Extinction, colonization, and persistence of rare vascular flora in the longleaf pine-wiregrass ecosystem: Responses to fire frequency and population size

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RESEARCH ARTICLE

Extinction, Colonization, and Persistence of Rare Vascular Flora in the Longleaf Pine–Wiregrass Ecosystem: Responses to Fire Frequency and Population Size

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ABSTRACT: We examined factors likely to be important in management of rare flora of the longleaf pine–wiregrass ecosystem on Fort Bragg and Camp Mackall Military Reservations in North Carolina, USA. We documented 1,268 occurrences of thirty-six rare plant species during two inventories conducted from 1991 to 1993 and 1998 to 1999. Of these occurrences, 891 (70.3%) persisted, 258 (20.3%) went extinct, and 119 (9.4%) colonized between the first and second inventories; extinctions exceeded colonizations by 139 occurrences. We used analyses of contingency table frequencies and logistic regressions to test hypotheses about temporal responses of local occurrences of rare flora. We found statistically significant effects of fire frequency on the colonization and extinction of rare flora; extinctions declined and colonizations increased with increasing fire frequency. There were statistically significant effects of both area occupied and stem number on the persistence and extinction of rare flora; extinctions declined and persistences increased with increasing area occupied and stem number. Our analyses emphasize the importance of fire and population size for the conservation of rare flora in this landscape.

Extinción, Colonización, y Persistencia de Flora Vascular Rara en los Ecosistemas de Longleaf Pine–Wiregrass: Respuestas a la Frecuencia del Fuego y el Tamaño Poblacional

RESUMEN: Examinamos factores que podrían ser importantes en el manejo de flora rara en el ecosistema de longleaf pine–wiregrass en las reservas militares de Fort Bragg y en Camp Mackall en Carolina del Norte. Documentamos 1268 ocurrencias de 36 especies de plantas raras durante dos inventarios realizados desde 1991 a 1993 y entre 1998 y 1999. De esas ocurrencias, 891 (70,3%) persistieron, 258 (20,3%) se extinguieron, y 119 (9,4%) fueron colonizadas entre el primer y el segundo inventario; las extinciones superaron a las colonizaciones por 139 ocurrencias. Usamos análisis de contingencia, tablas de frecuencias, y regresiones logísticas para testear la hipótesis sobre la respuesta temporal de ocurrencias locales de flora rara. Encontramos efectos significativos de los efectos de la frecuencia del fuego en la colonización y extinción de flora rara; las extinciones disminuyeron y las colonizaciones aumentaron con un aumento de frecuencia de fuego. Hubo efectos significativos del área ocupada y del número de troncos en la persistencia y la extinción de la flora rara; la extinción declinó y la persistencia aumentó con el aumento del área ocupada y el numero de troncos. Nuestro análisis enfatiza la importancia del fuego y del tamaño poblacional para la conservación de flora rara en el paisaje.

Index terms: rare species, fire frequency, longleaf pine, extinction, colonization

INTRODUCTION

Fire is the primary tool used in the management of rare flora associated with the longleaf pine-wiregrass ecosystem. The role of fire in increasing species richness (Sparks et al. 1998, Kush et al. 2000), causing seasonal effects (Sparks et al. 1998, Engle et al. 2000), altering phenology (Platt et al. 1988, Brewer and Platt 1994), influencing demographics (Menges and Kohfeldt 1995, Brockway and Lewis 1997), influencing open space (Hawkes and Menges 1996), and perpetuating longleaf pine itself (Heyward 1939, Glitzenstein et al. 1995) is well documented at the community level for the longleaf pine–wiregrass ecosystem. In addition, studies of individual taxon responses to fire are becoming more prevalent in the literature (Hawkes and Menges 1995, Menges and Kimmich 1996, Kirkman et al. 1998, Quintana-Ascencio et al. 1998, Lamont et al. 2000, Garnier and Dajoz 2001). Yet, there is an acute lack of knowledge of the temporal responses of rare vascular flora to fire, and, in particular, to fire frequency. Further, we know of no community-level analysis of the responses of rare flora to fire, where temporal responses are examined across suites of rare vascular species. Over time a rare plant occurrence will either persist or go extinct and new occurrences may become established, by way of colonization. Knowing how fire frequency drives and influences colonization, extinction, and persistence is crucial to the effective management of rare flora associated with the longleaf pine wiregrass ecosystem.

Fire suppression and habitat loss have directly contributed to the high incidence of rare flora associated with the longleaf pine–wiregrass ecosystem. Hardin and White (1989) identified 191 rare vascular species associated with longleaf pine-wiregrass, while Walker (1993) identified 389 rare vascular species associated with longleaf pine over the species' entire range (including areas where wiregrass does not grow). Many of the rare vascular species associated with this system are either federally protected or state listed and are highly restricted geographically. Department of Defense installations harbor a disproportionate number of rare species, as compared to lands managed by other federal agencies, due to the range of habitats sought for diversified military training (Leslie et al. 1996), and the protection and management afforded these habitats.

Increasing the population size of rare plants is central to their conservation because risk of extinction falls steeply with increasing population size. Because of the confluence of negative genetic and demographic factors, small occurrences may be doomed by an extinction vortex (Gilpin and Soulè 1986, Westemeier et al. 1998). Few studies in the plant literature have tested this largely theoretical hypothesis. The evaluation of abundance classes (Fischer and Stöcklin 1997), outcrossing rates (Van treuren et al. 1993), reproductive success (Widen 1993), and percentage of seed germination (Menges 1991) support the expectation that extinctions decline with increasing population size. Ouborg (1993) demonstrated that occurrences that went locally extinct were smaller on average and that larger occurrences were more likely to persist through time.

This study examined the interaction between fire frequency, and the extinction, colonization, and persistence of rare plant occurrences, responses likely to be important in the management of 36 rare species on Fort Bragg and Camp Mackall Military Reservations, North Carolina, USA. It is clear that with so many rare plant species imperiled, a single species approach to research and management is prohibitive and, in such a diverse system with one dominant disturbance regime, will not work. As it would not be feasible to develop separate management plans for each of these species, the Department of Defense has developed and implemented an ecosystem management policy for its land management activities. Budget constraints and lack of personnel require managing suites of species that inhabit an ecosystem (Leslie et al. 1996). A multiple-species approach may be particularly useful in the absence of individual life history information, a problem common to rare vascular flora (Walker 1993). Thus, the focus of our analyses are directed across species and functional groups. Such broad-based analyses represent a conservative approach. Given the diversity of species involved, detecting responses to fire frequency and population size will be more difficult when compared to detecting responses of individual species.

We specifically sought to quantify temporal responses of rare plant occurrences to fire frequency and population size by testing the following hypotheses: (1) frequent fire increases colonization rates and decreases extinction rates of rare plant occurrences; (2) there are differences between functional groups in response to fire frequency; (3) frequent fire increases both density and area occupied for persistent rare plant occurrences over time; (4) local extinctions decline and persistence of rare plant occurrences increases with increasing stem number and area occupied.

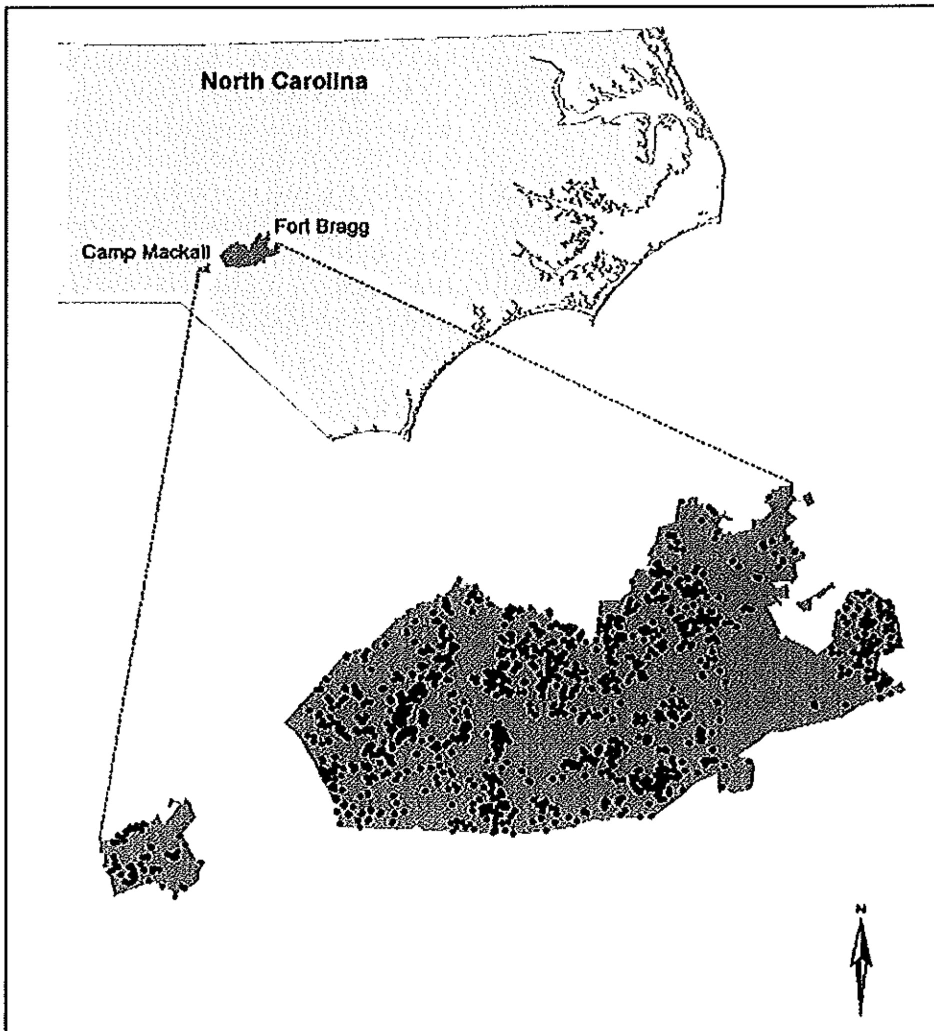

Figure 1. The rare plant occurrences found on Fort Bragg and Camp Mackall Military Reservations. Each dot represents a rare plant occurrence.

Table 1. List of rare flora, mean fires 1991-99, mean stem number 1998–99, total occurrences in 1991–93 and 1998–99, temporal responses, and state status. Botanical nomenclature follows Kartesz (1994). State statuses (Amoroso 1999) are abbreviated as follows: E=Endangered, T=Threatened, SR=Significantly Rare, SC=Special Concern, C=Candidate, and W1=Watch list.

Scientific Name	Mean Fires 1991–99	Mean Stem No. 1998–99	Total Pop. 1991–93	Persistence	Extinction	Colonization	Total Pop. 1998–99	State Status
Agalinis aphylla (Nutt.) Raf.	1.3	26.7	2	1	1	1	2	SR
Agalinis obtusifolia Raf.	1.5	5.0	2	1	1	0	1	W1
Amorpha georgiana var. *georgiana* Wilbur	1.9	55.6	30	26	4	3	29	E
Astragalus michauxii (Kuntze) F.J. Herm	2.1	10.7	88	69	19	18	87	T
Carex tenax Chapman	1.0	200.0	1	1	0	0	1	C
Cladium mariscoides (Muhl.) Torr.	2.0	535.0	5	5	0	0	5	SR
Danthonia sericea Nutt.	2.6	161.8	18	16	2	1	17	SR
Dionaea muscipula Ellis	3.8	89.2	9	9	0	1	10	C-SC
Eriocaulon texense Koern.	2.8	30.0	4	4	0	1	5	C
Eupatorium resinosum Torr. *ex* DC.	2.0	93.1	136	99	37	6	105	T-SC
Gaillardia aestivalis (Walt.) H. Rock	3.3	16.9	5	2	3	2	4	C
Gallactia mollis Michx.	3.0	4.8	7	4	3	0	4	C
Gnaphalium helleri var. *helleri* Britt.	1.6	26.1	5	2	3	2	4	SR
Kalmia cuneata Michx.	2.5	115.2	25	22	3	2	24	E-SC
Lilium iridollae Henry	2.7	0.5	12	2	10	10	12	T
Lindera subcoriacea B.E. Wofford	2.6	40.8	64	55	9	5	60	E
Muhlenbergia torreyana (J.A. Schultes) A.S. Hitchc.	2.0	100.0	1	1	0	0	1	E
Nestronia umbellula Raf.	1.5	541.9	25	23	2	2	25	W1
Parnassia caroliniana Michx.	3.4	92.9	3	2	1	4	6	E
Phaseolus polystachios (L.) B.S.P.	2.4	8.2	86	61	25	6	67	C
Physalis lanceolata Michx.	1.8	15.5	11	5	6	2	7	W1
Polygala grandiflora Walt.	2.1	48.5	7	5	2	1	6	SR
Pyxidanthera brevifolia Wells	2.2	2.0	255	238	17	11	249	E
Rhynchospora macra (C.B. Clarke) Small	2.5	125.2	10	8	2	0	8	E
Rhynchospora oligantha Gray	2.1	36.7	12	11	1	0	11	C
Ruellia ciliosa (Pursh) R.W. Long	3.0	12.5	1	0	1	1	1	C
Solidago gracillima Torr. and Gray	1.8	50.8	6	6	0	0	6	SR
Solidago pulchra Small	3.0	0.0	1	0	1	0	0	E
Solidago verna M.A. Curtis	1.9	59.8	17	14	3	2	16	T
Stylisma pickeringii var. *pickeringii* (Torr. *ex* M.A. Curtis) Gray	1.4	283.4	58	53	5	5	58	E
Tofieldia glabra Nutt.	2.5	8.3	145	79	66	17	96	C
Tridens carolinianus (Steud.) Henr.	2.4	21.5	43	29	14	1	30	C
Warea cuneifolia (Muhl. *ex* Nutt.) Nutt.	2.0	2.5	4	1	3	0	1	C
Xyris chapmanii Bridges and Orzell	2.1	31.2	26	21	5	5	26	C
Xyris elliottii Chapman	3.0	0.0	1	0	1	0	0	C
Xyris scabrifolia Harper	2.2	8.0	24	16	8	10	26	C
			1149	**891**	**258**	**119**	**1010**	

Table 2. Tests for fire frequency as a predictor of functional group proportions and persistence and colonization proportions using logistic regression.

Pairs of Functional groups	Per.-Col. Combined (n = 1010)	Persistence (n = 891)	Colonization (n = 119)
Monocot vs. dicot	P = < 0.0001	P =0.0036	P =0.0541
	X^2 = 15.32	X^2 = 8.50	X^2 = 3.71
Legume vs. non-legume	P = 0.7397	P = 0.8037	P = 0.5825
	X^2 = 0.11	X^2 = 0.06	X^2 = 0.30
Woody vs. herbaceous	P =0.4656	P = 0.9827	P = 0.2370
	X^2 = 0.53	X^2 = 0.00	X^2 = 1.40
Annual vs. perennial	P = 0.3735	P = 0.3649	P = 0.3001
	X^2 = 0.54	X^2 = 0.82	X^2 = 1.07

zero change, with high variability in changes in stem number at low fire frequencies and little variability in changes in stem number at high fire frequencies. There were statistically significant effects of fire frequency on changes in average area occupied at P = <0.0001. Area occupied exhibited a mean decline of –0.24 ha across all observations during the 9-y period. As was the case with changes in stem number, 50% of the observations were at or near zero change, with high variability in changes in area occupied at low fire frequencies and little variability in changes in area occupied at high fire frequencies.

Persistence versus Local Extinction as a Function of Population Size

We hypothesized that extinctions of rare plant occurrences would decline and the persistence of occurrences would increase with increasing stem number and area occupied. We chose to contrast persistence versus extinction as these occurrences differed the most in population size. The proportions of local extinctions declined and the proportions of persistent occurrences increased significantly as a function of stem number (P = 0.0002, Figure 4) and area occupied (P = < 0.0001, Figure 5). Occurrences that went locally extinct had the smallest stem numbers and occupied relatively small areas, while those of persistent occurrences had the largest stem numbers and occupied the largest areas (Figure 6). Small occurrences were disproportionately represented among extinctions. Of the rare plant occurrences that went extinct, 175 (71.1%) had 1–10 stems, and 164 (64.0%) occupied an area of 1 m^2.

DISCUSSION

We were able to assess with reasonable accuracy the extinction and persistence of rare plant occurrences. Return visits to occurrences recorded during the initial survey are likely to be accurate; either the occurrence was present or not. Like Harrison et al. (2000), we found that the majority of the species we studied were perennials. This is an advantage when censuses are infrequent, because occurrences of longer-lived species have greater intrinsic stability (Ricklefs 2001). Perhaps our least reliable data are those for colonizations. Psuedo-colonizations could exist if any occurrences were missed during the 1991–93 survey and then discovered during the 1998–99 survey. However, given the length of the initial survey and the highly trained botanists conducting the survey, missing existing plant occurrences was minimized to the maximum extent possible.

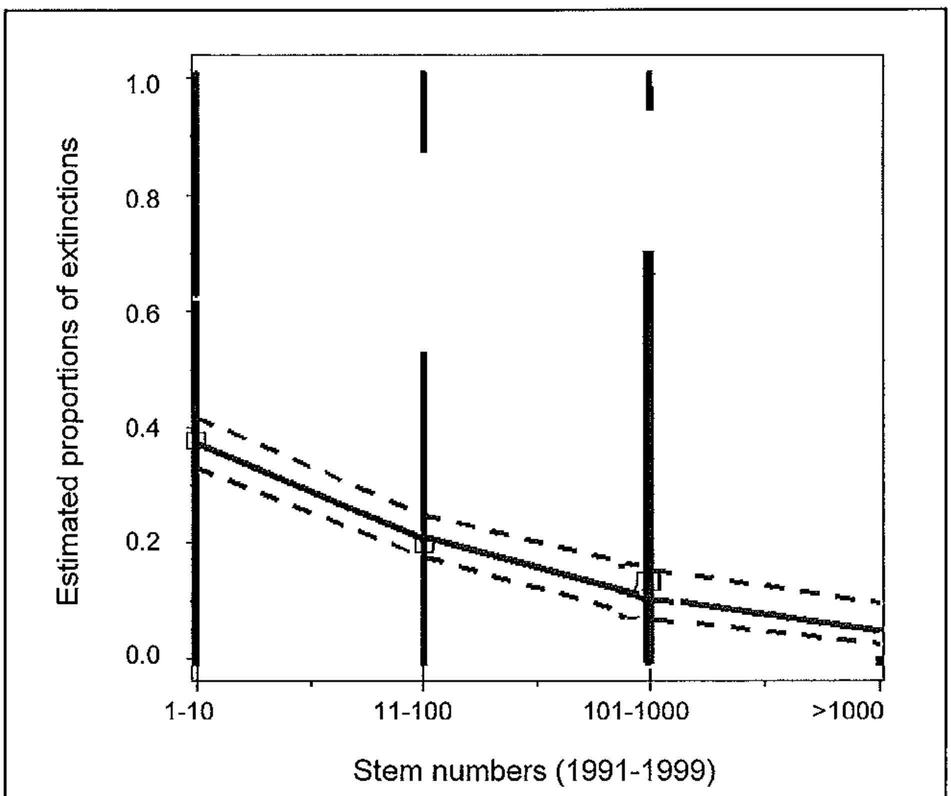

Figure 4. Proportions of extinctions (n=246), assigned a value of 1, contrasted with persistences (n=605), assigned a value of 0, as a function of stem number and as estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The relative numbers of extinctions and persistences are depicted as bars across the top and bottom of the graph, respectively. The relationship was significant at P = 0.0002, $X^2_{0.05(1)}$ = 13.83.

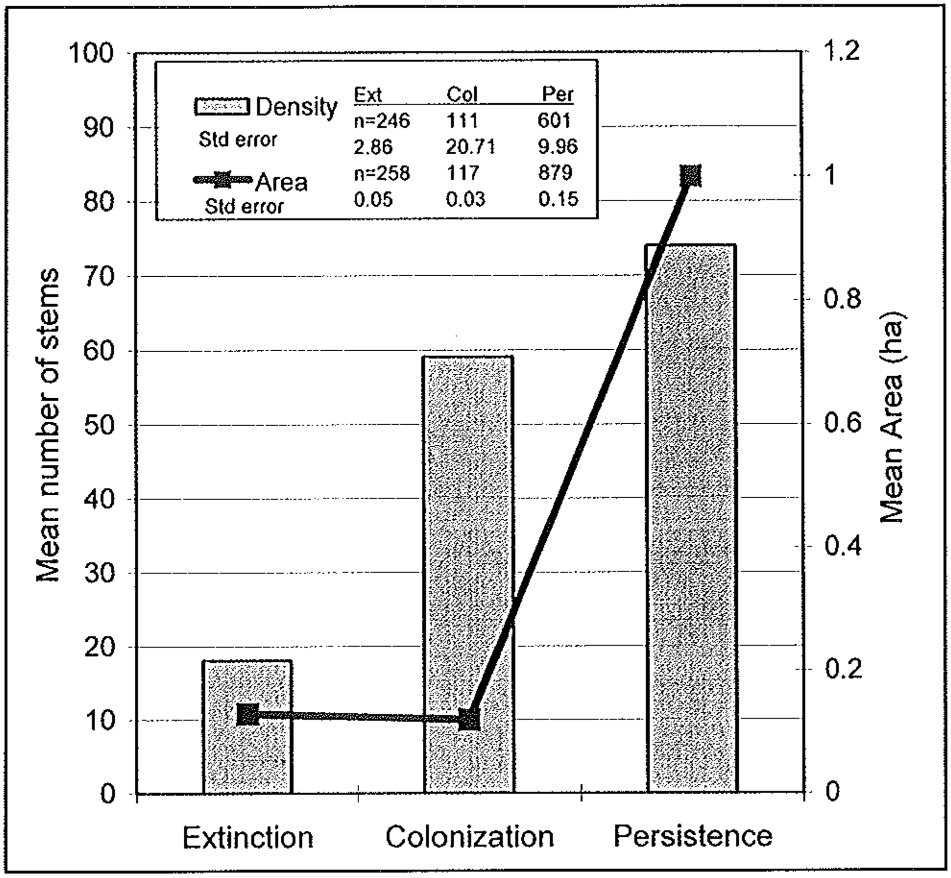

Figure 6. Mean population size of temporal responses. Values for extinction and persistence are based on 1991–93 data and values for colonization are based on 1998–99 data.

xeric sandhill communities are characterized by a sparse canopy and shrub layer, minimal ground litter and large areas of open sand. In contrast to communities that contain *Stylisma pickeringii* var. *pickeringii*, these areas are not subject to frequent mechanical disturbance. Persistence under these conditions is similar to that seen in some rare Florida scrub endemics adapted to fire cycles of 10 to 40 y. The persistence of these endemics is highly correlated with open sand conditions and is independent of fire (Hawkes and Menges 1995).

Extinctions declined and the persistence of rare plant occurrences increased with increasing population size (Figure 4 and 5). Is there a minimum population size that best promotes the persistence of rare plant occurrences? We found that 236 (96.0 %) of all extinctions occurred in the two smallest stem classes of 1–10 and 11–100 stems, suggesting that extinctions would be greatly reduced if a minimum population size in excess of 100 stems could be achieved for occurrences of rare plant species in this landscape. The finding that the average population size for persistent occurrences in 1991–93 was 74.0 (Figure 6) stems and rose to 98 stems in 1998–99 also supports our recommendation for minimum population size. Although not addressed in this study, a spatial analysis of the potential metapopulation structure of each rare species to include the variables of population size, location, and the distances among them will further enlighten our understanding of the dynamics of extinction, colonization, and persistence and could serve to direct future management efforts.

This study is a first step in elucidating the effects of prescribed fire as a management tool for rare vascular flora associated with the longleaf pine–wiregrass ecosystem. There are few studies in the literature that address the temporal responses of rare flora to fire frequency and few studies in the plant literature that address extinction and persistence as a function of population size.

The relationships among the three temporal states are complex and there are differences among species in their responses to fire. Despite the fact that this study involved multiple species with a diversity of life forms, life histories, and environmental relations, strong signals of effects of fire frequency and population size on temporal responses were apparent.

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