Spatial Distribution of *Penstemon grandiflorus* (Nutt.) and *Geomys bursarius* in a Fragmented Oak Woodland in Minnesota, USA

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ABSTRACT: We tested a method to evaluate the likely vulnerability of a species to the fragmentation of open area that occurs in oak savannas and woodlands in the absence of fire. This method is based on detailed analyses of the current spatial distribution of the species and does not depend on data obtained from long-term monitoring. We used this method to describe and analyze the spatial distribution of an herbaceous perennial, *Penstemon grandiflorus* (Nutt.) and pocket gophers, *Geomys bursarius*, in an oak savanna and woodland in east-central Minnesota (USA) that had not been burned for more than 30 years. In the absence of fire, woody canopy encroached into the open area of the savanna at an average rate of 7 cm $year^{-1}$ during this period. This increase in woody canopy resulted in a 50% reduction of open area and transformed the savanna landscape into a woodland containing 62 openings of different sizes. Analysis of the current spatial distributions of *P. grandiflorus* and *G. bursarius* showed that both species were primarily restricted to open areas and that the abundance of both declined rapidly in the woody edges surrounding openings. Occupancy rates for both species were significantly lower in small openings than in large openings. Both species were absent from most openings less than 100 m^2, while *G. bursarius* always occupied openings greater than 328 m^2 and *P. grandiflorus* always occupied openings greater than 670 m^2. The percent area that was occupied in openings was also positively correlated with opening size for both species. In the case of *G. bursarius*, a decline in opening size of an order of magnitude was associated with a 50% decline in the relative area occupied in openings. In the case of *P. grandiflorus*, an order of magnitude decline in opening size was associated with a decline of relative area occupied of nearly 60%. These results indicate that both species are likely to be vulnerable to further decline and fragmentation of open area in the study site.

Index terms: Geomys bursarius, habitat fragmentation, oak savanna, oak woodland, *Penstemon grandiflorus*

INTRODUCTION

Habitat loss and fragmentation are two of the most important causes of the decline of animal and plant populations worldwide (Klein 1989, Bierregaard et al. 1992, Primack 1993, Meffe and Carrol 1994). In east-central Minnesota, USA, decreased fire frequency has resulted in a decline and fragmentation of open area in native oak savannas (Tester 1989, Faber-Langendoen and Tester 1993, Faber-Langendoen and Davis 1995, Wovcha et al. 1995). Long-term monitoring is the only way to establish definitively if animal or plant species are declining in this threatened habitat as a result of the decline and fragmentation of open area. Unfortunately, few such studies have been undertaken in the past, and data are not available today to make these assessments for the vast majority of species. What is needed is an alternative method that would provide, if not definitive conclusions, a valid empirical basis on which to make such assessments.

One such approach is to analyze in detail the current spatial distribution of target species in the oak savanna/woodland. Such an analysis will provide clues as to whether the species may be in decline, and will indicate whether the species is likely to be vulnerable to further decline and fragmentation of open area. This analysis focuses on three aspects of the species' spatial distribution in the oak savanna/woodland: the relative abundance of the species in open areas compared to areas covered by tree canopy, the abruptness of species decline in the woody edges surrounding openings, and the rate of occupancy and relative abundance of the species in small openings compared to large openings.

The first two aspects of spatial distribution provide clues as to the species' vulnerability to further overall decline in open area. For example, a species commonly found under closed canopy is apparently quite tolerant of closed canopy habitat and, thus, probably would not be very sensitive to further decline of open habitat. On the other hand, a species primarily restricted to open areas, and which declined rapidly in the woody edges surrounding the openings, would appear to be relatively intolerant of closed canopy habitat and, thus, subject to decline if closed canopy habitat increased at the expense of open area.

The third aspect of spatial distribution provides a clue as to the species' vulnerability to further fragmentation of the open area in the oak savanna/woodland. A species that was found to be equally abundant in small openings and large openings would not appear to be experiencing any negative effects due to the fragmentation of open area that was occurring in the absence of fire. However, a species may be experiencing effects of fragmentation if it inhabits small openings less frequently than large openings, and if occupied small openings are more sparsely populated than occupied openings. (By itself, a finding of lower occupancy rates in small openings would not necessarily imply a fragmentation effect. For example, if individuals were independently randomly distributed throughout the open area in a landscape [null model], virtually all large openings would contain at least one individual. However, some small openings would be left unoccupied due to chance, and thus small openings would exhibit a lower rate of occupancy despite the fact that the occupancy sites were determined randomly and no fragmentation effects were involved. But the null model also predicts [based on the assumption of independence] that the relative amount of occupied area [percent area occupied] in small and large openings would be the same, on average.)

Cedar Creek Natural History Area (CCNHA) contains some of the last remnants of native oak savanna and woodland in east-central Minnesota (Wovcha et al. 1995). A controlled burning program was instituted at CCNHA in 1964 to reintroduce fire into parts of these habitats. In sites that experienced no or infrequent burns, woody vegetation has increased while the amount of open area has diminished (Tester 1989, Faber-Langendoen and Tester 1993). Although differences in the vegetation between burned and unburned sites have been documented at CCNHA (Tester 1989, Faber-Langendoen and Tester 1993), no study has quantified the nature and extent of fragmentation of open areas that has occurred in the absence of fire, nor the extent to which fragmentation can be reversed by the reintroduction of fire. Moreover, no one has described and analyzed the current spatial distribution of a resident plant or animal species in the context of the long-term decline and fragmentation of open habitat.

Two species common in the oak savanna/woodland at CCNHA are *Penstemon grandiflorus* (Nutt.), an herbaceous perennial, and the plains pocket gopher, *Geomys bursarius*. Previous studies of *P. grandiflorus* at CCNHA showed that it typically grows in association with the mounds and bare soil patches produced by *G. bursarius*, and that it grows fastest in bare soil and full sunlight (Davis et al. 1991a, Davis et al. 1991b, Davis et al. 1995). Because *G. bursarius* also primarily inhabits grassland and open woodland habitats (Hazard 1982), we anticipated that these two species would be very sensitive to the changing patterns of woody vegetation expected to occur in an oak savanna in the absence of fire. Moreover, owing to the association of *P. grandiflorus* with *G. bursarius*, we also predicted that the pattern of spatial distribution of both species would be similar.

We had three objectives in conducting this study. The first was to quantify the extent of decline and fragmentation of open area that has occurred in a portion of the CCNHA oak savanna/woodland over a 29-year period in the absence of fire. The second was to quantify the extent to which the reintroduction of fire altered the 29-year trend of decline and fragmentation in open area. The third objective was to describe and analyze the current spatial distributions at this site of *P. grandiflorus* and *G. bursarius*, using the approach described above. The combined efforts were undertaken to evaluate the likelihood that either or both species are subject to declining numbers in the absence of fire at this site.

MATERIALS AND METHODS

Study Site

The study area comprised 26.68 ha (460 m x 580 m) of oak savanna/woodland and wetland located at Cedar Creek Natural History Area, East Bethel, Minnesota. CCNHA is situated on a 2,200-km^2 sandplain formed 12,000–13,000 years ago by glacial outwash at the end of the Wisconsin glaciation. Soils in the Cedar Creek oak savanna are well drained and low in organic matter and total nitrogen (Grigal et al. 1974). Aerial photographs dating back to 1938 indicate that approximately 1 ha of the study area was under cultivation in the past and abandoned more than 35 years ago. Pieces of barbed wire on the site suggest that some grazing by domestic animals also took place. Prior to this study, the site had not been burned since 1955. Dominant trees in the study site are bur and northern pin oaks (*Quercus macrocarpa* and *Q. ellipsoidalis*). Openings are dominated by grasses and sedges, including *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans*, *Stipa spartea*, *Panicum* spp., *Carex* spp., and numerous forbs. Owing to the absence of fire for more than 30 years prior to the study, parts of the study area are covered by a nearly closed canopy of oaks and/or a prominent layer of shrubs and understory trees, particularly hazel, sumac, and choke cherry (*Corylus americana*, *Rhus glabra*, and *Prunus virginiana*). (Nomenclature follows Great Plains Flora Association 1986.)

The study site contained a 16-ha grid with 10-m x 10-m cells (Figure 1). Nodes (intersection points) were marked using 1.5-m steel reinforcing bars (9-mm diameter). Ten nodes were additionally marked by a brass plate set in concrete flush with the ground. The purpose of these ten nodes was to designate locations where a 2.4-m-diameter white plywood "X" was placed on the ground shortly before aerial photographs were taken of the study site. These targets, which are visible in the aerial photographs, permit the data obtained on the ground to be accurately linked to landscape patterns identified in the aerial photographs using a Geographic Information System (GIS).

In 1987, the study area was divided into three burn compartments (Figure 1). Burn compartment 1 was burned four times during the study (1987, 1989, 1990, 1992), burn compartment 2 was burned once (1992), and burn compartment 3 was not burned. All burns were conducted in early May in each of the years indicated.

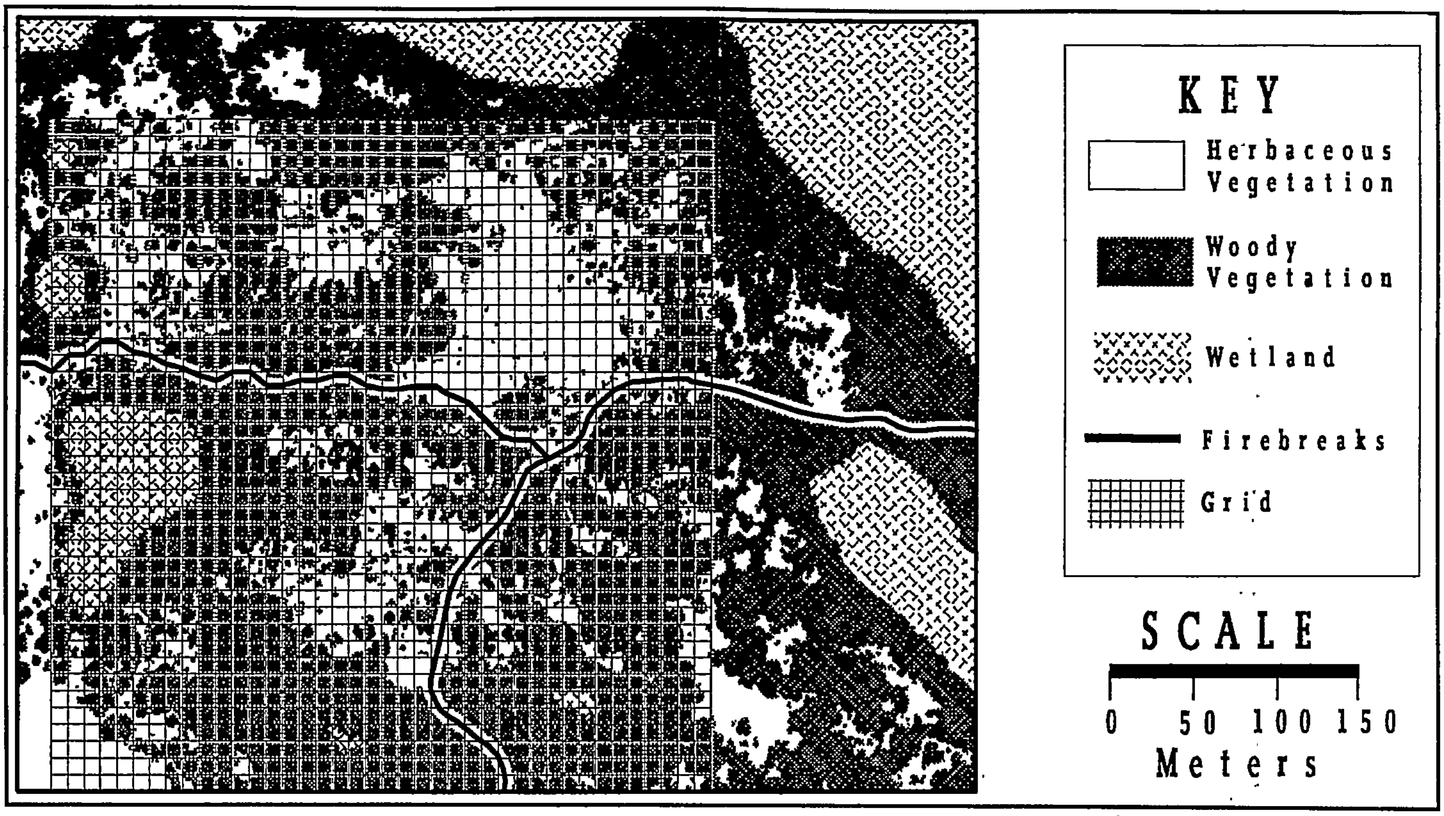

Figure 1. Map of the study area at Cedar Creek Natural History Area, Minnesota, showing 1988 vegetation boundaries, the location of the 16-ha ground grid and the location of the three burn compartments. Burn compartment 1 (burned in 1987, 1989, 1990, and 1992) is located in the lower left portion of the map. Burn compartment 2 (burned in 1992 only) is located above the fire breaks, and burn compartment 3 (unburned) is located in the lower right portion. The map was created by digitizing the vegetation boundaries from a 1988 aerial photograph of the site.

Study Organisms

Penstemon grandiflorus is a perennial forb that grows in well-drained, usually sandy soils in prairies and oak savannas in the Upper Midwest (Great Plains Flora Association 1986, Wovcha et al. 1995). First-year plants have a rosette growth form and usually consist of a single leafy rosette. The size, and sometimes the number, of rosettes increases with age, and eventually one or more flowering stems are produced (Davis et al. 1991a). At CCNHA, this species has been found to grow in association with the mounds and bare soil patches produced by the plains pocket gopher, *Geomys bursarius* (Davis et al. 1991a, Davis et al. 1991b). A previous study of *P. grandiflorus* showed that fire increases the mortality of very small plants; however, the overall impact on the population was found to be quite small (Davis et al. 1991b). The plains pocket gopher lives in grassland and open woodland habitats (Hazard 1982). It is strictly herbivorous, feeding principally on herbaceous vegetation (Behrend and Tester 1988); and its feeding and mound-building habits are known to influence composition and density of surrounding vegetation (Reichman and Smith 1985, Inouye et al. 1987, Reichman 1988, Martinsen et al. 1990). Owing to its fossorial habits, it is doubtful that *G. bursarius* experiences any harmful effects from burns of the type carried out at the study site.

Data Collection

During summer 1990, the number of *P. grandiflorus* plants growing in each of the 1,600 cells in the grid was recorded. The fossorial habits of *G. bursarius* made it impossible to census the animals directly. Instead, we used their mounds and the bare soil patches produced during their excavations as indications of their presence in each grid cell. In April 1992, the amount of bare soil in each cell was estimated using the line intercept method. A line was extended through the middle of each cell and the total length of the line intercepted by patches of bare soil 10 cm in diameter or greater was recorded for each cell. Ten centimeters was chosen as the minimum patch size because the primary interest was in the extent and distribution of bare soil produced by *G. bursarius*, and bare soil patches produced by gophers usually exceed 10 cm in diameter. In the study site, a small proportion of bare soil patches exceeding 10 cm in diameter are produced by thatch ants, *Formica obscuripes*, and woodchucks, *Marmota monax*. For the purposes of this study, bare soil patches created by these two species were ignored. In addition, grid cells containing the dirt fire breaks and the dirt road running through the site were excluded from the analyses.

Aerial photography

On August 9, 1988, a high-resolution overhead photograph was taken of the study site at an altitude of 3,500 m by a commercial photogrammetry firm, Markhurd Corporation, using a precision 24-inch focal length mapping camera and infrared sensitive film (Kodak 2443, 9-inch format). A similar photograph was taken by Markhurd on September 30, 1993, using a 12-inch mapping camera. For both years, Markhurd produced a print of the study site at a scale of 1:1,000. Boundaries of woody vegetation, openings, and wetlands were digitized from these prints using Arc/Info (Environmental Systems Research Institute) software installed on a Tektronix 4319 workstation. The digitized maps were registered to the ground grid using the ground targets described above. A black-and-white aerial photo of the study area taken in 1959 by Markhurd Corporation was also digitized and registered to the 1988 photo using common tree canopies identifiable in both photos.

Landscape analysis

Using a GIS (Arc/Info), separate maps were created for the vegetation boundaries obtained from the 1959, 1988, and 1993 aerial photographs and for the ground grid data (numbers of *P. grandiflorus* plants and percent bare soil per grid cell). Openings were defined to be those areas of herbaceous habitat, excluding wetlands, that were completely surrounded by woody canopy.

Previous studies have shown that most of the woody plant increase in North American savannas that takes place in the absence of fire is the result of perimeter expansion of existing patches of woody plants (Archer et al. 1988, Faber-Langendoen and Davis 1995). This process consists of canopy expansion of existing trees and autogenic succession processes that, driven by soil and microclimate changes produced under existing trees (Callaway et al. 1991, Ko and Reich 1993, Belsky 1994, Belsky and Canham 1994), favor the recruitment of additional woody plants (Archer et al. 1988, Archer 1989). Inspection of the 1988 and 1959 aerial photos indicated that the rate of perimeter expansion was not uniform throughout the study site. To quantify the rate of woody canopy increase in the study site, we used Arc/Info to produce a landscape-wide average rate of perimeter expansion of the woody canopy. This was accomplished by placing succeedingly larger concentric border zones (buffers) around the tree polygons digitized from the 1959 photo until the total tree coverage best approximated the tree coverage of the 1988 photo. The width of this final buffer divided by 29 years was used to calculate a mean annual rate of canopy encroachment. The buffer selected for this calculation produced a "projected" 1988 map that was 99.7% accurate with respect to the percent cover of trees and openings in the "actual" 1988 map.

To record occupancy rates and quantify the area occupied by *P. grandiflorus* plants and patches of bare soil in openings of different sizes and under tree canopies, we used Arc/Info to overlay the grid data with the 1988 vegetation map. An opening was defined as occupied by either *G. bursarius*

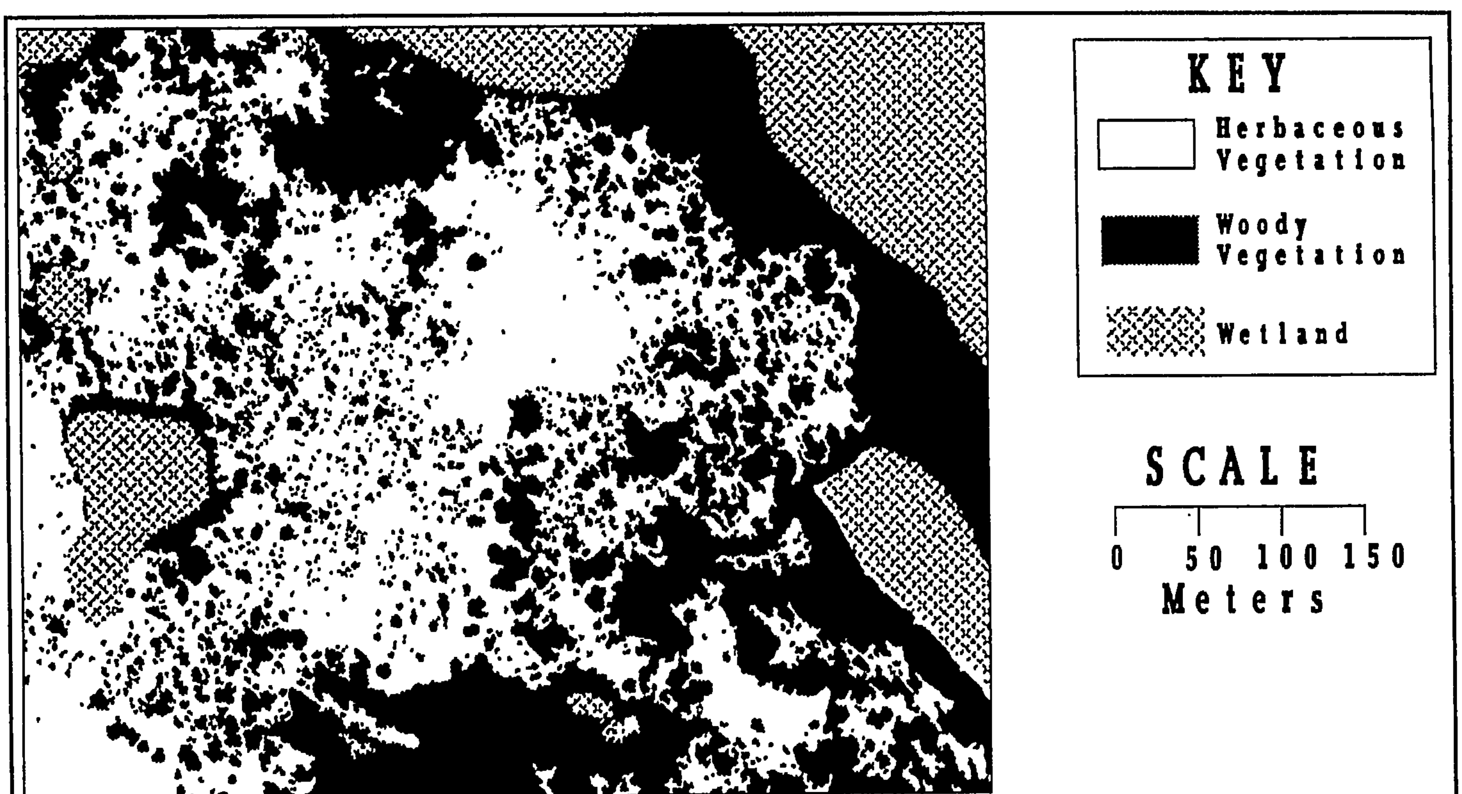

Figure 2. Map of the study area at Cedar Creek Natural History Area, Minnesota, showing 1959 vegetation boundaries. The map was created by digitizing a 1959 aerial photograph of the study site.

or *P. grandiflorus* if the opening overlapped one or more cells that contained at least 1% bare ground, or one *P. grandiflorus* plant, respectively. Arc/Info was also used to quantify the total area of overlap. To quantify the extent to which *P. grandiflorus* plants and bare soil patches extended into the woody vegetation surrounding openings, we used Arc/Info to create a series of six concentric border zones around the openings in the 1988 vegetation map of the study site. These concentric zones extended into the closed canopy area at distances from the woodland edge of 0–1, 1–3, 3–5, 5–7, 7–10, and 10–15m. Arc/ Info was then used to overlay these concentric zones with the grid data, and to calculate the area of overlap as described above.

RESULTS

Vegetation Changes 1959–1993

In 1959 (Figure 2), 41.4% of the 26.68-ha study site was covered by woody canopy, 47.5% was open area, and 11.0% was wetland. In 1959, 95.9% of all open area was contiguous, while the largest tree polygon represented 47.2% of the total tree area. In 1988 (Figure 1), woody canopy cover had increased to 65.8% of the study site and open area had declined to 23.8%. Wetland cover (10.5%) had changed little. In 1988, the largest opening represented only 29.4% of the total open area, while the largest tree polygon represented 95.5% of the total tree area, meaning that virtually all woody canopy had become contiguous, while open area had become fragmented. Total edge area (boundary between tree canopy and opening) declined by 34% during the same time (Table 1). A buffer of 2.05 m around the 1959 tree polygons produced a map that was closest to the actual 1988 landscape. Boundary movement of 2.05 m over 29 years means that, in the absence of fire, woody canopy encroachment into open areas averaged 7 cm year^{-1}.

Between 1988 and 1993, during which east-central Minnesota experienced a major drought and there were three controlled burns on portions of the study site, tree canopy coverage declined by 12.9% (Figure 3, Table 1). Open area increased by 30.5% and many of the openings separated by trees in 1988 had reconnected into a large contiguous opening representing 88.0% of all open area (Figure 3, Table 1). The length of edge area changed little during the same 5-year span, declining by just 1% (Table 1). Tree canopy coverage declined by 21.1% in the area burned three times between 1988 and 1993. In the unburned area, tree canopy coverage declined by 1% during the same period.

Table 1. Changes in the oak woodland landscape of the study area at CCNHA, Minnesota, between 1959 and 1993. Fire was introduced into part of the landscape between 1988 and 1993. The "1988 Projected" column was produced by Arc/Info (see text).

	1959	1988 Actual	1988 Projected	1993
Open Area (m^2) (% of Study Site)	126,860 (47.6%)	63,388 (23.8%)	63,828 (23.9%)	83,327 (31.2%)
No. of Openings	22	98	103	31
Largest Contiguous Opening (m^2) (% of Total Open Area)	121,642 (95.9%)	18,620 (29.4%)	16,689 (26.1%)	73,350 (88.0%)
Woody Canopy Area (m^2) (% of Study Site)	110,588 (41.4%)	175,495 (65.8%)	175,741 (65.9%)	152,787 (57.3%)
No. of Woody Canopy Patches	143	340	173	416
Largest Contiguous Woody Area (m^2) (% of Total Woody Canopy Area)	53,793 (48.6%)	167,626 (95.6%)	156,752 (89.2%)	127,787 (81.0%)
Opening-Woody Canopy Edge (m)	29,855	19,648	23,809	19,860

Spatial Distribution and Occupancy Rates of *P. grandiflorus* and Soil Disturbances by *G. bursarius*

The dirt road and firebreaks occupied portions of 112 of the 1,600 grid cells. Of the 1,488 remaining cells, 564 (37.9%) contained at least 1% bare ground, as recorded by the line transect. *Geomys bursarius* was responsible for the majority (93.2%) of these bare ground patches. The remainder were accounted for by soil rings around thatch ant mounds (4.8%), bare soil around the bases of some of the oak trees (1.6%), and bare soil around woodchuck burrows (0.4%). An analysis of the overlay of the 1988 vegetation map using the 1% bare ground map showed that 70.1% of area in openings overlapped grid cells containing bare ground patches. By comparison, only 24.5% of the wooded area intersected cells containing bare ground patches 10 cm or greater in diameter. These results show the strong association of *G. bursarius* with openings in the woodland. A comparable analysis for *P. grandiflorus* coverage yielded similar results, with 43.5% of the area in openings overlapping with cells containing *P. grandiflorus*, and only 5.0% of the wooded area intersecting with *P. grandiflorus* cells. Of 1,451 *P. grandiflorus* plants recorded in the grid, 1,305 (89.9%) were located in cells with bare ground patches. A log-likelihood G test (Zar 1974) showed that *P. grandiflorus* and bare soil patches are positively associated with one another at the scale of the grid cells ($G=173.53$, $p < 0.0001$).

An examination of bare ground cover in the concentric border zones of woody vegetation surrounding the openings showed that the proportion of woody canopy area overlapped by cells containing at least 1% bare ground was inversely correlated with the

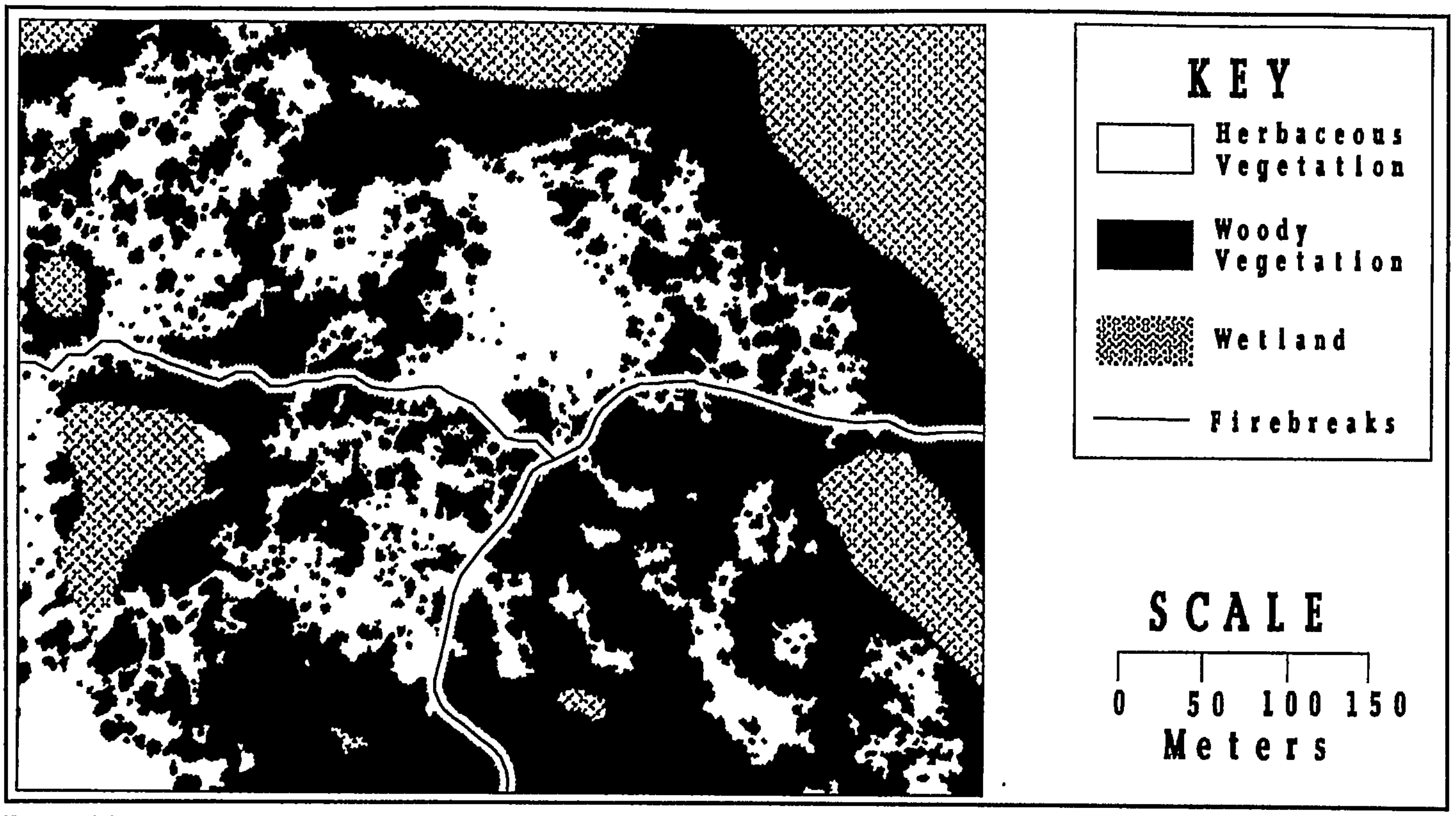

Figure 3. Map of the study area at Cedar Creek Natural History Area, Minnesota, showing 1993 vegetation boundaries. The map was created by digitizing a 1993 aerial photograph of the study site.

distance from the opening (Figure 4a). As shown in Figure 4a, the proportion of woody edge area that overlapped bare ground cells declined by 50% 2 m from the edge of the opening. The same analysis for the *P. grandiflorus* showed that its abundance declined even more abruptly in the woody vegetation surrounding the openings, and that no plants were found more than 8 m from an opening (Figure 4b).

The 16-ha grid encompassed 62 openings, which ranged in size from 7.7 m^2 to 15,153 m^2, with a mean of 699 m^2 ($\pm$ 314) and a median size of 59 m^2. *Geomys bursarius* occupied 33 of these openings, and the mean area of the occupied openings (1,270 $\pm$ 576 m^2) was significantly larger than that of unoccupied openings (49.8 $\pm$ 11.7 m^2, t=3.915, $p < 0.0002$, area log transformed prior to analysis). *Geomys bursarius* was always found in openings larger than 328 m^2. Fourteen openings were occupied by *P. grandiflorus*, and the mean area of these openings (2873 $\pm$ 336 m^2) was also significantly larger than the area of unoccupied openings (65.4 $\pm$ 12.3 m^2, t=5.51, $p < 0.0001$). *Penstemon grandiflorus* was always found in openings larger than 670 m^2 and never occupied an opening that was not also occupied by *G. bursarius*. The occupancy rates of small (<100 m^2, n=42), medium (100–999 m^2, n=15) and large (>1,000 m^2, n=5) openings differed significantly for both species (*G. bursarius*: X^2=16.31, $p < 0.001$; *P. grandiflorus*: X^2=35.02, $p < 0.001$), with small openings having the lowest rates of occupancy and large openings the highest (Figure 5a). Overall, the two species were found to be positively associated with each other at the level of the opening (X^2 = 12.18, $p < 0.001$).

The percent area of an opening that was occupied increased with opening size for both species (*G. bursarius*: r= 0.405, $p < 0.002$; *P. grandiflorus*: r=0.711, $p < 0.001$; Spearman Rank Correlation Analysis). The three opening sizes differed in the percent area occupied by both species (*G. bursarius*: H=13.51, $p < 0.001$; *P. grandiflorus*: H=18.95, $p < 0.001$; Kruskal-Wallis Test), with the percent area occupied being lowest in the small openings and highest in the large openings (Figure 5b).

DISCUSSION

The current spatial distributions we documented for *P. grandiflorus* and *G. bursarius* are consistent with what would be expected for species that had been experiencing a long-term decline in abundance due to the decline and fragmentation of open area. Specifically, both species showed a strong association with openings and both declined greatly in the wooded area surrounding the openings. Both species also exhibited occupancy rates that were lower in small openings than in large openings, and the percent area occupied was also lower in the small openings. In the case of *G. bursarius*, the data showed that a reduction in opening size of an order of magnitude was associated with a 50% reduction in the relative area occupied in openings. In the case of *P. grandiflorus*, an order of magnitude reduction in opening size was associated with a nearly 60% reduction of relative area occupied, with

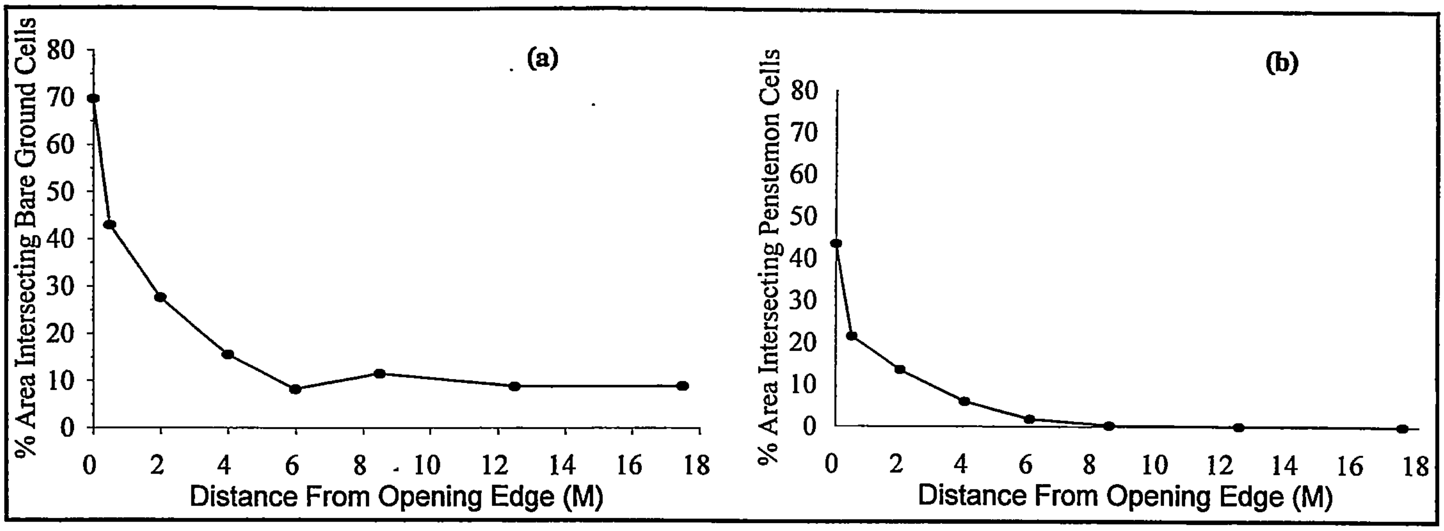

Figure 4. The percent of 1988 woody canopy area intersecting grid cells containing (a) bare ground, and (b) *Penstemon grandiflorus*, shown as a function of distance from the edge of the openings in the study site. Data were obtained for concentric border zones around the openings. These border zones extended 0–1, 1–3, 3–5, 5–7, 7–10, 10–15, and >15 m from the opening edges. The values are presented at the midpoint of the respective concentric zones: 0.5, 2, 4, 6, 8.5, and 12.5. The value given for a distance of 0 m is the percent of area in the openings that intersected grid cells containing bare ground. The value provided for a distance of 17.5 m is the percent area under woody canopy that was >15 m from the opening edge.

openings less than 100 m^2 in size being almost entirely unoccupied by *P. grandiflorus*. The results indicate that both species probably are vulnerable to further decline and fragmentation of open area in the study site.

The question remains as to why occupancy rates of both species were lower in small openings. Apparently not due to chance, this finding must be the result of either unfavorable conditions in small openings or difficulties faced by both species in finding the small openings in the first place, or it may result from a combination of these two factors. Data are not available to assess the importance of the second possibility, but it is likely that small openings do provide suboptimal conditions for both species. Since territories of *G. bursarius* at Cedar Creek typically exceed 1,000 m^2 (Zinnel 1992), many small openings are not large enough to support an individual, even assuming some foraging beyond the edge of an opening or in nearby openings. Similarly, since *P. grandiflorus* is known to grow best in patches of bare soil in the open sun (Davis et al. 1991a, 1991b, 1995), small openings with less bare soil (this study) and more shade from the trees surrounding the opening would provide less favorable habitat than large openings.

In conclusion, the results from this study indicate that both *P. grandiflorus* and *G.*

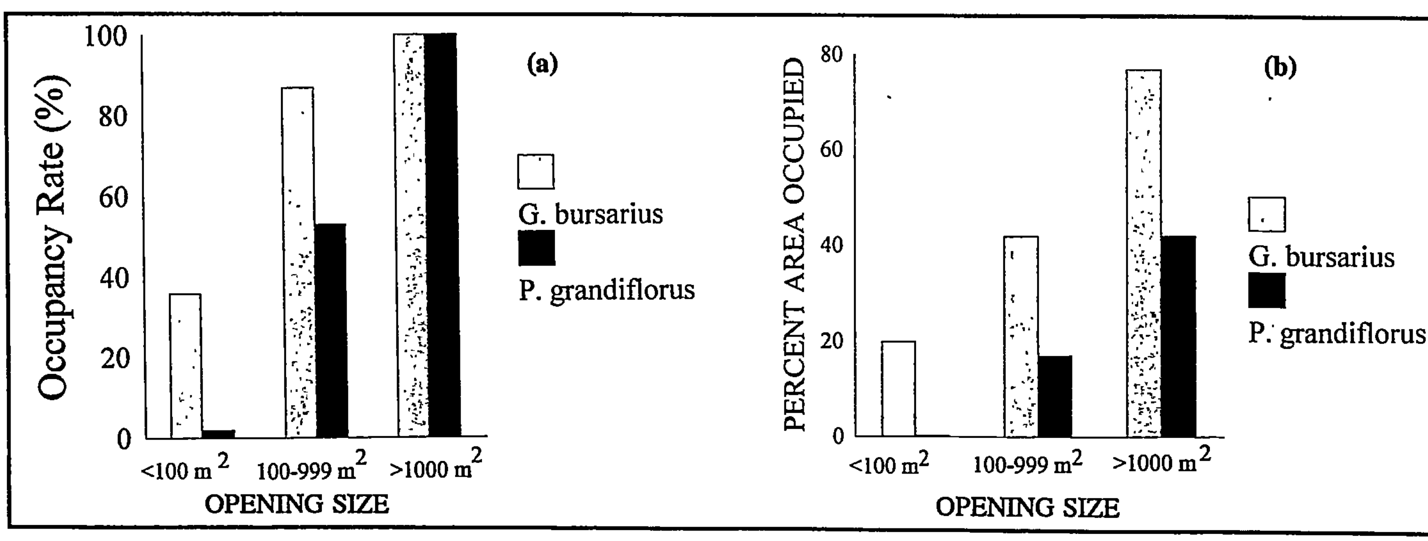

Figure 5. (a) The rate of occupancy by *G. bursarius* and *P. grandiflorus* in openings of different size in the oak savanna/woodland. Data based on 42 small (< 100 m^2), 15 medium (100–1,000 m^2), and 5 large (>1,000 m^2) openings. (b) The mean percent area occupied by *G. bursarius* and *P. grandiflorus* in openings of different size in the oak savanna/woodland.

bursarius would most likely become less abundant if the decline and fragmentation of open area were to continue at the study site. Conversely, the results indicate that both species should benefit from the increase of connected open area that has begun to occur with the reintroduction of fire. Finally, this study shows how a detailed analysis of current spatial patterns of a species can be used to evaluate the species' vulnerability to future decline and fragmentation of its habitat. It should be noted that although the examples presented here are of species inhabiting fragmented open areas, the approach should be equally applicable to species inhabiting forest fragments.

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Mark Davis is Professor of Biology at Macalester College, where he teaches and provides undergraduates with field research opportunities. During the past 10 years, 22 Macalester undergraduates have worked with him on his research in the oak savanna and woodland at Cedar Creek. Four of these students were coauthors on this paper.

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