas con horizonte de tierra friable superior A provisto de escasas raíces de plantas vivas. Las especies que viven en sustrato herbáceo presentan una preferencia de al menos* $p < 0{,}05$ *por las zonas cuyo horizonte se mantiene unido por raíces de plantas vivas. Las especies sin preferencias resultaron excesivamente infrecuentes según* NEKOLA *(in press a) para consignarlas estadísticamente: AvU. Medias en áreas no quemadas; Abb. Abundancia en áreas quemadas; Ecp. Preferencia ecológica (T. Sustrato herbáceo; D. Sustrato húmico; G. Generalista.)*

Species	AvU	Abb	*P*–value	Ecp
Negative responses				
Carychium exiguum (Say, 1822)	273.607	90.250	0.0000000	T
Carychium exile H. C. Lea, 1842	5.196	0.000	0.0000000	D
Catinella exile (Leonard, 1972)	58.446	1.625	0.0000000	T
Catinella "vermeta"	1.482	0.000	0.0000001	T
Deroceras laeve (Müller, 1774)	4.036	1.188	0.0000050	G
Discus cronkhitei (Newcomb, 1865)	16.143	5.000	0.0000000	G
Euconulus alderi (Gray, 1840)	43.054	8.375	0.0000000	T
Gastrocopta contracta (Say, 1822)	21.232	5.875	0.0000000	G
Gastrocopta holzingeri (Sterki, 1889)	36.196	17.938	0.0000000	D
Gastrocopta pentodon (Say, 1821)	9.661	4.875	0.0000072	D
Gastrocopta procera Gould, 1840	2.304	0.000	0.0000000	T
Gastrocopta rogersensis Nekola & Coles, 2001	5.518	0.062	0.0000000	T
Gastrocopta similis (Sterki, 1909)	21.518	4.125	0.0000000	T
Gastrocopta tappaniana (C. B. Adams, 1842)	112.929	33.375	0.0000000	T
Hawaiia minuscula (A. Binney, 1840)	36.286	23.062	0.0000000	G
Helicodiscus n. sp.	1.071	0.062	0.0001509	T
Nesovitrea binneyana (Morse, 1864)	1.500	0.000	0.0000001	D
Nesovitrea electrina (Gould, 1841)	80.179	22.688	0.0000000	T
Oxyloma retusa (I. Lea, 1834)	21.268	8.750	0.0000000	T
Pomatiopsis lapidaria (Say, 1817)	1.196	0.000	0.0000021	–
Punctum minutissimum (I. Lea, 1841)	26.286	10.500	0.0000000	D
Punctum n. sp.	41.982	12.625	0.0000000	T
Punctum vitreum H. B. Baker, 1930	16.536	2.812	0.0000000	D
Stenotrema leai leai (A. Binney)	2.696	0.375	0.0000004	T
Striatura milium (Morse, 1859)	0.714	0.000	0.0002470	G
Strobilops affinis Pilsbry, 1893	74.911	4.312	0.0000000	T
Triodopsis multilineata (Say, 1821)	1.571	0.062	0.0000016	G
Vallonia pulchella (Müller, 1774)	23.321	11.688	0.0000000	T

Tabla 2. (Cont.)

Species	AvU	Abb	*P*–value	Ecp
Vertigo elatior Sterki, 1894	41.875	5.875	0.0000000	T
Vertigo milium (Gould, 1840)	59.357	36.375	0.0000000	T
Vertigo morsei Sterki, 1894	3.589	0.375	0.0000000	T
Vitrina limpida Gould, 1850	1.143	0.000	0.0000035	G
No response				
Anguispira alternata (Say, 1817)	0.018	0.000	0.5622176	D
Catinella avara (Say, 1824)	7.286	8.000	0.5185276	T
Cochlicopa lubrica (Müller, 1774)	0.464	0.000	0.0031253	D
Cochlicopa lubricella (Porro, 1838)	1.714	1.938	0.6798546	G
Columella simplex (Gould, 1841)	0.071	0.188	0.4068651	D
Discus catskillensis (Pilsbry, 1898)	0.357	0.000	0.0095467	D
Euconulus fulvus (Müller, 1774)	3.429	1.625	0.0040433	D
Euconulus polygyratus (Pilsbry, 1899)	0.018	0.000	0.5622176	D
Gastrocopta abbreviata (Sterki, 1909)	0.000	0.062	0.2039785	–
Gastrocopta armifera (Say, 1821)	1.232	1.188	0.9197258	G
Glyphyalinia indentata (Say, 1823)	2.732	3.250	0.4543545	D
Haplotrema concavum (Say, 1821)	0.411	0.000	0.0054455	G
Hawaiia n. sp.	2.571	1.750	0.1616094	T
Helicodiscus inermis H. B. Baker, 1929	0.679	1.812	0.0089186	–
Helicodiscus parallelus (Say, 1817)	5.393	6.438	0.2831711	G
Helicodiscus shimeki Hubricht, 1962	0.286	0.000	0.0204383	D
Helicodiscus singleyanus (Pilsbry, 1890)	0.375	1.125	0.0247064	G
Hendersonia occulta (Say, 1831)	0.036	0.062	0.7606162	D
Mesodon clausus clausus (Say, 1821)	0.054	0.000	0.3154693	D
Oxyloma peoriensis (Wolf in Walker, 1892)	0.125	0.000	0.1251903	–
Pupoides albilabris (C. B. Adams, 1821)	8.393	7.062	0.2324971	T
Stenotrema barbatum (Clapp, 1904)	0.107	0.000	0.1557229	D
Stenotrema fraternum fraternum (Say, 1824)	0.054	0.062	0.9262276	D
Succinea indiana Pilsbry, 1905	0.000	0.188	0.0277912	–
Succinea ovalis Say, 1817	0.143	0.188	0.7834904	D
Triodopsis alleni (Wetherby in Sampson, 1883)	0.071	0.000	0.2464148	D
Vallonia gracilicosta Reinhardt, 1883	11.500	11.062	0.7459095	D
Vertigo arthuri (von Martens, 1884)	0.643	0.000	0.0005065	–
Vertigo gouldi (A. Binney, 1843)	0.018	0.000	0.5622176	D
Vertigo nylanderi Sterki, 1909	0.036	0.000	0.4124393	T
Vertigo ovata Say, 1822	5.750	4.000	0.0472312	T
Vertigo tridentata Wolf, 1870	0.375	0.062	0.0738709	D
Zonitoides arboreus (Say, 1816)	4.143	4.625	0.5650976	D
Zonitoides nitidus (Müller, 1774)	0.464	0.000	0.0031253	T
Positive response				
Gastrocopta corticaria (Say, 1816)	0.732	3.500	0.0000003	D
Strobilops labyrinthica (Say, 1817)	9.661	22.375	0.0000000	D
Vallonia costata (Müller, 1774)	1.804	6.438	0.0000000	G
Vallonia parvula Sterki, 1892	8.250	13.250	0.0001267	T
Vallonia perspectiva Sterki, 1892	2.143	5.625	0.0000055	D
Vertigo pygmaea (Draparnaud, 1801)	0.000	0.562	0.0001385	G

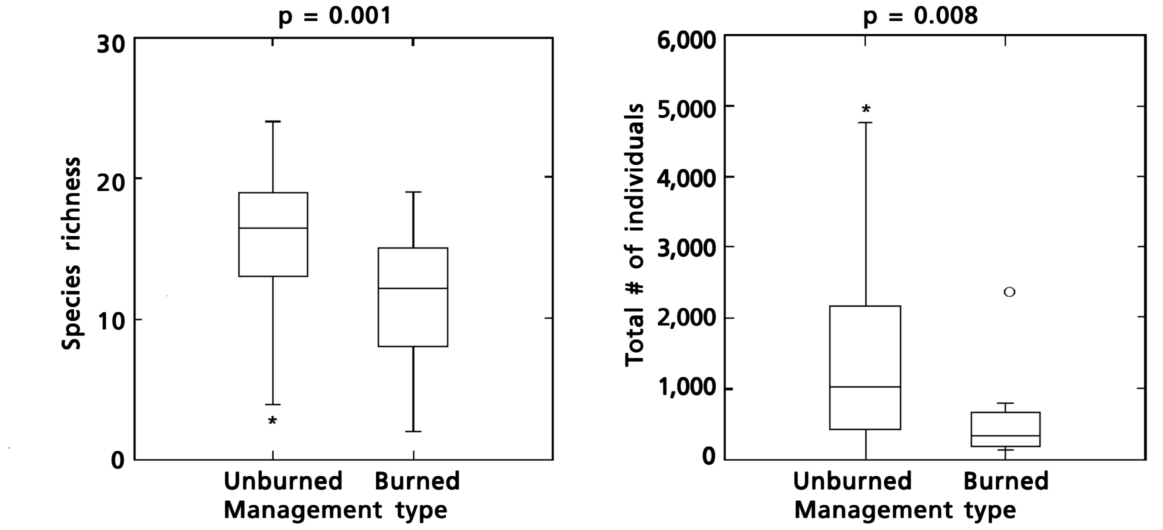


Fig. 2. Box–plot diagram of the response of species richness and abundance to management type on all sampled sites.

Fig. 2. Diagrama de la respuesta en riqueza y abundancia de especies al tipo de actuación desarrollado en todas las áreas estudiadas.

frequency. This null expectation was calculated by assigning 88% of all encountered individuals to unburned sites, with the remaining 22% to burned sites. This procedure was necessary as the number of unburned vs. burned sites was not balanced (88% vs. 22%). A two–tailed significance threshold was employed so that species with positive and negative responses to fire could both be identified. As these analyses were repeated for each species, a Bonferroni correction was used to adjust the significance threshold. Differences between fire responses across the three general ecological preference types were documented via a contingency table, with significance being estimated using both log–linear modelling and Fisher's Exact test.

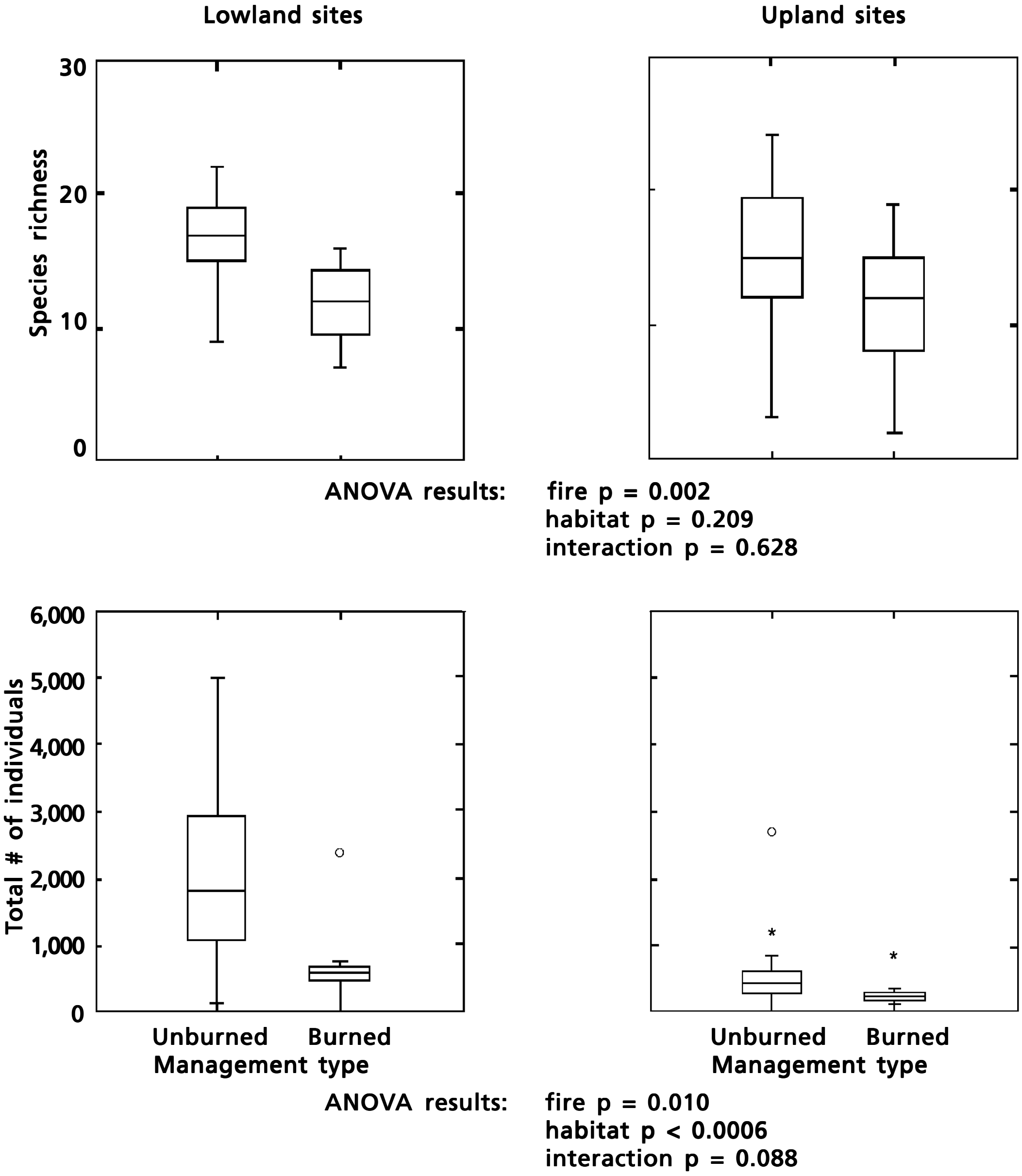
Results

These grassland habitats were generally found to support a diverse and abundant land snail fauna. A total of 91,074 individuals in 72 different species were recovered from the 72 surveyed sites (tables 1, 2). The number of species per each 4 l litter sample ranged from two (Chicog gravel prairie) to 24 (Twin Pines Farm sandstone glade). Average richness ranged from roughly 15 in upland sites, to 17 in lowland. Snail abundance per site ranged from 6 (Point Beach State Forest dunes) to 5,001 (Ogema West fen). Average abundance ranged from roughly 500 in upland sites to 2,000 in lowlands.

One–way ANOVA, using all sites, demonstrated that both species richness (p = 0.001) and abundance (p = 0.008) were significantly lower on sites that had experienced fire management (fig. 2). Median species richness was approximately 18 on unburned vs. 12 on burned sites. Likewise, median shell abundance was 1,000 on unburned vs. 300 on burned sites.

Full 2–way ANOVA, using all sites and considering both management type and habitat type (upland vs. lowland) as independent variables, demonstrated a highly significant (p = 0.002) reduction (approximately 30%) in species richness in both upland and lowland sites (fig. 3). Habitat type and the interaction between habitat and fire history were not significant predictors (p = 0.209 and p = 0.628, respectively). Likewise, a significant (p = 0.010) reduction in shell abundance (50–70%) was noted on burned sites (fig. 3). In this case, however, habitat type was a more significant (p < 0.0005) predictor, with lowlands having 4–10 times the number of shells as uplands. Additionally, a marginally significant (p = 0.088) interaction between management and habitat was observed, with the reduction appearing to be roughly 50% greater in lowlands.

Two–way ANOVA restricted to the 26 paired sites (fig. 4) demonstrated that even after blocking of variation due to site pair identity, a significant reduction in richness (p < 0.0005) and abundance (p = 0.015) still occurred on fire–managed sites.



ANOVA results: fire p = 0.002
habitat p = 0.209
interaction p = 0.628

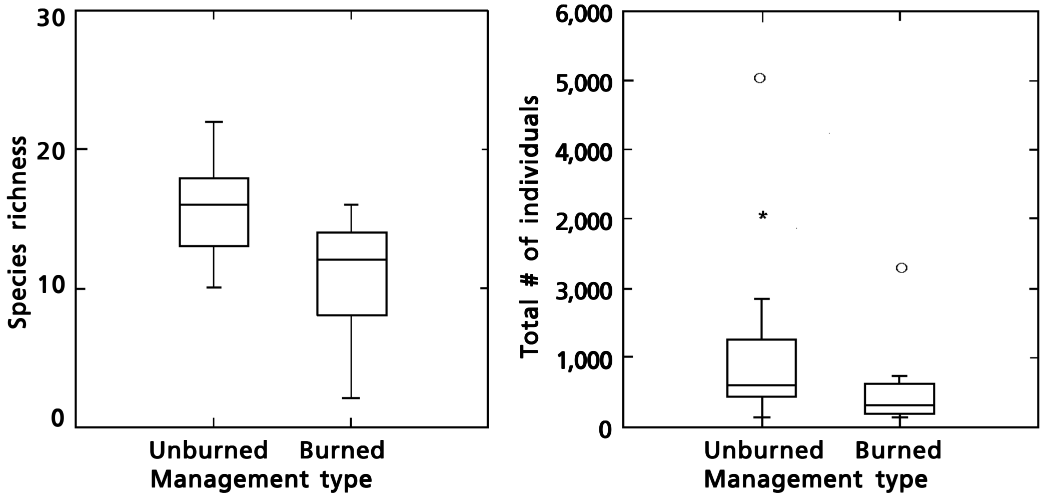
ANOVA results: fire p = 0.010
habitat p < 0.0006
interaction p = 0.088

Fig. 3. Box–plot diagram of the response of species richness and abundance to management and habitat type on all sampled sites.

Fig. 3. Diagrama de la respuesta en riqueza y abundancia de especies al tipo de actuación desarrollado y el hábitat en todas las áreas estudiadas.

Comparison of dominance–diversity diagrams for these sites (fig. 5) demonstrates that both burned upland and lowland sites have truncated curves, with the rarest 40–50% of species being much less common as compared to unburned sites. However, the more common species appear to have largely similar dominance–diversity diagrams.

Contingency table analysis of individual species responses to fire (table 2) indicate that 32 (44%) experience a significant reduction in abundance on fire–managed sites, even following use of a Bonferroni–corrected two–tailed significance threshold (p = 0.000347). Only six species (8%) demonstrated positive responses to fire, while the remaining 34 (47%) demonstrated no



ANOVA results:
Pairs p = 0.001
Fire p < 0.0005

ANOVA results:
Pairs p = 0.009
Fire p = 0.015

Fig. 4. Box–plot diagram of the response of species richness and abundance to management on 26 sites paired by habitat type and geographic location.

Fig. 4. Diagrama de la respuesta en riqueza y abundancia de especies a la actuación desarrollada en 26 áreas emparejadas según el tipo de hábitat y localización geográfica.

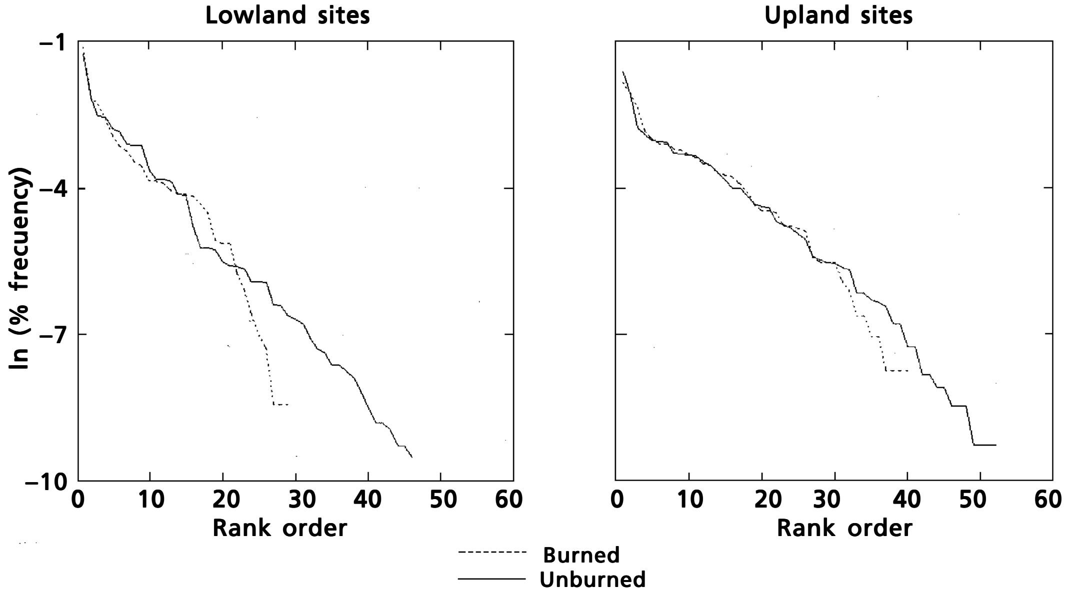


Fig. 5. Dominance–diversity curve for upland/lowland sites which have been burned/unburned.

Fig. 5. Curva de la dominancia–diversidad para las mesetas/llanuras que hayan sido quemadas/ no quemadas.

significant changes in population size. Contingency table analysis of ecological preference vs. fire response indicated that fully 72% of turf–specialists were negatively impacted by fire (table 3). However, only 22% of duff–specialists exhibited negative responses. While 67% of duff–specialists demonstrated no significant response to fire only 24% of turf–specialists were unaffected. Generalist species demonstrated little discernable trend to fire, with seven decreasing, two increasing, and five with no response. Log–likelihood ratio and Fisher's Exact tests both indicated these differences as being highly significant (p = 0.0006 and p = 0.004, respectively).

Table 3. Contingency table analysis of fire response vs. general ecological preferences. Log–likelihood ratio p = 0.000634; Fisher's Exact Test p = 0.004 (Ecological preferences: T. Turf; D. Duff; G. Generalist.)

Tabla 3. Análisis de la tabla de contingencia de la respuesta al fuego frente a las preferencias ecológicas generales. Logaritmo de la razón de verosimilitudes p = *0,000634; Test exacto de Fisher* p = *0,004 (Preferencias ecológicas: T. Sustrato herbáceo; D. Sustrato húmico; G. Generalista.)*

	Ecological preferences		
Fire response	T	D	G
Negative	18	6	7
None	6	18	5
Positive	1	3	2

Discussion

These data clearly indicate that fire management causes significant reductions in land snail community richness and abundance in both upland and lowland grasslands throughout a significant section of the tallgrass prairie biome in central North America. At a species–level, fire most strongly impacts the rarest species, and causes significant population reductions in 44% of the 72 encountered taxa. These negative impacts were most strongly felt in turf–specialists, where almost 75% experienced significant reductions. Thus, statements regarding the benign nature of fire on snail populations (FREST & JOHANNES, 1995), and the beneficial impact of fire on North American grassland faunas (THELER, 1997) can be proven false. Rather, frequent use of fire management appears to represent a significant threat to the health and diversity of North American grassland land snails.

It is not possible through these analyses to definitively identify the factors that directly lead to these impacts. However, at least part of the answer must lay in grassland detritusphere removal. This will lead to direct mortality, as the great majority of land snails are limited to this layer (HAWKINS et al., 1998). As land snail abundance (BERRY, 1973), diversity (CAIN, 1983; LOCASCIULLI & BOAG, 1987), and composition (CAMERON & MORGAN–HUWS, 1975; BAUER et al., 1996; BARKER & MAYHILL, 1999) is often positively correlated with litter depth, detritusphere removal would be expected to have a strong negative impact on land snail community structure.

Redevelopment of an equilibrium thickness of organic detritus takes at least five years in southern Plains grasslands (KUCERA & KOELLING, 1964), with even longer intervals being required in more northern locations (HILL & PLATT, 1975). The optimal interval between fires for land snails might be even longer, depending upon the time required for more refractory plant debris (such as lignified grass stems) to break down, allowing a complete suite of decompositional microhabitats to develop. Litter architecture is known to effect snail community composition in forests of Virginia (BURCH, 1956), British Columbia (CAMERON, 1986), and Puerto Rico (ÁLVAREZ & WILLIG, 1993) and grasslands of England (YOUNG & EVANS, 1991). It should thus not be surprising that in the current data set, sites burned up to 15 years ago have maintained lowered land snail richness and abundance as compared to unburned sites.

As grassland land snails presumably evolved in conjunction with natural fire regimes, it is also intriguing to note that turf–specialists experienced the most severe negative impacts to fire. If fire was a common process structuring central North American grasslands, evolution should have selected for individuals that were more tolerant of, or favored by, this disturbance. Like other native grassland invertebrate groups (SWENGEL, 1996; HARPER et al., 2000), land snails in the presettlement landscape may have been able to tolerate fires by being able to easily recolonize from source pools in adjacent unburned areas. Even when such adjacent source pools are present, recolonization may take over a dozen years (MÄND et al., 2001). In modern landscapes, where grasslands are highly fragmented and surrounded by agricultural, urban, or forest habitats, such recolonization has become much more difficult. Thus, turf–specialist taxa may continue to decrease in burned grasslands due to a lack of recolonization sources, while generalist and duff-specialist woodland taxa, which are more common in the surrounding landscape, may be able to maintain their populations through mass effect (SHMIDA & ELLNER, 1984).

The depression of land snail richness and abundance following fire episodes, the length of time required to redevelop a mature detritusphere, and the greater sensitivity of turf–specialist taxa to fire casts doubt on the wide–

held belief (e.g., Pauly, 1985) that North American grasslands should be burned at 2–6 year intervals. Rather, these data support the contention that presettlement return intervals ranged between 20–30 years (Sims, 1988). These data also strongly suggest that other factors, such as large herbivore grazing (Collins et al., 1998) and periodic drought (Borchert, 1950), may have also played essential roles in keeping prairies treeless, as these processes do not lead to the wholesale detritusphere removal.

Protecting the health of North American grassland land snail populations will require the preservation of mulch layers on sites. Such efforts will also help protect a large percentage of the entire grassland soil biota. The detritusphere can only be protected if more realistic fire return intervals (20–30 years) are adopted by conservation agencies, and used in conjunction with more diversified approaches towards woody and invasive plant removal. Activities like grazing, haying, and hand cutting/pulling will not cause widespread removal of the detritusphere, and should thus be more compatible with land snail (and soil biodiversity) conservation.

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