ABSTRACT

GRAY, JANET BRACEY. Rare vascular flora of the longleaf pine-wiregrass ecosystem: temporal responses to fire frequency and population size. (Under the direction of Dr. Thomas R. Wentworth)

We examined factors likely to be important in the management of rare flora occurring in the longleaf pine-wiregrass ecosystem on Fort Bragg and Camp Mackall Military Reservations in North Carolina. Thirty-six rare plant species, comprising 1,268 records, were documented during the course of two inventories of rare flora conducted during the periods 1991-93 and 1998-99. There were 891 (70.3%) records of persistence, 258 (20.3%) records of extinction, and 119 (9.4%) records of colonization; extinctions exceeded colonizations by 139 records. We used analyses of contingency table frequencies and logistic regressions to test hypotheses about temporal responses of local populations 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. Relative turnover increased with increasing fire frequency and declined with increasing population size. Our analyses indicate the importance of fire and population size for the conservation of rare flora in this landscape.

Rare Vascular Flora of the Longleaf Pine-Wiregrass Ecosystem: Temporal Responses to Fire Frequency and Population Size.

By

Janet Bracey Gray

A thesis submitted to the Graduate Faculty
of North Carolina State University
in partial fulfillment of requirements for the degree of
Master of Science

Department of Botany

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Approved By

_____   _____
Nick Haddad   Jon M. Stucky

_____
Chair of Advisory Committee
Thomas R. Wentworth

DEDICATION

to my son
Zachary Mills Shipley
1996 -

mother
Frances Bracey Gray
1921 -

grandmother
Gladys Grant Bracey
1904-1983

Great grandmother
Nettie Pierce Bracey
1887-1950

Great great grandmother
Diana Pierce

BIOGRAPHY

<u>Windsor, Virginia, 1956</u>. I was born and raised in Tidewater, Virginia, sandwiched between Suffolk, the peanut capitol of the world and Smithfield, the birthplace of the Virginia country ham. They remain my favorite foods today.

I can trace my mother's family back to Exum and Sally Bracey and according to the 1832 Isle of Wight County population census, Sally was illiterate; but she was the only relative recorded as such. Mills Valentine Bracey, the son of Exum and Sally, fought in the Civil War, and was wounded in the neck at the battle of the Wilderness. He ended up in Chimborozo, the largest Confederate hospital in the south and was released after a month. He was among those who surrendered at Appomattox courthouse.

Mills Valentine Bracey's son was Robert Sisco Bracey. His wife, my great-grandmother Nettie was a fervent believer in God, and kept journals in which she wrote in reverse and backwards, left to right. I have her journals. I've read them all by holding them up over my shoulder and looking into a mirror. It was passed down to me that this oddity was a sudden event corresponding to her eventual admission into Eastern Central Hospital in Williamsburg Va. She never left. Even when she could, she didn't want to. She stayed on for 21 years and helped nurse the sick and preached the word of God. Before you begin to think that this is a biography of Nettie, I have one more thing to say; Nettie was an environmentalist. To quote her own written words from one of her earlier journals "Automobiles are the beasts of the earth, fed by sucking all the oil out of the

cracks of the earth". Perhaps these words spun the thread that ties my childhood to what I am doing today as an adult.

Madison, Wisconsin, 1972. Oddly enough, I was attending a Catholic high School and working as a "salad girl" at the Edgewater Hotel, three or four nights a week. Jim Colby, a graduate student in the Arts was the broiler chef. One weekend, Jim invited me to accompany him and his girlfriend to some local greenhouses to track down heirloom tomatoes. I went along and that was it. I knew instinctively what I wanted to do! After high school, I attended the University of Wisconsin-Madison, enrolled in the horticulture program and ended up taking a work-study job in the Botany Department's herbarium. I pressed, mounted and filed plant specimens. That was it. I knew instinctively what I wanted to do. The world of native plants was far more interesting than anything cultivated that you could put before me! Any free time I had was spent alone, documenting with film the wonderful flora associated with prairie remnants. From time to time, I still get out that collection of slides and admire what I think is halfway decent photography. Years later, a 20-day rare plant survey contract behind me, in which my split was $1,500.00, I bought a great camera. It was stolen. I haven't photographed anything since.

Wilmington, North Carolina, 1986. While working as the greenhouse manager for the Biology Department at the University of North Carolina at Wilmington, Dr. David Sieren, a quiet and modest man, did things for me that I didn't know about and have only come to realize within the last few years. He introduced me to the flora of North Carolina by way of an independent study project, "Wetland Flora of Brunswick County".

I had the freedom to explore and a nook in the herbarium to key plants to my hearts content. Someday, I knew I'd formally go back to school.

<u>Raleigh, North Carolina, 1999.</u> I had to finish graduate school. It was "a thorn in my side" that I had more or less quit and my mother was always there to remind me how it grieved her so that I didn't finish. I look back and it's hard to believe that I started the program, came fairly close to finishing and then did not follow through. Another good reason to finish, was that I was working as a botanist with endangered species on Fort Bragg Military Reservation and knew that the only way to elevate the quality of my work was to get some additional training, training in research.

One day, I found myself driving up to Raleigh to meet with Dr. Nina Allen, graduate advisor. Any doubts I had about going back to school she immediately dispelled. Fortuitously, I ran into Dr. Tom Wentworth in the hallway. We had met for the first time a couple of months earlier at a meeting held at Weymouth Woods. He said to me "I've been thinking about what you told me concerning the two rare plant surveys conducted on Fort Bragg and how you are interested in seeing where plant sites were blinking on and off". I said yes, that I was very much interested in doing that but at the moment I was trying to get back into graduate school. He immediately asked if he could be my advisor. With this said, here I am, with a research project near completion. This one's for you Mom!

Janet Bracey Gray

15 July 2001

ACKNOWLEDGEMENTS

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Introduction

Prescribed fire is the primary tool used in the management of rare flora contained in the longleaf pine-wiregrass ecosystem. Yet, there is an acute lack of knowledge of the temporal responses of rare vascular flora to fire, and in particular, to fire frequency. By temporal responses, we mean that over time a rare plant occurrence will either persist or go extinct and new populations, by way of colonization, may become established. Knowing which factors drive and influence colonization, extinction, and persistence is crucial to the effective management of rare flora associated with the longleaf pine wiregrass ecosystem.

The role of fire in increasing species richness (Lemon 1949, Hodgkins 1958, Sparks et al. 1998, and Kush & Meldahl 2000), causing seasonal effects (Robbins & Myers 1992, Sparks et al. 1998, and Engle et al 2000), altering phenology (Stone 1951, Platt et al. 1988, Brewer & Platt 1994, and Menges 1995), influencing demographics (Menges & Kohfeldt 1995, and Brockway & Lewis 1997), influencing open space (Hawkes & Menges 1996), and perpetuating longleaf itself (Heyward 1939 and Glitzenstein et al. 1995) is well documented at the community level. In addition, studies of individual taxon responses to fire are becoming more prevalent in the literature (Menges & Kimmich 1996, Menges 1995, Hawkes & Menges 1995, Kirkman et al. 1998, Quintana-Ascencio et al. 1998, Brown & Wheelan 1999, Wardell-Johnson 2000, Lamont et al. 2000, and Garnier & Dajoz 2001). However, there has been no community-level analysis of temporal responses of rare flora to fire.

Fire frequency, along with timing and intensity, can have both positive and deleterious effects on the persistence, colonization, and extinction of small, rare populations even

when the species are fire adapted. Fires that are too frequent, or too infrequent, can decrease the resiliency of rare plant populations (Kirkman et al. 1998). The effects of varying fire frequencies are often exacerbated because most local populations of rare flora have few individuals, thus making them particularly vulnerable to extirpation (Walker & Peet 1983).

The effects of fire frequency are tightly linked to habitat quality. In longleaf pine ecosystems, high quality habitat is indicated by open understory conditions and an intact ground cover. As in Florida scrub habitat, the availability of open space and fire regime most likely influence the abundance patterns of rare flora (Hawkes & Menges 1996). Natural longleaf pine-wiregrass communities burned frequently in presettlement times and prescribed fire now replaces lightning-ignited fires that once occurred regionally. Fire suppression has resulted in the deterioration of habitat quality by allowing the accumulation of litter. A dense layer of litter can shade out and eliminate the pyrophytic herb layer containing many rare species (Frost 1998).

Fire suppression and habitat loss have directly contributed to the high incidence of rare flora associated with the longleaf pine-wiregrass ecosystem (Hardin & White 1989). Approximately 3% remains of an estimated 92 million acres of the longleaf pine ecosystem that once swept the coastal plain from Virginia to Texas (Frost 1993). Yet, despite this staggering loss, the longleaf pine-wiregrass ecosystem is one of the most spectacularly species rich ecosystems in North America with much of this diversity in the herb stratum. Values up to 42 species/0.25 m^2 and 84 species/625 m^2 have been reported on mesic sites by Walker & Peet (1983) and 140 species per 1000 m^2 by Peet & Allard

(1993). Many of the rare vascular species associated with this system are either federally listed or state protected and are highly restricted geographically. 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 entire range, to include areas where wiregrass does not grow.

Increasing abundances of rare plants is central to their conservation. The risk of extinction falls steeply with increasing population size. This has been particularly well documented for bird populations, both mainland and island, and orb spiders (Diamond 1984 and Toft & Schoener 1983). Few studies in the plant literature test this largely theoretical hypothesis. Among the various approaches used are the evaluation of abundance classes (Fischer & Stöcklin 1997), outcrossing rates (Van treuren et al. 1993), reproductive success (Widen 1993), and percentage of seed germination (Menges 1991). These studies support the expectation that extinctions decline with increasing population size.

In order to best direct management efforts, some understanding of the volatility or turnover of individual rare species is needed. This is particularly crucial in the absence of life history information, a problem common to rare vascular flora of the longleaf pine-wiregrass ecosystem (Walker 1993). The persistence of rare plants in managed landscapes is dependent on extinction and colonization rates across multiple populations. Management of single populations is risky, because individual populations are prone to extinction (Soulé 1987).

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This study examines factors likely to be important in the management of 36 rare

species on Fort Bragg and Camp Mackall Military Reservations, North Carolina. First,

we evaluated the effects of fire frequency on habitat quality. We then specifically sought

to quantify temporal responses to fire frequency, persistence, and local extinction as

functions of density and area and to examine relative turnover rates of rare flora by

testing the following hypotheses: (1) frequent fire increases colonization rates and

decreases extinction rates of rare plant populations; (2) within various mutually exclusive

pairs of functional groups (monocots versus dicots, etc.) there are marked differences in

response to fire frequency, and in rates of persistence and colonization relative to fire

frequency; (3) frequent fire increases both density and area occupied for persistent rare

plant populations over time; (4) the rate of local extinction of rare plant populations

declines and their persistence increases with increasing stem number and area occupied;

and (5) relative turnover of rare flora increases with increasing fire frequency and

declines with increasing stem number. The results of this study provide management

guidelines for the use of prescribed fire in the conservation of rare flora.

Methods and Study Area

Study area — Lying within 45,528 ha of the longleaf pine-wiregrass ecosystem are our

study areas, Fort Bragg (lat 35°07′30′ N, long 79°08′30′ W) and Camp Mackall (lat

35°01′45′ N, long 79°28′45′ W) Military Reservations. The reservations are located

within the sandhills region of the inner coastal plain physiographic province, North

Carolina, USA (Fig. 1).

The longleaf pine communities of the region vary along a moisture gradient from xeric entisols to mesic/wet ultisols. Soils are derived from Cretaceous and/or Tertiary deposits of fluvial and marine sediments, ranging from arkosic, feldspar-rich sands to micaceous, arenaceous, compact clays. The underlying sediments have a basal conglomerate of pebbles and cobbles (Daniels et al. 1984). Mean annual temperature is 22.2 º C and mean annual precipitation for 30 years prior to and including 1999 was 1,186.2 mm/yr.

Within the last 10 years, there has been a heightened awareness of the effectiveness of fire, particularly during the growing season, in maintaining suitable habitat for the federally endangered red-cockaded woodpecker that occurs in our study areas. The reservations are burned on a 3- to 5-year rotation with an emphasis on growing season burns to control encroaching hardwoods. This burning regime has been of positive benefit for many other rare flora and fauna associated with the longleaf pine-wiregrass ecosystem. In the absence of fire, shrubs and scrub oaks quickly invade and compete with the rich herbaceous understory that typifies this system (Hodgkins 1958, Streng et al. 1993, Glitzenstein et al. 1995, and Brockway & Lewis 1997).

To date, 58 rare plant species have been identified on Fort Bragg and Camp Mackall Military Reservations. These 58 rare species inhabit a number of communities contained in the longleaf pine-wiregrass ecosystem, including xeric sandhill scrub, pine scrub/oak sandhill, mesic pine flatwoods, streamhead pocosins, and sandhill seeps (nomenclature after Schafale & Weakley 1990). Due to the range of habitats sought for diversified military training, and the protection and management afforded these habitats, Department

of Defense installations harbor a disproportionate number of rare species, as compared to other federal agencies (Leslie et al. 1996).

For our study, we considered 36 of the 58 rare species that inhabit those longleaf pine communities that are most influenced by fire. Vascular plant nomenclature for these species follows Kartesz (1994). Of the species not considered, 3 are federally endangered and are actively managed using silvicultural methods in addition to fire. The other 19 species occur in aquatic or wetland habitats where fire is not a frequent occurrence or in areas of the reservations with highly restricted access. Of the 36 rare plant species considered, 27 (75.0%) are herbaceous perennials, a proportion consistent with previous findings that the vast majority of herbaceous rare flora associated with longleaf pine throughout its range are perennials (Walker & Peet 1983, Hardin & White 1991, and Walker 1993). In addition, 23 (64.0%) inhabit mesic to wetland communities. This is also consistent with the finding that rare vascular flora associated with longleaf pine are more likely found in wetter habitats (Walker 1993) and thus are now limited to pocosin/savanna ecotones (Frost 1995).

Surveys for rare flora — A comprehensive survey for rare flora including species considered in this study was conducted over 44,000 hectares on Fort Bragg and Camp Mackall during the period 1991-1993 (Table 1). A two-step process was used to identify rare plant populations. The first consisted of habitat assessment surveys conducted from October 1991 to November 1992 using a parallel, zigzag transect surveying technique. A group of trained biologists/botanists walked parallel, zigzag transect lines. Spacing between transects varied; team members were spaced 100 meters apart in degraded,

uniform areas and were spaced 50 meters apart in areas of higher quality. Binoculars were used as an aid in finding rare plants.

Habitat was assessed by each transect team as having a low, medium, or high priority for more intensive inventory based on the likelihood of containing rare plants. This evaluation of rare plant potential was based on observations of degree of fire suppression, amount of soil disturbance, level of species diversity, and presence of rare and/or indicator species (i.e., species which indicate the presence of certain environmental conditions and which can be used to characterize the type and quality of the plant communities in which they occur). The acres surveyed, the location and number of acres requiring a return visit, and the number of acres completed and not requiring more intensive inventory were recorded. Habitats recorded as low priority were re-visited during the 1992 and 1993 growing season to correct for assessments made during winter months when rare plant populations might have been missed.

Phase two of the inventory for rare flora consisted of return visits to high and medium priority areas identified during the initial habitat assessment. A zigzag transect method was employed in upland areas and linear parallel transects were walked along wetland ecotones. Because of the visual difficulty associated with surveying into the interiors of wetland areas, such as streamhead pocosins and swamps, surveys for rare wetland populations were concentrated during late summer and fall when most of these species were flowering and /or fruiting (Russo et al. 1993).

Rare plant populations encountered by the habitat assessment teams throughout the two assessment periods were mapped on 1990 black and white aerial photographs (scale

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1:12,000) and later transposed into a geographic information layer (GIS). Biological data recorded, pertinent to this study, included the scientific name of each population, exact and categorical counts of individuals, and area occupied. When ranges of stem counts were given, the highest value was used for our analyses (Sutter 2001 pers. comm.). Stem counts recorded as "many" or "few" and values preceded by a plus (+) sign were not considered in our analyses.

The reservations were surveyed again in 1998-1999. Local populations documented during the initial survey were revisited to determine presence or absence. The area occupied by each persistent population was globally positioned to the nearest meter and the number of stems was recorded. Suitable habitat was systematically surveyed for newly colonized populations with an emphasis on areas surrounding existing populations. Areas occupied by new populations were globally positioned to the nearest meter and the number of stems was recorded. When considering colonizations, we used only the observed colonizations in our analyses. Suitable habitats for potential colonizations were not identified, thus the proportion of colonizations to potential colonizable sites is not known.

Fire histories, comprising both dormant and growing season burns, were obtained for each occurrence for the period 1991 through 1999. The 14 populations impacted by military training activities and/or project construction were not considered in this study.

We feel reasonably confident that we were able to accurately assess extinction, colonization and persistence of rare plant populations. Like Harrison et al. (2000), we found that the majority of the species were perennials. Return visits to populations

recorded during the initial survey are likely to be accurate; either the population was present or not. Perhaps the most unreliable data are those of colonizations. Psuedo-colonizations could exist if any populations were missed during the 1991-93 survey and then recorded as colonizations during the 1998-99 survey.

Mapping quality of vegetative communities — In 1996-97, we determined the quality of all vegetative communities. The following criteria defined the levels of quality (1, 2, 3): Level 1 vegetative communities were in their natural state, or closely approximating their natural state. These areas showed negligible human disturbance with minimal ground-disturbing events. Little to no hardwood mid-story was present and the ground cover was intact. Prescribed fire had been the primary management tool. Level 2 vegetative communities still retained a good representation and distribution of associated species that had been exposed to moderate amounts and intensities of human disturbance that had caused ground disturbance. Midstory hardwoods were present but controlled by prescribed burning, supplemented by mechanical methods of hardwood removal. Level 3 vegetative communities had extensive hardwood encroachment and/or were devoid of ground cover, with severely altered natural vegetative components. Pine plantations and human-dominated areas are examples of extensively altered vegetation and were automatically assigned a level 3 designation. Because of similar habitat quality conditions and ease of discussion, levels 1 and 2 were grouped into high quality habitat and level 3, differing the most in quality, was assigned low quality.

Statistical analyses — Logistic regression analyses of contingency table frequencies were used to test extinction and colonization rates of rare flora as functions of fire frequency

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during the period 1991-1999, high and low habitat quality as functions of fire frequency during the period 1991-1997, and extinction and persistence as functions of both 1991 area and stem number. In all analyses where fire frequency was the independent variable, frequency classes were 1, 2, 3, 4 and 5 fires. Because of the low number of populations that burned 6 and 7 times, these populations were pooled and assigned to the class of 5 fires.

In logistic regression, Y represents the binary response variable with outcomes 0 and 1 (for example, colonization and extinction). The model describes the natural logarithm (the logit) of the odds of the outcome that Y = 1 as a linear function of a predictor or independent variable X. A '1' is the number of observations offering a given response to the independent variable X (fire). The larger the logit, the more the '1' responses outweigh the '0' responses. The smaller the logit, the more the '0' responses outweigh the '1' responses (ter Braak & Looman 1995). Departures from the logistic model can be assessed by graphing the fitted equation together with the observed binary responses and proportions.

Where data were not binary, chi-square analyses of contingency table frequencies were used to test for independence/dependence of temporal responses to fire frequency and to examine for independence/dependence of habitat quality on vegetative communities. It is important to note that the chi-square statistic is based on the actual observed cell frequencies and the test criterion is

$$X^2 = \sum \frac{(\text{obs} - \text{exp})^2}{\text{exp}} \ .$$

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We used the nonparametric Kruskal-Wallis test to examine differences in the change in stem number and area of rare plant populations across fire frequencies during the period 1991-1999. Area and stem number were not normally distributed and could not be transformed to normality, and therefore were not suited to analysis of variance (ANOVA). The Kruskal-Wallis technique is a distribution free method assuming a specific parametric distribution for the data (Sokal & Rohlf 1969).

Relative turnover index — To examine the level of volatility or the relative turnover of each taxon during the period 1991-1999, we calculated the relative turnover rate (modified after Schoener 1988). It is calculated by

$$\text{Trel} = \frac{E_i + C_i}{X_1 + X_2}$$

where E_i is the number of extinctions unique to taxon i, C_i is the number of colonizations unique to taxon i, and X_1 and X_2 are the total number of populations at each of the two censuses. The nature of the turnover index is that it considers extinction and colonization within the context of persistence. This index ranges from 0 (no turnover) to 1 (complete turnover). The correlation procedure was then used to examine for linear relationships of relative turnover to both fire frequency and stem number, by using the 36 pairs of values corresponding to each rare plant species. Regression analyses were used to determine if there was a significant difference in the behaviors of functional group pairs in their relative turnover response to fire and stem number.

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Results

Effects of fire frequency on habitat quality — There was a significant positive

relationship between habitat quality and fire frequency. Proportions of high quality

habitat increased and proportions of low quality habitat declined as a function of fire

frequency at $P = < 0.0001$, $X^2_{0.05 (1\ df)} = 30.95$ (logistic regression). There were highly

significant differences in habitat quality among the 14 vegetative communities examined

at $P = <.0001$, $X^2_{0.05 (11\ df)} = 340.667$ (2 x 14 contingency table), although 75% of the

vegetative community units typed out as low quality. The three dominant vegetative

communities in descending order of the number of units occurring across the landscape

were pine scrub/oak sandhill, xeric sandhill scrub and streamhead pocosin. Of these

three communities, the greatest proportion of high quality habitat is found in streamhead

pocosins. Because fire frequency and habitat quality are correlates, we only considered

fire frequency in subsequent analyses.

Survey results for rare flora — Of 1,268 rare plant populations, there were 891 (70.3%)

persistences, 258 (20.3%) extinctions, and 119 (9.4%) colonizations (Fig. 2). Twenty-

two (61.1%) of the 36 species considered declined in the number of populations between

the two surveys. At one extreme, two rare species, *Solidago pulchra* and *Xyris elliotti,*

represented by one population each in 1991 went locally extinct in 1999. At the other

extreme, the state endangered sandhills pyxie moss (*Pyxidanthera brevifolia*) extant in

1999 contributed 249 (25%) of the total number of populations, while the state threatened

Eupatorium resinosum and state candidate *Tofieldia glabra* each contributed 105 (10.4%)

and 96 (9.6%) populations, respectively (Table 1).

The 1,268 rare populations were burned in 2,829 instances during the period 1991-

1999. Of these 2,829 populations being burned, 1,917 (67.8%) were burned during the

growing season (April through June) and 912 (32.2%) were burned during the dormant

season (December through February). There were 1,181 rare plant populations that

burned at least once, and these experienced an averaging of 2.38 fires during the study.

Fire frequency was highest where rare plants colonized, lower where they persisted and

lowest where they went extinct (Fig. 3).

Effects of fire frequency on temporal responses — There were statistically significant

differences in the proportions of persistence, colonization, and local extinction of rare

plant populations in response to fire frequency when examined across all species

(P=0.0005, $X^2_{0.05 (10 df)}$ = 31.42, contingency table analysis). Observed frequencies were

higher than expected for both persistent populations and those that went locally extinct.

The observed frequency for colonizations was one below that of the expected value.

Using logistic regression, we then examined extinction and colonization in response to

fire frequency. We chose to contrast extinction and colonization as these are the most

dynamic processes and differ the most in response to fire. Colonizations significantly

increased and extinctions significantly declined as a function of fire frequency at P=

0.0009 (Fig. 4).

Effects of fire frequency on functional groups — We used logistic regression to test fire

frequency effects on functional group proportions by classifying 1999 populations

(combining colonization and persistence) into one of two functional groups and assigning

a 1 to the functional group of interest and a 0 to the contrasting functional group.

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Colonization and persistence were chosen for this analysis as these represent successful

populations extant in 1999. Proportions of monocot populations increased while

proportions of dicot populations declined with increasing fire frequency, significant at P

$= < 0.0001$ (Table 2). It is noteworthy that monocots comprise (14) 38.9% of the 36

species considered.

We found no statistically significant relationships between proportions of annuals

versus perennials, woody versus herbaceous species, and legumes versus non-legumes as

a function of fire frequency (Table 2, left side). We then evaluated separately proportions

of functional group persistences and proportions of functional group colonizations as

functions of fire frequency. Proportions of monocot colonizations and persistences each

increased with increasing fire frequency at $P = < 0.0541$ and $P = 0.0360$, respectively,

while those of dicots declined (Fig. 5). We found no statistically significant

relationships between the individual temporal responses of annuals versus perennials,

woody versus herbaceous species, and legumes versus non-legumes to fire frequency

(Table 2, right side).

Changes in stem number and area occupied as a function of fire frequency — We

hypothesized that fire frequency increases both stem number and area occupied for

persistent rare plant populations over time. There were statistically significant positive

effects of fire frequency on changes in stem number between fire frequencies during the

period 1991-1999 at $P = 0.0023$ (Fig. 6), resulting in a mean increase of 24.5 stems

across all observations. Fifty percent of the observations were at or near zero change,

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with high variability in changes in stem number with low fire frequency and little change in stem number at high fire frequencies. Area occupied exhibited a mean decline of −0.24 ha across all observations during the nine-year period. Fifty percent of the observations were at or near zero change, with high variability in changes in area occupied with low fire frequency and little change in area occupied at high fire frequencies at $P = < 0.0001$ (Fig. 7).

Persistence versus local extinction as a function of population size — We hypothesized that extinctions of rare plant populations would decline and the persistence of populations would increase with increasing stem number and area occupied. We chose to contrast persistence versus extinction as these responses differed the most in population size. Populations that went locally extinct had the fewest number of stems while those of persistent populations had the largest. The proportions of local extinctions declined and the proportions of persistent populations increased significantly as a function of stem number at $P = 0.0002$ (Fig. 8) and area occupied ($P = < 0.0001$), (Fig. 9). Small populations were disproportionately represented among extinctions. Of the rare plant populations that went extinct, 175 (71.1 %) had 1-10 stems, and 164 (64.0%) occupied an area of $1m^2$. Among persistent populations, 289 (47.8%) had 1-10 stems and 296 (33.5%) occupied an area of $1m^2$.

On average, extinctions had the smallest number of stems and area occupied and persistent occurrences had the largest. Colonizations were intermediate between the two. However, our data show that rare plant populations, regardless of temporal state, are small (Fig. 10).

Relative turnover rates in relation to stem number and fire frequency — We tested the

hypothesis that relative turnover of rare flora would decrease with stem number and

increase with increasing fire frequency. There were declines in relative turnover of rare

flora with increases in stem number and increases in relative turnover with increasing fire

frequency. The relationships were statistically significant at $r = -0.6981$ and $r = 0.3590$,

respectively (Figs. 11 & 12).

   In testing for a significant difference between the relationship of relative turnover to

density and mean fires of the functional groups considered, we found that both annuals

and perennials exhibit increasing relative turnover with increasing fire frequency.

However, annuals exhibit consistently higher relative turnover at any given fire frequency

than do perennials, significant at $F = 6.74$, $P = 0.0140$. We found no statistically

significant relationships between relative turnover rates of monocots versus dicots,

woody versus herbaceous species and legumes versus non-legumes with respect to fire.

There were also no statistically significant differences in relative turnover between all

functional groups considered with respect to stem number (Table 3).

Discussion

Effects of fire frequency on temporal responses — Increased fire frequency increases the

proportion of colonizations of rare flora and decreases the proportion of extinctions (Fig.

4). Interestingly, what appears to be a subtle difference in the average number of fires

experienced by rare plant populations could be decisive in maintaining the delicate

balance between extinction and colonization.

Although most populations in this study were burned during the period 1991-1999, there were more than twice as many extinctions as colonizations. The relatively small number of colonizations may reflect a limited number of potential colonizable sites, or utilization of a small fraction of suitable sites. The former explanation is the more plausible one. Seventy-five percent of Fort Bragg and Camp Mackall was characterized as low quality; relatively little suitable habitat may have been available for occupation. Establishment of a new population is dependent on the ability of an individual to make use of favorable conditions in resource-concentrated microsites within a highly variable landscape (van der Maarel & Sykes 1993). The large percentage of unsuitable habitat on these military reservations may also serve to explain the high number of extinctions. Populations that went locally extinct burned the fewest number of times, indicating that increased fire frequency is warranted in areas across the reservations with infrequent fire. In this study, habitat degradation is a correlate to low fire frequency. If local extinction is the result of habitat degradation (Harrison 1991), sites are no longer available for colonization (Thomas 1994). The longleaf pine-wiregrass ecosystem is dynamic and other factors related to fire behavior, such as the fire return interval, fire intensity, and burn season, as well as climatic conditions, may also play roles in providing habitat suitability for rare flora.

During the period 1991-1999, 70.3% of the 1991 rare plant populations contained within Fort Bragg and Camp Mackall Military Reservations persisted and 20.3% went extinct. The 3.5 ratio of persistence to extinction represents a layer of small, ephemeral populations superimposed against a backdrop of larger, persistent populations, a similar

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finding to that of Schoener & Spiller (1987) in their analysis of turnover rates of orb spiders. Multiple survey points in time are needed to more fully understand the dynamics of extinction and colonization as they relate to persistence and to discern what are normal "background" rates.

Effects of fire frequency on functional groups — The proportion of monocots increased at the expense of dicots as a function of increasing fire frequency at $P = < 0.0001$, $X^2 = _{0.05}$ $_{(1\ df)}$ 15.32. There were also increases in monocot persistences and monocot colonizations versus those of dicots as a function of fire frequency (Fig. 5). It is plausible that monocots are more sensitive to fire and more responsive to the open conditions created by frequent fire than are other functional groups. This may be particularly true for the four perennial grasses considered in our study. Seeds of perennial grasses are light and require openings for seedling establishment. Persistent pappus-like hairs and awns aid in dispersal to newly created seedbeds created by fire. Infrequent fire encourages encroaching woody vegetation, thus eliminating open areas for seedling establishment (Keeley 1981). This explanation is supported by the finding that monocots in general show habitat specificity to streamhead pocosins where we found the largest proportion of high quality habitat among the vegetative communities.

Changes in stem number and area occupied as a function of fire frequency — There were declines in area occupied and increases in stem number among observations in response to fire frequency, but gains and losses were small. Fifty percent of the observations were at or near zero change in both stem number and area. Across the range of fire frequencies populations exhibited the least change in stem number and area at the highest fire

frequencies (Figs. 6 & 7). This may be indicative of the resilience of rare flora after fire

disturbance and suggests that high fire frequencies are conducive to equilibrium

conditions.

In contrast to the small fluctuations in stem number and area at the highest fire

frequencies were large spikes of both stem number and area gained at zero fire frequency.

These large gains in stem number and area were primarily attributable to *Stylisma*

pickeringii var. *pickeringii* and *Pyxidanthera brevifolia*. Large, densely populated areas

of *Stylisma pickeringii* var. *pickeringii* are common in physically disturbed areas, such as

roadsides and the edges of drop zones, areas which are subject to frequent mechanical

disturbance and which have low to no canopy cover. This appears to be indicative of the

species' ability to proliferate under a disturbance regime other than fire, as long as

competition for light and nutrients is reduced by another form of disturbance. Contained

within xeric sandhill communities that were not burned during the time frame of this

study are small widely scattered clumps of *Pyxidanthera brevifolia*. These communities

are characterized by a sparse canopy and shrub layer, minimal ground litter and large

areas of open sand. In contrast to sites that contain S*tylisma 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 ten to forty years. The persistence of these endemics is highly correlated with

open sand conditions and independent of fire (Hawkes & Menges 1995).

Persistence versus local extinction as a function of population size — There are robust

relationships of extinction and persistence as functions of stem number and area (Figs. 8

& 9). This study confirms the hypothesis that large stem numbers and areas occupied promote the persistence of populations, while small stem numbers and decline in areas occupied lead to local extinctions. This finding supports the earlier work of Fischer and Stöcklin (1997) who found statistically significant trends in local extinction among both rare and non-sensitive flora in small abundance classes. However, extinction rates among rare flora are likely exacerbated by highly restricted geographical ranges and habitat specificity. Our results parallel faunal studies documenting high extinction rates among small populations of breeding birds and orb spiders. Extinctions declined with increases in density and area (Diamond 1984 and Toft & Schoener 1983).

Relative turnover rates in relation to stem number and fire frequency — Relative turnover of rare plant populations declines with increasing stem number (Fig. 11). This was expected as large population sizes would tend to buffer populations from single and recurring disturbance events. Representative among species with larger population sizes and no turnover are *Carex tenax*, *Solidago gracillima, Muhlenbergia torreyana*, and *Cladium mariscoides*. Relative turnover increased with increasing fire frequency (Fig. 12). This was also expected as fire maintained ecosystems are highly dynamic. The highest average fire frequencies were experienced by *Xyris elliotti, Solidago pulchra,* and *Ruellia ciliosa. Solidago pulchra* and *Ruellia ciliosa* experienced complete turnover by going locally extinct. *Xyris elliotii* experienced complete turnover by way of one colonization and one local extinction. A comparison of Figs. 11 and 12 supports another conclusion: large population size negates the effect of high fire frequency on relative turnover. *Dionaea muscipula* had an average density of 200 individuals and experienced

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the greatest average number of fires among the 36 species, yet had a very low turnover rate. *Danthonia sericea, Cladium mariscoides, Eriocaulon texense, Kalmia cuneata,* and *Lindera subcoriacea* had large average population sizes and also followed this pattern of low turnover with frequent fire (Table 1). Although we did not correlate relative turnover to the number of occurrences per species, we note that *Pyxidanthera brevifolia, Eupatorium resinosum,* and *Tofieldia glabra* had the greatest number of persistent populations and experienced low relative turnover, even though *Tofieldia glabra* and *Eupatorium resinosum* experienced the most extinctions among all species considered (Table 1).

The results of this study show that fire frequency accounts for differences in turnover rates between annuals and perennials. One probable explanation is that seed germination of annuals typically occurs post-fire. Seeds lie dormant between disturbance events (Keeley 1981 and Tyler 1995). Annual species are short-lived, with naturally high rates of colonization and extinction, and relative turnover is expected to be greater in these species than in long-lived perennials (Fisher & Stöcklin 1997, Margules et al. 1994, van der Maarel & Sykes 1993, and Robinson & Quinn 1988). Similarly, Fisher and Stöcklin (1997) found that extinction rates varied depending on the functional group and were highest for annuals and biennials, lower for perennials and lowest for colonizing perennials. Species differ in vulnerability to turnover (Schoener & Spiller 1987) and the large amount of scatter in fig. 12 may be indicative of species differences in sensitivity to fire frequency.

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Implications for management — Is there a minimum fire frequency that best promotes the persistence of rare flora? Our data suggest there is. For long-term stability of the number of populations of rare species, extinctions must be offset by colonizations. Our evidence suggests that the rate of colonization balances the rate of extinction between fire frequencies of 4 and 5 times during the 9-year study period (Fig. 4). This finding would indicate that a fire return interval of approximately 2 years would suffice for balancing rates of extinction and colonization. A case may also be made for reduction in the fluctuation of stem number and area as a means of stabilizing populations of rare plants. Stem number and area occupied by rare plant populations were less volatile when burned 4 or 5 times during the 9-year study period (Figs. 6 and 7), suggesting that burning every 2 years would be sufficient to minimize volatility. Thus, we propose that 2 years be considered the minimum fire return interval for rare vascular flora in this longleaf pine-wiregrass ecosystem. This fire return interval is in the mid-range of a presettlement fire regime of 1-3 years reported by Frost (1998) for the southeastern coastal plain of the United States, where 50 % to 90 % of the landscape probably burned that frequently and in which many rare, fire dependent plant species appear to require a 1-3 year fire return interval.

Is there a minimum population size that best promotes the persistence of rare plant populations? 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 of 100 stems could be achieved for populations of rare plant species in this landscape. The finding that the average population size for

persistent populations was 98 stems in 1998-1999 (Fig. 10) also supports our

recommendation of a 100-stem minimum. However, special management efforts should

be directed towards increasing stem numbers in the 1-10 stem class, which accounted for

175 (71.1 %) of the extinctions observed. If none of these extinctions had occurred, the

remaining 71 extinctions observed would have been more than offset by the 119

colonizations that occurred during the same period. Managing the smallest populations is

clearly important, as 289 (47.8 %) of all persistent populations (of known stem number)

on Fort Bragg and Camp Mackall Military Reservations were in this stem class.

Increases in stem number (and area occupied) promote the persistence of rare plant

populations and reduce the risk of extinction. Increasing abundances of rare plant

populations may promote stability by minimizing fluctuation in stem number and area.

Increased population size can also serve as a buffer against stochastic events that lead to

local extinction. Large population size also appears to negate the tendency of frequent

fires to increase turnover rates. Although not addressed in this study, the spatial

arrangement of these small persistent populations could direct future management efforts.

This study is a first step in elucidating the effects of prescribed fire as a management

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

Scientific Name	Mean Fires 1991-1999	Mean Stem. No. 1998-1999	Total Pop. 1991-1993	Persistence	Extinction	Colonization	Total Pop. 1998-1999	Relative Turnover	State Status
Agalinis aphylla	1.3	26.7	2	1	1	1	2	0.50	SR
Agalinis obtusifolia	1.5	5.0	2	1	1	0	1	0.33	W1
Amorpha georgiana var. georgiana	1.9	55.6	30	26	4	3	29	0.12	E
Astragalus michauxii	2.1	10.7	88	69	19	18	87	0.21	T
Carex tenax	1.0	200.0	1	1	0	0	1	0.00	C
Cladium mariscoides	2.0	535.0	5	5	0	0	5	0.00	SR
Danthonia sericea	2.6	161.8	18	16	2	1	17	0.09	SR
Dionaea muscipula	3.8	89.2	9	9	0	1	10	0.05	C-SC
Eriocaulon texense	2.8	30.0	4	4	0	1	5	0.11	C
Eupatorium resinosum	2.0	93.1	136	99	37	6	105	0.18	T-SC
Gaillardia aestivalis	3.3	16.9	5	2	3	2	4	0.56	C

Table 1. (continued)

Gallactia mollis	3.0	4.8	7	4	3	0	4	0.27	C
Gnaphalium helleri var. helleri	1.6	26.1	5	2	3	2	4	0.56	SR
Kalmia cuneata	2.5	115.2	25	22	3	2	24	0.10	E-SC
Lilium iridollae	2.7	0.5	12	2	10	10	12	0.83	T
Lindera subcoriacea	2.6	40.8	64	55	9	5	60	0.11	E
Muhlenbergia torreyana	2.0	100.0	1	1	0	0	1	0.00	E
Nestronia umbellula	1.5	541.9	25	23	2	2	25	0.08	W1
Parnassia caroliniana	3.4	92.9	3	2	1	4	6	0.56	E
Phaseolus polystachios	2.4	8.2	86	61	25	6	67	0.20	C
Physalis lanceolata	1.8	15.5	11	5	6	2	7	0.44	W1
Polgala grandiflora	2.1	48.5	7	5	2	1	6	0.23	SR
Pyxidanthera brevifolia	2.2	2.0	255	238	17	11	249	0.06	E
Rhynchospora macra	2.5	125.2	10	8	2	0	8	0.11	E
Rhynchospora oligantha	2.1	36.7	12	11	1	0	11	0.04	C

table 1. (continued)

Ruellia ciliosa	3.0	12.5	1	0	1	1	1	1.00	C
Solidago gracillima	1.8	50.8	6	6	0	0	6	0.00	SR
Solidago pulchra	3.0	0.0	1	0	1	0	0	1.00	E
Solidago verna	1.9	59.8	17	14	3	2	16	0.15	T
Stylisma pickeringii var. pickeringii	1.4	283.4	58	53	5	5	58	0.09	E
Tofieldia glabra	2.5	8.3	145	79	66	17	96	0.34	C
Tridens carolinianus	2.4	21.5	43	29	14	1	30	0.21	C
Warea cuneifolia	2.0	2.5	4	1	3	0	1	0.60	C
Xyris chapmanii	2.1	31.2	26	21	5	5	26	0.19	C
Xyris elliottii	3.0	0.0	1	0	1	0	0	1.00	C
Xyris scabrifolia	2.2	8.0	24	16	8	10	26	0.36	C
			1149	**891**	**258**	**119**	**1010**		

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

Pairs of Functional groups	FUNCTIONAL GROUP RESPONSE		FUNCTIONAL GROUP PERSISTENCES AND COLONIZATIONS TESTED SEPARATELY	
	Pers. and col. combined (n = 1060)		**Temporal responses to fire frequency**	
			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	$P =$ .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

Table 3. *F* values and statistical significances for regressions of relative turnover (for 36 species) on mean fire frequency and the log of mean population density and the effects of functional groups on these regressions.

	Independent Variable: Mean fires			
	Rel. turnover vs fire		Effect of functional groups	
Functional groups	*F*	*P*	*F*	*P*
Annual and perennial	8.67	0.0059	6.74	0.0140
Woody and herbaceous	4.56	0.0403	2.49	0.1243
Legume and non-legume	5.14	0.0301	0.69	0.4134
Monocot and dicot	4.87	0.0343	0.02	0.9020
	Independent Variable: Log of Mean Density			
	Rel. turnover vs density		Effect of functional groups	
Functional groups	*F*	*P*	*F*	*P*
Annual and perennial	28.72	<0.0001	1.64	0.2094
Woody and herbaceous	29.86	<0.0001	1.96	0.1709
Legume and non-legume	36.30	<0.0001	0.97	0.3325
Monocot and dicot	31.55	<0.0001	0.12	0.7338
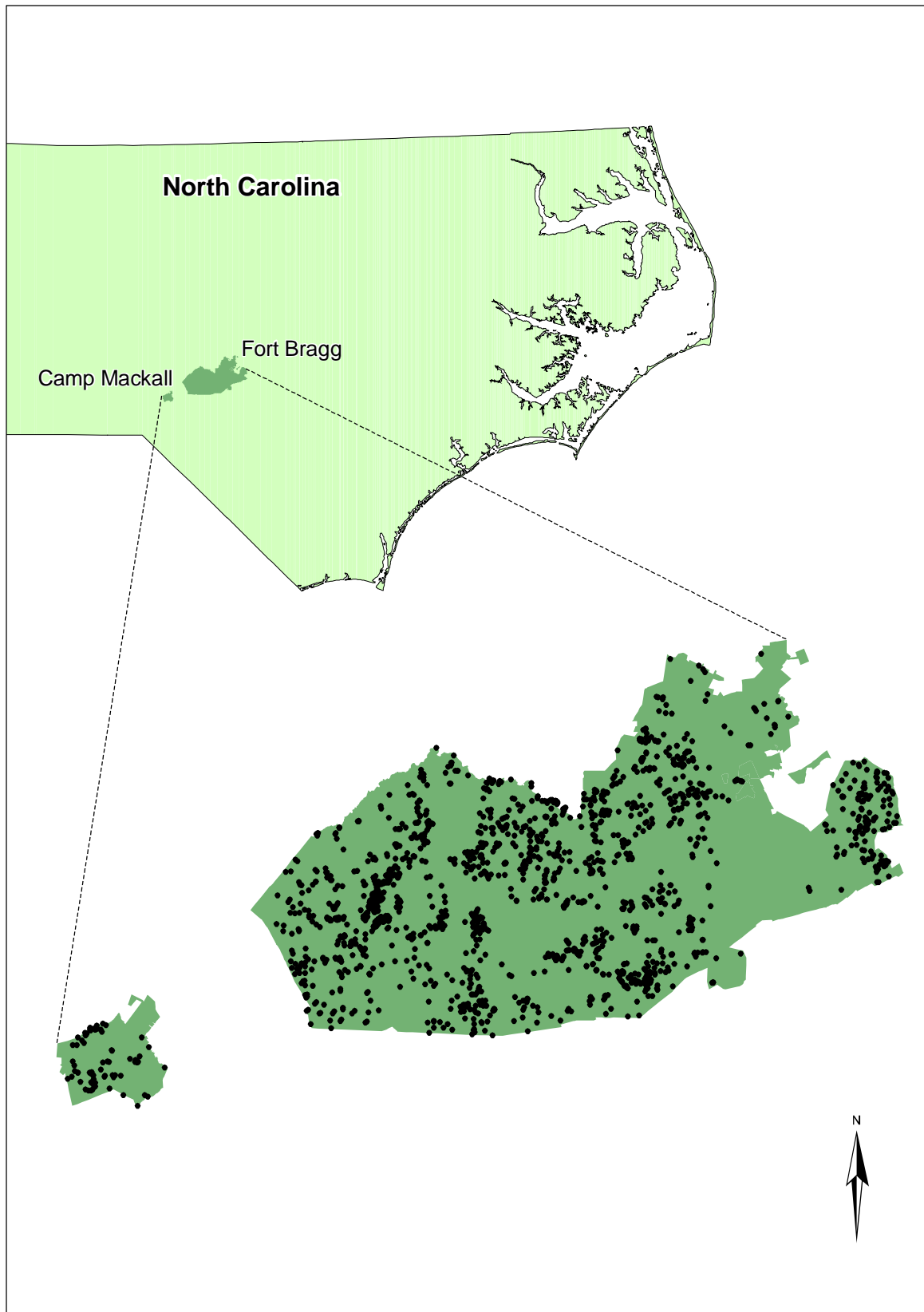
Fig. 1. The rare plant occurrences found on Fort Bragg and Camp Mackall Military Reservations.

1998-1999 Survey

	1	**0**
1	Per +/+ 891	Ext +/- 258
0	Col -/+ 119	N/A

1991-1993 Survey (vertical axis label)

Fig. 2. Presence/Absence model defining the three temporal responses as defined by the 1991-1993 and 1998-1999 surveys. (1 indicates presence, 0 indicates absence)
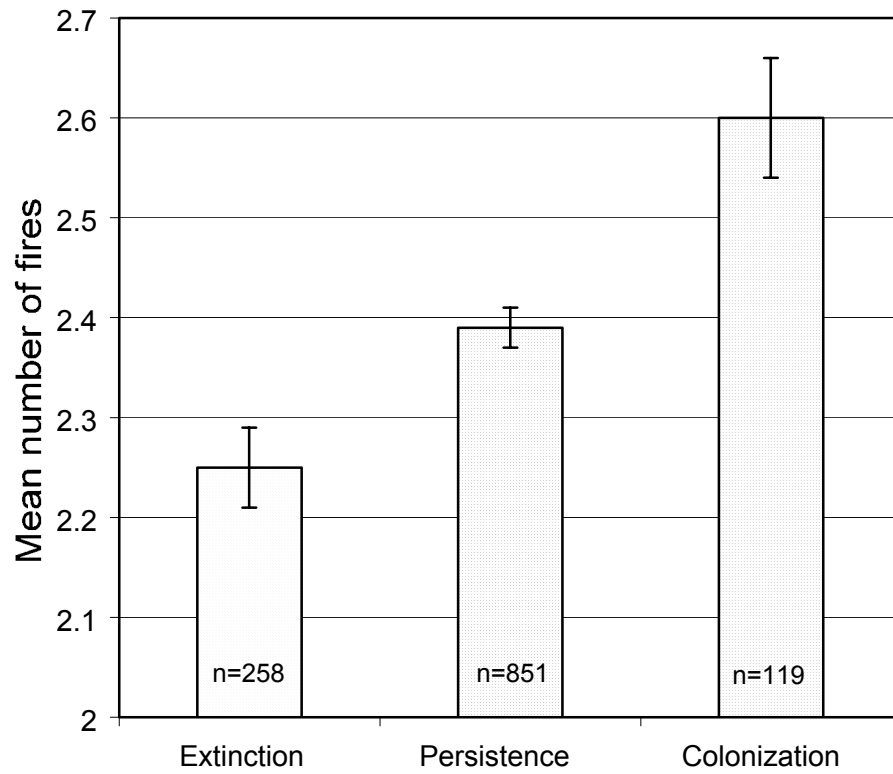
Fig. 3. Mean number of fires incurred for each temporal state, during the period 1991-1999.
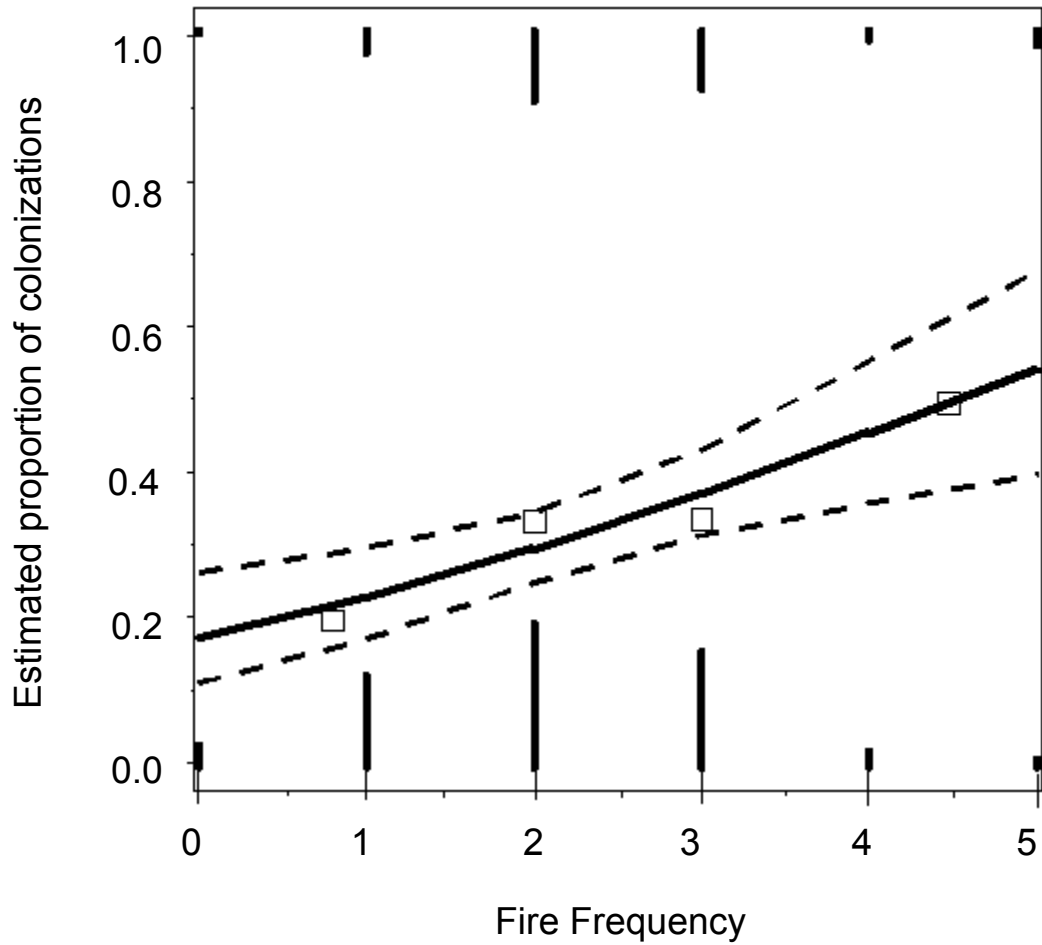
Fig. 4. Proportions of colonizations (n=119), assigned a value of 1, contrasted with extinctions (n=258), assigned a value of 0 as a function of fire frequency and estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The relative numbers of colonizations and extinctions at each fire frequency are depicted as bars across the top and bottom of the graph. The relationship was significant at P = 0.0009, $X^2_{0.05(1)}$ = 11.06. A mirror image of this graph is achieved by assigning extinction a value of 1 and colonization a value of 0.
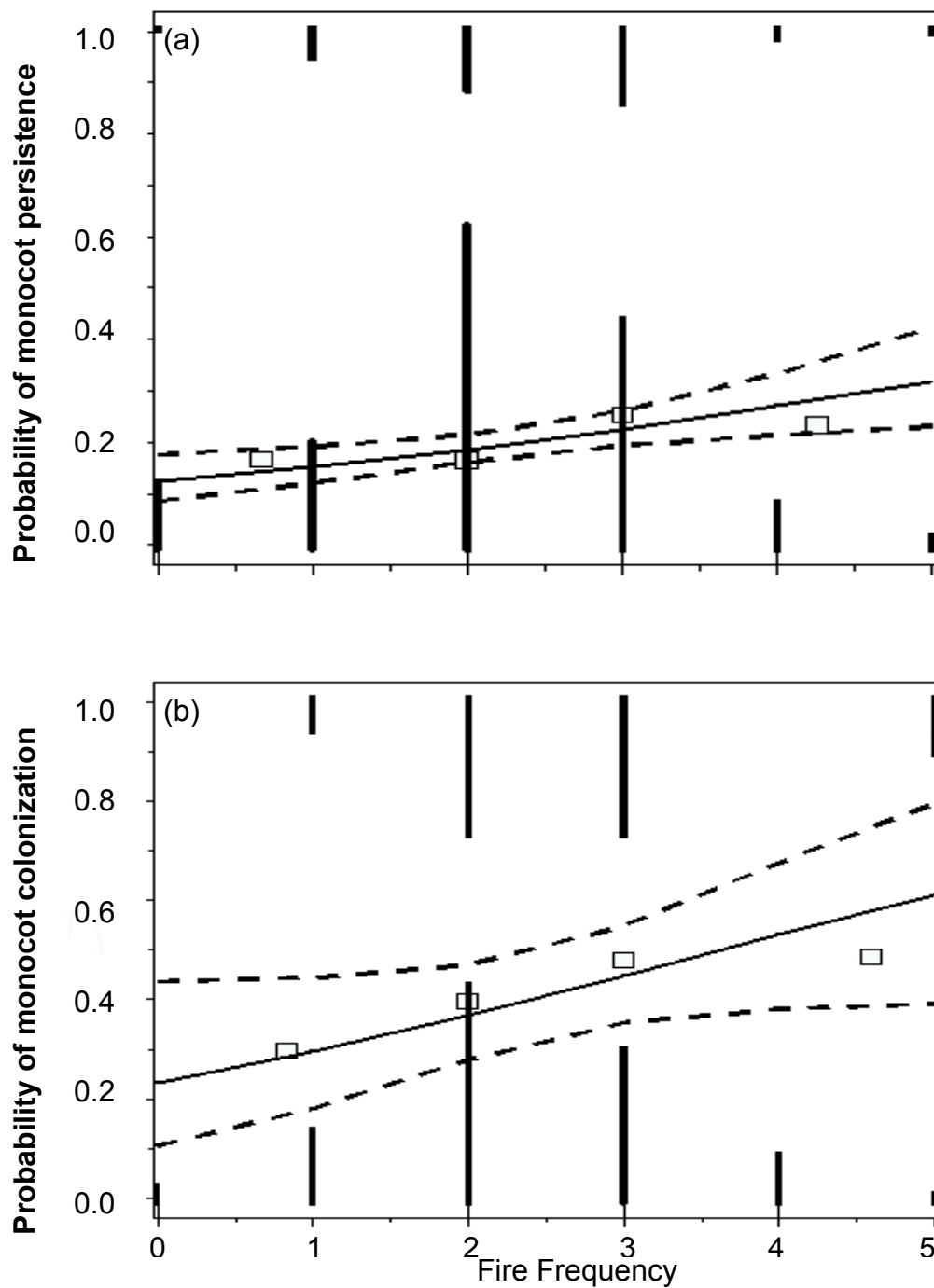
Fig. 5. Proportions of monocots for (a) persistence (n=258) and (b) colonizations (n=119) as a function of fire frequency and estimated using logistic regression. Monocots are depicted as 1 and contrasted with dicots assigned a value of 0. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The relative numbers of persistences and colonizations are depicted as lines across the top and bottom of each graph. The relationship was significant for (a) persistence at $P = 0.0036$, $X^2_{0.05(1)} = 8.50$ and (b) colonization at $P = 0.0541$, $X^2_{0.05(1)} = 3.71$.

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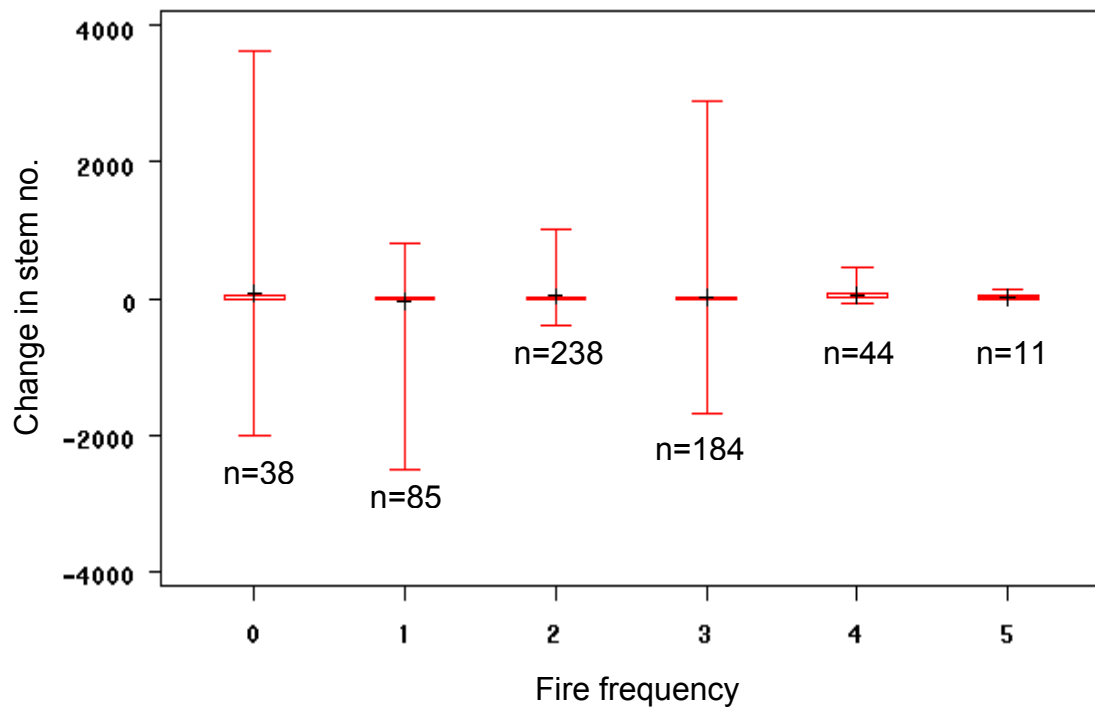
Fig. 6. Boxplot depicting fire frequency effects on the change in stem number of observations across fire frequencies between 1991 and 1999. Fifty percent of the observations were at or near zero as represented by the flat boxes. The relationship was significant at $P = 0.0023$, $X^2_{0.05(5)} = 18.608$ (Kruskal-Wallis).
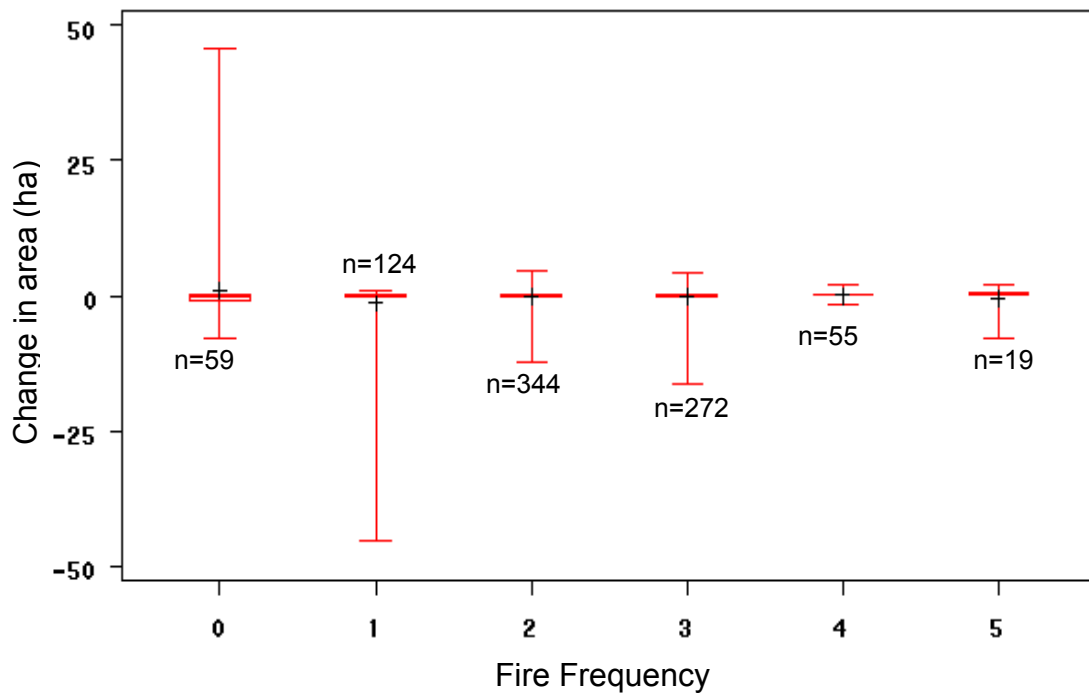
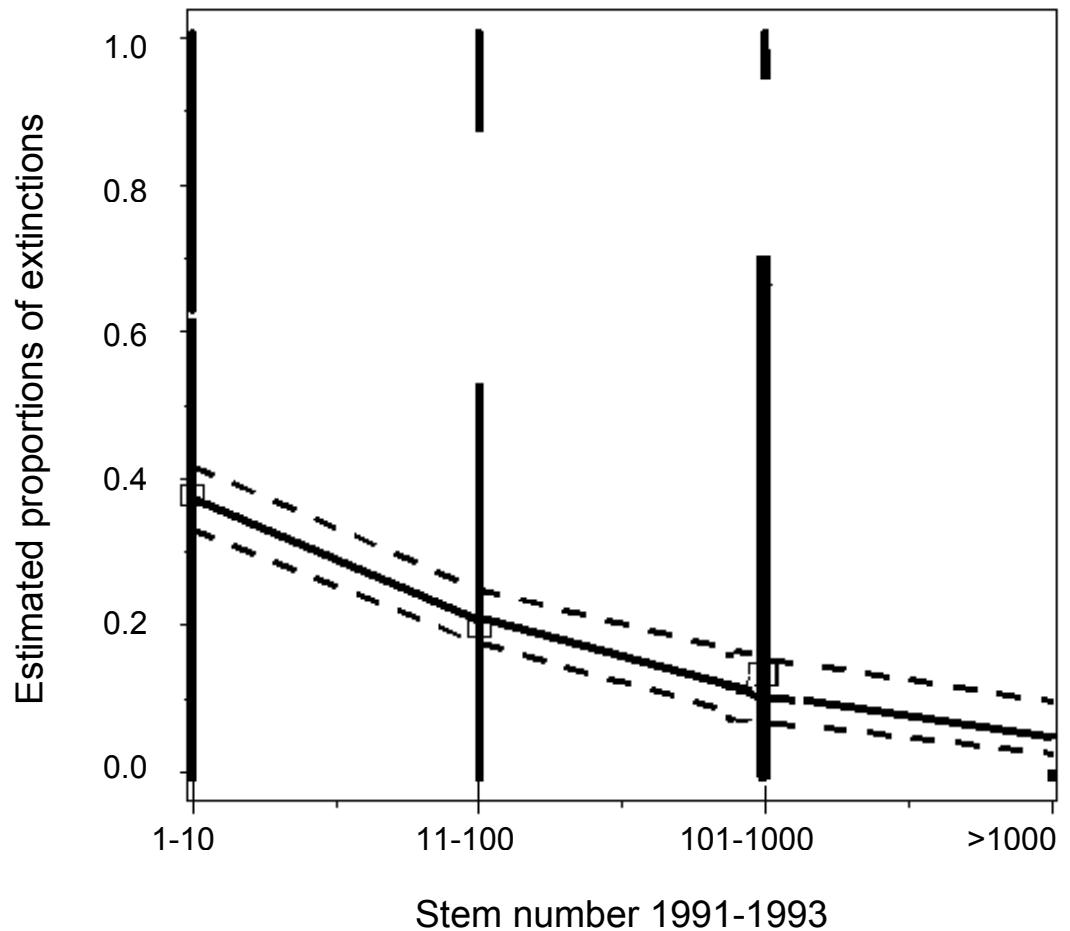Fig. 7. Boxplot depicting fire frequency effects on the change in area occupied of observations across fire frequencies between 1991 and 1999. Fifty percent of the observations were at or near zero as represented by the flat boxes. The relationship was highly significant at P = <0.0001, $X^2_{0.05(5)}$ = 26.309 (Kruskal-Wallis).

Fig. 8. Proportions of extinctions (n=246), assigned a value of 1, contrasted with persistence (n=605), assigned a value of 0 as a function of stem number and 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. The relationship was significant at P = 0.0002, $X^2_{0.05(1)}$ = 13.83. A mirror of this graph is achieved by assigning persistence a value of 1 and extinction a value of 0.
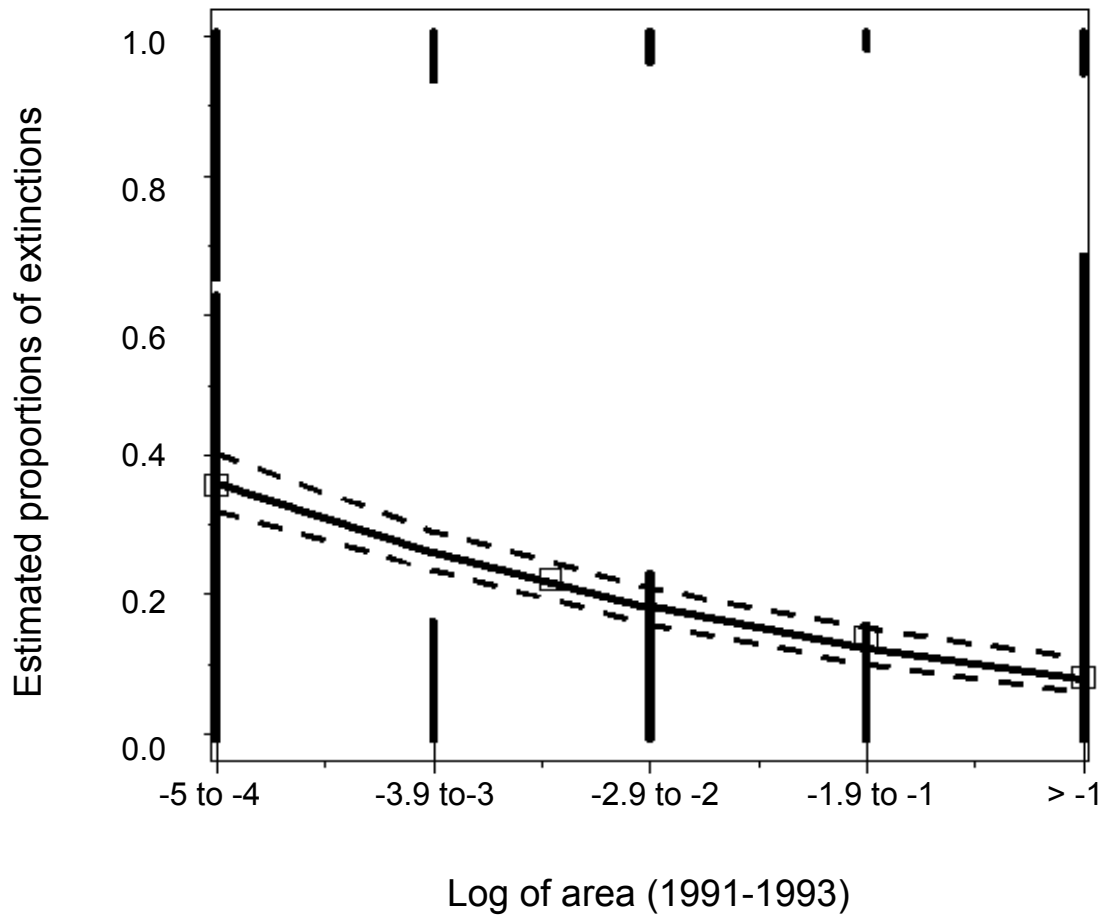
Fig. 9. Proportions of extinctions (n=258) assigned a value of 1, contrasted with persistence (n=885) given a 0 as a function of the log of area and estimated by logistic regression. The broken lines represent the 95% confidence bands on each side of the fitted logistic relation. The observed responses of extinction and persistence at each fire frequency are depicted as bars across the top and bottom of each graph. The relationship was highly significant at P = <0.0001, $X^2_{0.05(1)}$ = 84.10. A mirror image of this graph is achieved by assigning persistence a value of 1 and extinction a 0.
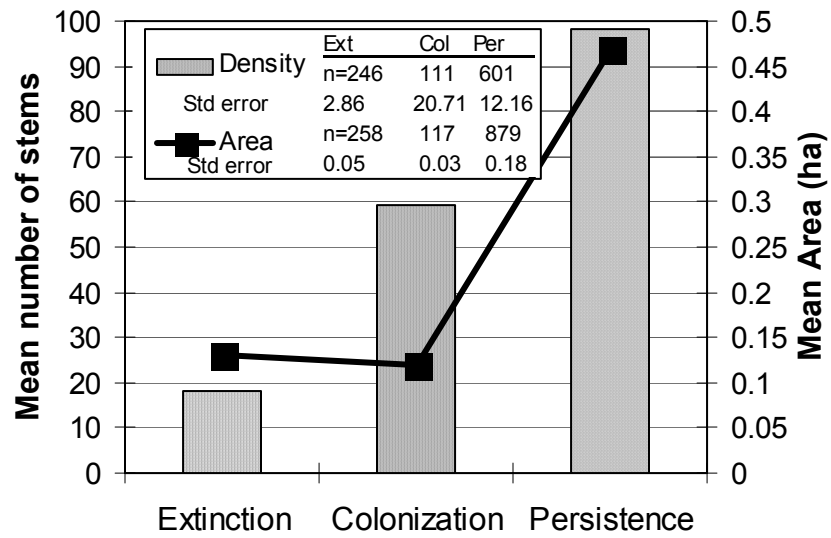
Fig. 10. Mean population size of temporal responses.
Values for colonization and persistence are based on
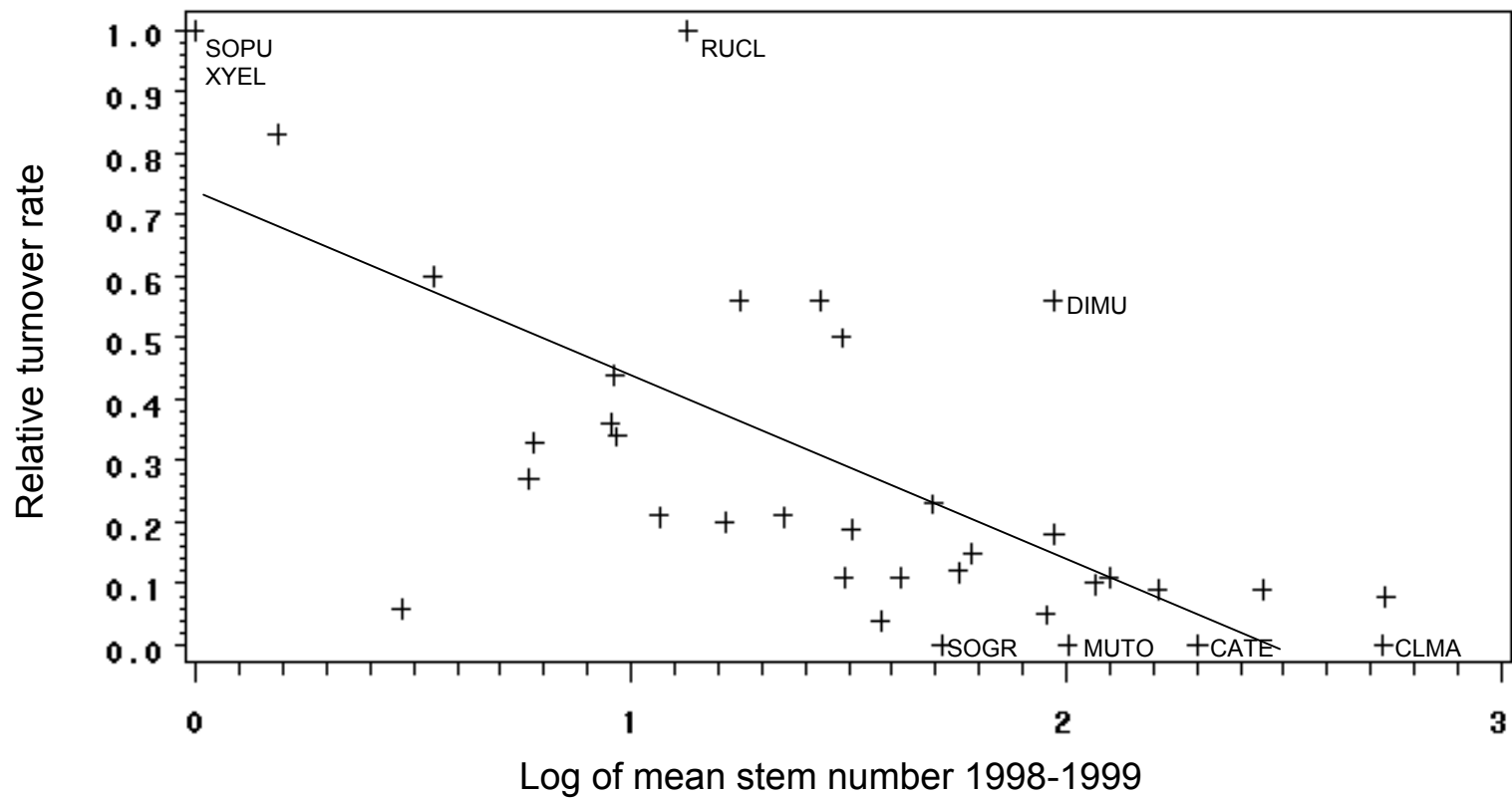1999 data and values for extinction are based on 1991
data.

Fig. 11. Relationship between relative turnover and log of mean stem number of rare flora (n = 36) using 1999 stem counts. The correlation was highly significant at r = -0.6981, P = <0.0001. Species names are abbreviated as follows: CATE: *Carex tenax*, CLMA: *Cladium mariscoides*, DIMU: *Dionaea muscipula*, MUTO: *Muhlenbergia torreyana*, RUCL: *Ruellia ciliosa*, SOGR: *Solidago gracillima*, SOPU: *Solidage pulchra*, XYEL: *Xyris elliotti.*
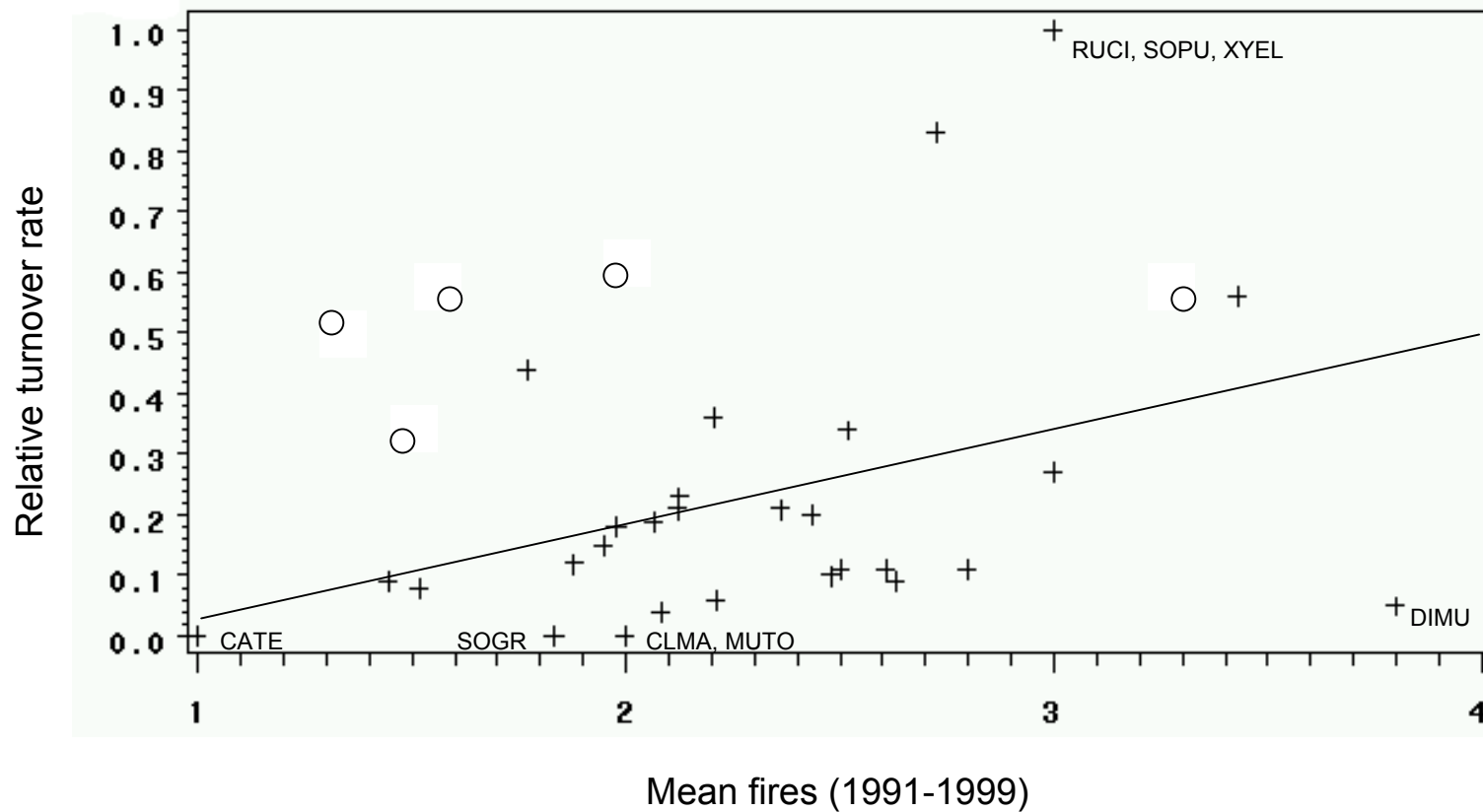
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Fig. 12. Relationship between relative turnover and mean number of fires of rare flora (n=36). The correlation was significant at $r = 0.3590$, $P = 0.0315$. Species names are abbreviated as follows: CATE: *Carex tenax*, CLMA: *Cladium mariscoides*, DIMU: *Dionaea muscipula*, MUTO: *Muhlenbergia torreyana*, RUCI: *Ruellia ciliosa*, SOGR: *Solidago gracillima*, SOPU: *Solidage pulchra*, XYEL: *Xyris elliotti.* Annuals are depicted by circles.