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ORIGINAL PAPER

# Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone

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**Abstract** Disturbances and environmental heterogeneity are two factors thought to influence plant species diversity, but their effects are still poorly understood in many ecosystems. We surveyed understory vegetation and measured tree canopy cover on permanent plots spanning an experimental fire frequency gradient to test fire frequency and tree canopy effects on plant species richness and community heterogeneity within a mosaic of grassland, oak savanna, oak woodland, and forest communities. Species richness was assessed for all vascular plant species and for three plant functional groups: grasses, forbs, and woody plants. Understory species richness and community heterogeneity were maximized at biennial fire frequencies, consistent with predictions of the intermediate disturbance hypothesis. However, overstory tree species richness was highest in unburned units and declined with increasing fire frequency. Maximum species richness was observed in unburned units for woody species, with biennial fires for forbs, and with near-annual fires for grasses. Savannas and woodlands with intermediate and spatially variable tree canopy cover had greater species richness and community heterogeneity than old-field grasslands or closed-canopy forests. Functional group species richness was positively correlated with functional group cover. Our results suggest that annual to biennial fire frequencies prevent shrubs and trees from competitively excluding grasses and prairie forbs, while spatially variable shading from overstory trees reduces grass dominance and provides a wider range of habitat conditions. Hence, high species richness in savannas is due to both high sample point species richness and high community heterogeneity among sample points, which are maintained by intermediate fire frequencies and variable tree canopy cover.

**Keywords** Community heterogeneity · Intermediate disturbance hypothesis · Oak savanna · Oak woodland · Prescribed fire · Species richness

## Introduction

Competitive exclusion, disturbance processes, and environmental heterogeneity are three key determinants of plant species diversity in terrestrial ecosystems (Whittaker 1975; Connell 1978;

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Huston 1994). Competitive exclusion reduces species diversity as strong competitors first suppress lesser competitors and later drive them to local extinction. Environmental heterogeneity can promote high species diversity by promoting spatial niche partitioning and heterogeneity in plant community composition across environmental gradients ($\beta$ diversity; Whittaker 1975). Disturbances can reduce plant species diversity by eliminating disturbance-sensitive species, increase species diversity by opening up growing space and resources for use by colonizing species, maintain species richness by slowing or preventing competitive exclusion, and alter spatial heterogeneity in plant community composition (Huston 1994).

Ecological theory predicts important linkages between disturbance frequency and species diversity (Grime 1973; Connell 1978; Huston 1979). The intermediate disturbance hypothesis (IDH, Connell 1978; Huston 1979) predicts that species diversity will be maximized at intermediate disturbance frequencies and severities that minimize species losses due to competitive exclusion and direct disturbance effects, while maintaining opportunities for establishment of new species. Although the IDH is well studied (Roxburgh et al. 2004), species diversity responses to fire frequency often do not follow predicted patterns. In tallgrass prairie, species richness declines with increasing fire frequency as higher fire frequencies favor the dominant $C_4$ grasses and reduce community heterogeneity (Collins 1992; Collins et al. 1995; Collins and Steinauer 1998). In savannas and woodlands, species richness often increases with increasing fire frequency up to biennial (Tester 1989; Brockway and Lewis 1997) or annual (Walker and Peet 1983) fires. However, rigorous tests of the IDH have been few in savannas and woodlands, in part due to the scarcity of long-term studies using a wide range of fire frequency treatments applied to large plots. Without sufficient replication of treatments in time and space, tests of the IDH may produce ambiguous results (Beckage and Stout 2000).

Fire frequency may also influence understory species richness indirectly in savanna, woodland, and forest ecosystems through its influence on overstory tree density and canopy cover. Huston (1994) proposed that high fire frequencies promote high species richness in savannas by preventing competitive exclusion of grasses and forbs by woody plants. Furthermore, understory plant community composition and diversity in savannas often varies across gradients in understory light and soil resources associated with spatial variability in overstory tree cover (Bray 1958; Belsky et al. 1989; Vetaas 1992; Scholes and Archer 1997; McPherson 1997; Brewer 1998). Thus, high plant community heterogeneity and overall species richness may be observed in savannas with intermediate and spatially variable tree canopy cover (Leach and Givnish 1999) due to high plant resource heterogeneity. High species richness in fire-maintained savannas (compared to neighboring forests and grasslands) may also be the result of intermediate resource availability that reduces dominance and competitive exclusion by both woody plants and grasses and allows greater forb species richness (Leach and Givnish 1999). Although fire frequency and tree canopy (or understory light) effects on species diversity have each been investigated separately, we are aware of only one previous study that explicitly examined the potential influence of tree canopy structure (basal area) on the relationship between fire frequency and plant species diversity (Mehlman 1992).

Prior to modern settlement, fires annually burned large areas of the tallgrass prairie biome of North America (Gleason 1913). At the forest-prairie biome transition zone, topographic barriers to the spread of wildfire created spatial heterogeneity in fire frequency and vegetation structure (Gleason 1913; Grimm 1984; Leitner et al. 1991). Grasslands and oak savannas occupied areas with high and medium fire frequencies, while oak woodlands and deciduous forests occupied areas with low fire frequencies (Gleason 1913; Grimm 1984; Leitner et al. 1991). Decades of land-use change, landscape fragmentation, and active fire suppression have largely excluded wildfires and produced dramatic losses of intact oak savannas to the point where they are now rare (Nuzzo 1986). Management with prescribed fire (or fire surrogates) may be necessary if restoration of oak savanna ecosystems is a priority. Yet, long-term effects of different prescribed fire regimes on oak savanna vegetation, and particularly plant species diversity, are not well understood.

The purpose of this study was to assess the combined effects of fire frequency and overstory canopy structure on plant species diversity within an area of the prairie-forest biome transition zone in central North America. Plant species diversity was assessed in terms of species richness and community heterogeneity (a measure of $\beta$ diversity). Fire frequency and tree canopy cover effects on species richness were assessed at both the plant functional group (grasses, forbs, and woody plants) and whole plant community levels. We tested the following hypotheses related to fire frequency and canopy cover effects on plant species diversity:

1. Species richness will be greatest at an intermediate fire frequency that minimizes species losses due to fire and competition while promoting new species establishment (intermediate disturbance hypothesis).
2. The fire frequency at which species losses to fire and competition are minimized will vary among plant functional groups due to mean differences in fire adaptations, ability to colonize following disturbance, and competitive ability (vital attributes corollary to IDH).
3. Species richness will be higher in savannas than in grasslands or woodlands due to intermediate resource availability that limits dominance by grasses and woody plants and promotes high forb diversity (intermediate resource hypothesis).
4. Community heterogeneity will be higher in savannas than in grasslands or forests due to spatial variability in overstory canopy structure and associated plant resources (resource heterogeneity hypothesis).

While the focus of this paper is on plant species diversity, related papers from this study provide information about overstory tree structure and dynamics (Peterson and Reich 2001), factors influencing plant functional group cover (Peterson et al. 2007), and carbon and nitrogen dynamics (Reich et al. 2001).

## Methods

### Study area

The study was conducted at Cedar Creek Natural History Area (CCNHA), a 2,300 ha reserve located on the Anoka Sand Plain in east-central Minnesota (45°25′ N, 93°10′ W). The climate is humid continental, with cold winters and warm summers. Mean daily temperature ranges from –11°C in January to 22°C in July. Mean annual precipitation is 790 mm, more than half of which falls during the growing season (May–September). Soils are well-drained sands of the Sartell and Zimmerman series (Grigal et al. 1974), terrain is relatively flat, and erosion after prescribed fires is minimal.

CCNHA lies within the transition zone between the tallgrass prairie and temperate deciduous forest biomes in central North America. Upland areas currently support a mosaic of forests, woodlands, savannas, and old fields, which are floristically similar to the southern dry forest, oak barren, and dry-mesic prairie types described by Curtis (1959). Northern pin oak (*Quercus ellipsoidalis* E.J. Hill) and bur oak (*Quercus macrocarpa* Michx.) are the dominant tree species.

### Prescribed burning experiment

Prescribed fire programs were initiated at CCNHA and the adjacent Helen Allison Savanna (a 20-ha oak savanna reserve owned by the Nature Conservancy) in the early 1960s within more than 200 ha of mixed oak woodlands, oak savannas, and old-field grasslands. Treatments were designed to test fire frequency effects on the structure and species composition of oak savannas and woodlands and to restore and maintain the historically important oak savanna ecosystems (Irving 1970; Faber-Langendoen and Davis 1995). Management units (1–30 ha each) originally containing savanna and/or woodland structure were randomly assigned fire frequency treatments ranging from annual and biennial fires to complete fire exclusion. Additional management units were added to the prescribed fire programs in the 1980s. Canopy cover has increased with continued fire exclusion in some unburned units (Faber-Langendoen and Davis (1995), adding closed-canopy forest conditions to the structural gradient. Old-fields were embedded within some management units and have remained relatively stable structurally. Management units are protected from livestock grazing, but herbivory by white-tailed deer (*Odocoileus virginianus*), pocket gophers (*Geomys bursarius*), and insects does influence plant and nutrient dynamics in these systems (Inouye et al. 1987; Ritchie et al 1998).

Prescribed fires were conducted mostly between mid-April and mid-May, prior to leaf expansion in overstory trees (Peterson and Reich 2001). Most understory plants (except for some cool-season grasses and spring forbs) do not initiate aboveground growth until mid-May, so the fires generally consumed dead plant material. Fires were usually ignited using the strip headfire technique with prescribed weather conditions of 15–25°C air temperature, 25–45% relative humidity, and winds less than 20 kph. Fire behavior varied with weather conditions and fuel loads, but fire prescriptions were written to produce fires of low intensity, and mean flame lengths were typically less than 1 m (personal observation). Management units were burned 0–26 times during 1962–1995. We defined realized fire frequency as the total number of prescribed fires divided by the number of years the unit was part of the prescribed fire experiment. We defined the starting year as the year prior to the first fire. Realized fire frequencies ranged from complete fire exclusion to about eight fires per decade for the near-annual fire treatment.

## Field sampling

We sampled vegetation on 26 permanent plots established in savanna, woodland, and forest stands within the prescribed fire management units. Each plot consisted of four parallel 50-m long sampling transects placed 25 m apart, encompassing a total area of 0.375 ha. We placed understory vegetation sampling points at 10-m intervals along each transect (24 sample points per plot). Management units contained one or two plots each; where management units contained two plots, the plots represented areas with different initial overstory structural conditions. In three prescribed fire management units, we also sampled vegetation on temporary plots in old-field grassland areas to expand the range of overstory structural conditions studied (total = 29 plots).

In summer 1995, we surveyed understory vegetation at each of the 696 sample points using quadrat sampling methods adjusted for herbaceous and woody plants. We assessed herbaceous species richness (and cover) at each sample point based on visual cover estimates within a rectangular frame (0.5 $m^2$). We assessed woody plant species richness (shrubs, trees, and vines) based on stem count surveys within a 1-m radius circular quadrat (3.14 $m^2$), but estimated total woody plant cover using the 0.5-$m^2$ rectangular frames (Peterson et al. 2007). We used larger sampling areas for woody plant species richness to compensate for larger mean plant sizes and generally lower plant densities. We obtained overstory tree species richness for each plot from a complete survey of living trees (diameter ≥5 cm). Most of the units receiving prescribed fire treatments had been burned within 2 years of sampling. We attempted to survey plots at times when understory plant cover was near maximum and most species could be detected and accurately identified. As a result, we surveyed woodland and forest plots in late June and July and savanna plots in August.

We measured tree canopy cover, the fraction of sky obscured by overstory trees, at each sample point (24 per plot) during the summer growing season using a Plant Canopy Analyzer (LAI-2000, LI-COR, Lincoln, Nebraska, USA). To measure tree canopy cover, we positioned the sensor at the top of the shrub layer at each sample point (up to a maximum height of about 2 m), using a 270° lens cap (90° occluded), and matched readings with simultaneous readings from a paired sensor in a nearby old-field grassland. Canopy cover values are closely related to understory light levels (Machado and Reich 1999) and local stand basal area (Peterson 1998). Averaged over a plot, canopy cover is also a good indicator of aboveground net primary productivity and nitrogen cycling rates (Reich et al. 2001).

### Data analysis

We calculated species richness, the number of unique species in a sample or group of samples, for individual sample points (quadrat species richness) and for all samples pooled within a plot (plot species richness). We calculated quadrat species richness as the sum of herb species richness (grasses and forbs) from the herbaceous survey (0.5 $m^2$ quadrat) and woody plant species richness from the understory shrub and tree survey (3.1 $m^2$ quadrat). Plot species richness was the number of unique plant species in the pooled sample from all 24 sample points in a plot. We also calculated species richness for three plant functional groups: woody plants (understory trees, shrubs, and vines), forbs, and grasses (grasses and sedges).

We calculated community heterogeneity as the mean dissimilarity of species lists for all pairwise combinations of sample points within a plot. We used the Sorensen similarity index, $C_s = 2j/(SR_a+SR_b)$, to calculate similarity between pairs of sample points, where $SR_a$ and $SR_b$ are quadrat species richness values for quadrats a and b, and j is the number of species common to both quadrat samples. We calculated dissimilarity as the complement of similarity, $1 - C_s$. To quantify community heterogeneity among plots, we used Whittaker's beta statistic, $\beta_W = TSR/PSR_{avg}$, where TSR is the number of unique plant species in the pooled sample from all 29 plots in the study and $PSR_{avg}$ is the mean plot species richness (Magurran 1988).

We used hierarchical linear modeling (Raudenbush and Bryk 2002) with SAS PROC MIXED (Littell et al. 1996) to model combined fire frequency and tree canopy cover effects on total and plant functional group species richness at the sample point level. To reduce heteroscedasticity in model residuals, we transformed sample point species richness values with a square root function prior to analysis. The level-1 model was $SR_{ij} = \beta_0 + \beta_1 \cdot CC_{ij} + \beta_2 \cdot CC_{ij}^2 + r_{ij}$, where $SR_{ij}$ is species richness, $CC_{ij}$ is local tree canopy cover, and $r_{ij}$ is a random error for sample point j on plot i. We modeled the $\beta_0$ coefficient as a function of fire frequency (linear and quadratic) and a plot-level random variable, and modeled the $\beta_1$ and $\beta_2$ coefficients as functions of fire frequency (linear term only) and plot-level random variables.

## Results

We encountered 190 vascular plant species. Of this total, 38 were grass and sedge species, 39 were shrubs and trees, and 113 were forbs. Plot species richness varied between 32 and 71 species (mean = 55) and mean quadrat species richness varied between 8.8 and 16.6 species. Beta diversity among plots was 2.6 for woody species, 3.0 for grasses, 4.2 for forbs, and 3.5 for all plants. About half of the plant species were relatively rare, being recorded at fewer than 10 sample points.

Overstory tree species richness was highest on plots protected from fire and declined with increasing fire frequency (Fig. 1). Only two tree species, bur oak (*Quercus macrocarpa*) and northern pin oak (*Q. ellipsoidalis*), were present on plots with the highest fire frequencies. Plots protected from fire typically contained shade-tolerant, fire-sensitive species (e.g., *Acer*

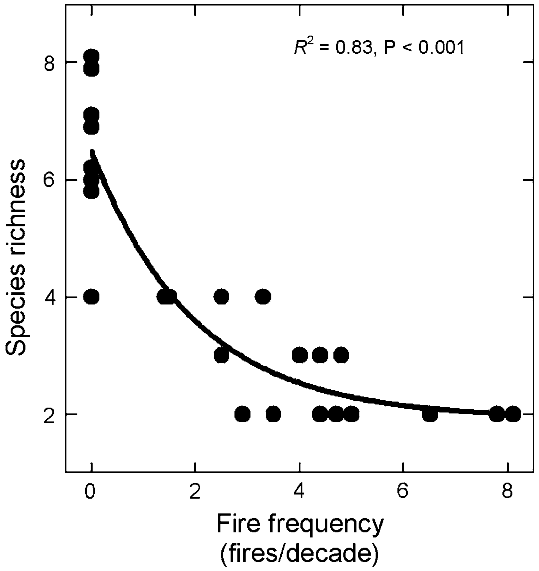

**Fig. 1** Fire frequency effects on overstory tree species richness. Regression line is based on a negative exponential function. Old-field plots were omitted from this analysis because the absence of overstory trees (SR = 0) on these plots was caused primarily by human removal prior to cultivation rather than by fire effects

*rubrum*, *Prunus serotina*) in addition to the oaks. Old-field grassland plots contained no overstory trees.

Total understory plant species richness (plot level) was maximized at an intermediate fire frequency of about five fires per decade, consistent with the predictions of the intermediate disturbance hypothesis (Fig. 2a). The fire frequency at which plot-level species richness was maximized varied among plant functional groups, however, consistent with the predictions of our vital attributes corollary to the IDH. Woody plant species richness was highest in plots protected from fire and declined with increasing fire frequency (Fig. 2b). Forb species richness increased with fire frequency to a maximum at about five fires per decade, but declined somewhat at higher fire frequencies (Fig. 2c). Grass species richness was lowest in plots protected from fire and generally increased with fire frequency, although grass richness tended to level off at fire frequencies greater than five fires per decade (Fig. 2d).

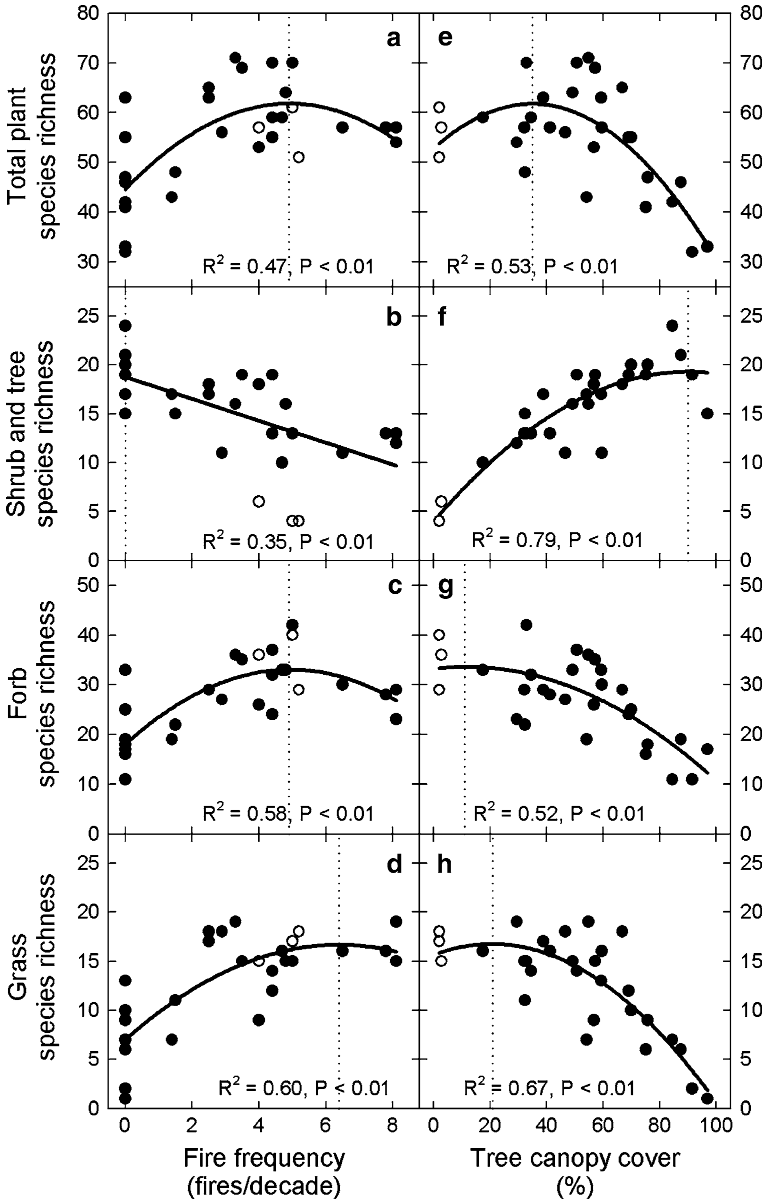

**Fig. 2** Fire frequency and tree canopy cover effects on plant species richness at the plot level. Species richness values are for all plants (**a**, **e**), woody plants (**b**, **f**), forbs (**c**, **g**), and grasses (**d**, **h**). Open circles indicate old-field grassland plots. Solid lines indicate significant linear or quadratic relationships based on regression analysis. Vertical dotted lines indicate fire frequency or mean tree canopy cover values with maximum predicted species richness

Plant species richness was highest on savanna and woodland plots with intermediate mean tree canopy cover (20–70%), as predicted by our intermediate resource and resource heterogeneity hypotheses (Fig. 2e). Woody plant species richness increased monotonically with mean tree canopy cover up to about 95% (Fig. 2f). Grass and forb species richness were maximized on grassland and savanna plots with mean tree canopy cover up to 50%, but then declined with further increases in canopy cover (Fig. 2g, h).

Plant functional group species richness was significantly correlated with mean functional group cover both within and between most plant functional groups. Understory woody plant species richness increased with mean understory woody plant cover to a maximum at about 60% cover and remained relatively constant at higher cover levels (Fig. 3c). In contrast, forb and grass species richness declined with increasing understory woody plant cover (Fig. 3a, b), with the relationship particularly strong for grasses.

Functional group species richness was also significantly correlated with mean grass cover (Fig. 3g–i), but only weakly correlated with mean forb cover (Fig. 3d–f). Grass species richness increased with mean grass cover up to a maximum at 20–35% grass cover, but declined slightly with higher cover (Fig. 3g). Forb species richness was positively correlated with mean grass cover (Fig. 3e) and mean forb cover (Fig. 3h). In contrast, species richness of understory woody plants declined with increasing mean grass cover (Fig. 3i). Grass species richness was unrelated to mean forb cover (Fig. 3d), and woody plant species richness was only weakly related to forb cover after low values from old-field plots were dropped from the analysis (Fig. 3f).

The mixed model analysis indicated significant combined effects of fire frequency and tree canopy cover on total plant species richness and functional group species richness at the sample point level (Fig. 4). Total plant species richness was maximized on partially shaded sites (30–60% tree canopy cover) within units burned

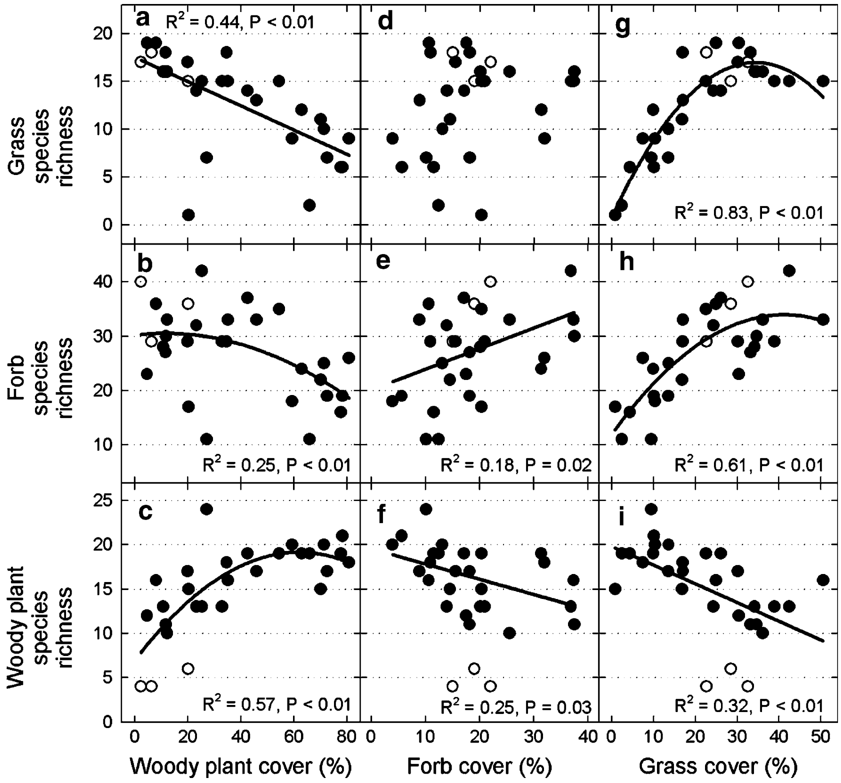

**Fig. 3** Relationships between cover and species richness, within and between plant functional groups. Open symbols represent old-field plots. Lines indicate significant linear or quadratic relationships based on regression analysis

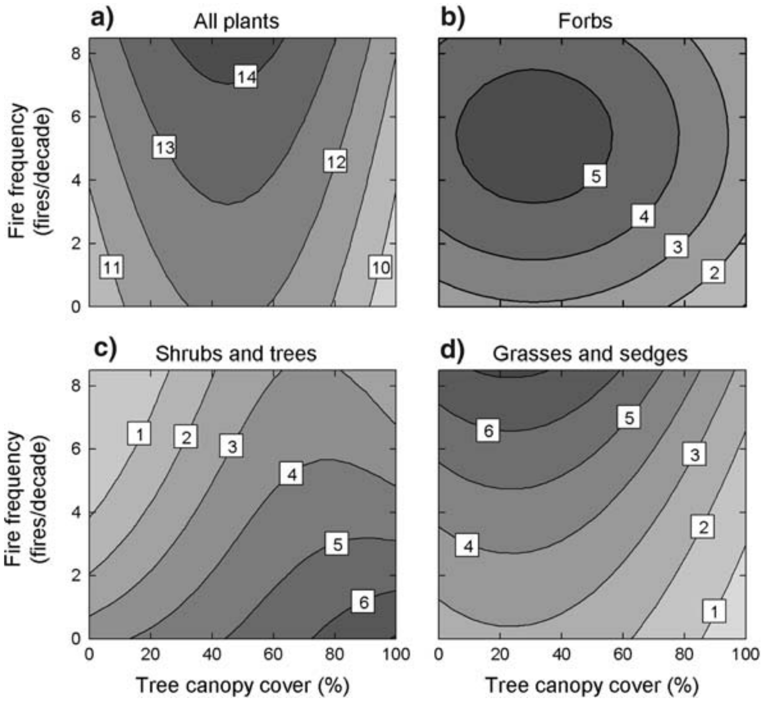

**Fig. 4** Response-surface models of fire frequency and tree canopy cover effects on plant species richness at the sample point (0.5–3.1 m$^2$) scale for (**a**) all plants, (**b**) forbs, (**c**) woody plants, and (**d**) grasses. Contour lines indicate predicted species richness from hierarchical linear modeling

6–8 times per decade (Fig. 4a). Forb species richness was maximized on partially shaded sites (10–50% tree canopy cover) within units burned 4–7 times per decade (Fig. 4b). Understory woody species richness was highest on shaded sites (70–100% tree canopy cover) that were protected from fire, and declined at higher fire frequencies and with reduced shading (Fig. 4c). In contrast, grass species richness was highest on open to partially shaded sites (0–60% local tree canopy cover) with near-annual fire frequencies and declined at lower fire frequencies and with increased shading (Fig. 4d).

Community heterogeneity within plots varied from a low near 0.4 in closed canopy oak forest to a high near 0.7 for savannas with well-defined tree and grass patches (Fig. 5). On average, community heterogeneity was greatest at intermediate fire frequencies (about five fires per decade) and in savannas and woodlands with 30–60% mean tree canopy cover (Fig. 5a, b). Consistent with our resource heterogeneity hypothesis, community heterogeneity was positively correlated with the variance in tree canopy cover (Fig. 5c), which was also greatest on sites with 30–60% mean tree canopy cover. Combined, fire frequency and the variance in tree canopy cover accounted for 57% of the variability in community heterogeneity among plots.

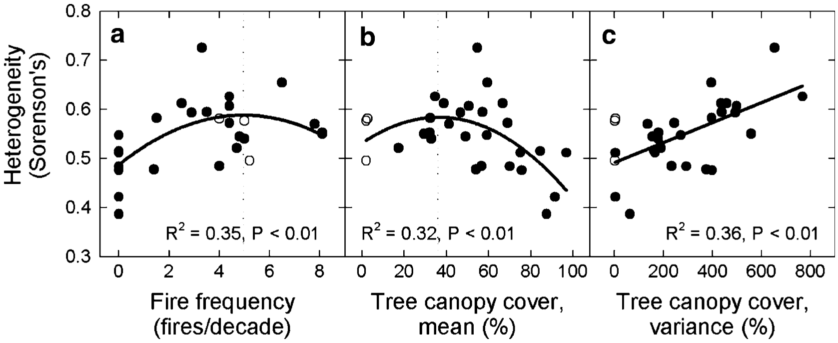

**Fig. 5** Fire frequency and canopy cover effects on community heterogeneity, as measured by mean dissimilarity among all pairs of samples within plots. Lines indicate statistically significant linear or quadratic regression relationships. Open circles represent old-field plots

## Discussion

### Fire frequency effects on plant species richness

Our results were consistent with the predictions of the intermediate disturbance hypothesis (IDH), with total species richness maximized under fire regimes of about five fires per decade. Maximum species richness at biennial fire frequencies has been reported previously for oak savannas (Tester 1989) and longleaf pine woodlands (Brockway and Lewis 1997), but other studies have reported maximum species richness in annually burned savannas and woodlands (Lewis and Harshbarger 1976; Walker and Peet 1983). To fully assess the applicability of the IDH, however, we must determine if the results are also consistent with assumptions about the underlying mechanisms in the IDH.

One assumption of the IDH is that disturbances (fires, in this case) reduce the abundance and competitive ability of the dominant species, thereby slowing rates of competitive exclusion. Trees and shrubs are the dominant competitors at Cedar Creek and most other temperate savannas, and history shows that tree and shrub dominance increases on these sites in the absence of fire (Curtis 1959; Nuzzo 1986; Faber-Langendoen and Davis 1995). Fires kill aboveground stems of most shrubs and tree saplings, thereby reducing their ability to preemptively intercept light and competitively exclude grasses and forbs via shading. However, most shrub and tree species at Cedar Creek can resprout following fire and can regain lost biomass in as little as 3–4 years (Axelrod and Irving 1978). Biennial fire frequencies appear sufficient to limit understory woody plant cover to less than 40% (Peterson et al. 2007) and to maximize grass and forb species richness. Higher fire frequencies reduce woody plant species richness without producing equivalent increases in grass and forb species richness. Fires also modify and constrain overstory tree cover and diversity by periodically killing overstory trees, limiting growth of saplings into the overstory canopy, and eliminating regeneration of shade-tolerant, but fire intolerant, tree species (Peterson and Reich 2001).

Another assumption of the IDH is that reductions in species richness at low disturbance frequencies is due to competitive exclusion, where competitive exclusion can include loss of extant species and prevention of establishment by new species. Our data showed that total species richness was low at low fire frequencies, due primarily to reductions in grass and forb species richness (Fig. 2a, c, d). These reductions in grass and forb species richness were associated with higher tree canopy cover (Fig. 2g, h) and higher cover of understory shrubs and trees (Fig. 4a–c). Again, the evidence suggests that competitive exclusion of species of low stature is reducing total plant species richness at low fire frequencies.

Fire frequency also influenced community heterogeneity, with greatest expected community heterogeneity occurring at intermediate fire frequencies. Biennial fire frequencies appear to promote the highest community heterogeneity primarily by promoting high cover, species richness, and spatial heterogeneity within the forbs functional group. At low fire frequencies, tree canopy cover is generally high, understory plant communities tend to be dominated by a few woody species (e.g., *Quercus ellipsoidalis*, *Corylus americana*, *Rhus radicans*, and *Parthenocissus vitacea*), and community heterogeneity is low. At near-annual fire frequencies, tree canopy cover is generally low and understory plant communities feature high and consistent cover of $C_4$ grasses (e.g., *Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*), a few persistently sprouting woody species (e.g., *Q. ellipsoidalis*, *Q. macrocarpa*, and *Rhus glabra*), and some common prairie forbs (Peterson 1998; Peterson et al. 2007); again, community heterogeneity is lower than for biennial fire frequencies.

These responses differ somewhat from those in floristically similar tallgrass prairie communities, where species richness and community heterogeneity responses to fire frequency do not follow the patterns predicted by the intermediate disturbance hypothesis (Collins 1992; Collins et al. 1995). In both systems, dominance by $C_4$ grass species declines from annual to biennial fire frequencies, with corresponding increases in species richness and community heterogeneity (Collins et al. 1995; Peterson et al. 2007). However, in tallgrass prairie, species richness and community heterogeneity can increase with longer mean fire return intervals (up to 20 years) without significant net losses due to woody plant dominance (Collins 1992; Collins et al. 1995), probably due to the absence of trees and to relatively slow rates of shrub population establishment and expansion without fire in prairie grasslands (Bragg and Hulbert 1976). The dominance of woody plants in Cedar Creek savannas may be enhanced by sandy soils, which have been shown to reduce the ability of grasses and forbs to prevent establishment of woody plants (Knoop and Walker 1985). On savannas with finer textured soils, woody plant dominance and the fire frequency at which species richness is maximized may both be reduced.

The fire frequency at which species richness was maximized varied among plant functional groups, consistent with the vital attributes corollary to the IDH, and the differences appear to be at least partially related to differences in fire severity. Effective fire severity is highest for woody plants. Fires damage or kill woody plants, reduce woody plant cover, and reduce woody species frequencies (Axelrod and Irving 1978; Waldrop et al. 1992; Peterson 1998), and understory woody species richness was maximized at the lowest fire frequencies. In contrast, most grasses sustain little damage from spring fires, so effective fire severity is low, and species richness in the grasses group is maximized at very high fire frequencies that minimize competition from woody plants. Forb species richness was maximized at biennial fire frequencies, as would be predicted if fire effects were slightly more severe for forbs than for grasses.

Although we found that overstory tree species richness declined with increasing fire frequency, this result is not necessarily inconsistent with the predictions of the IDH. High fire frequencies kill (or prevent establishment of) seedlings and saplings of fire-sensitive species, prevent seedlings and saplings from growing into the overstory, and slowly kill overstory trees, thereby limiting overstory tree species composition to highly fire resistant oaks (Peterson and Reich 2001). There is currently little evidence that species richness is declining with fire exclusion (our longest fire-free intervals), although oaks appear to be losing dominance to *Acer rubrum* (red maple) in the oldest stand (>125 years since major disturbance). However, it might be that overstory tree diversity is maximized at an ‘‘intermediate’’ fire frequency with mean fire return interval greater than 125 years.

## Tree canopy cover effects on species richness

As predicted, plant species richness was highest in savannas and woodlands (areas with mean tree canopy cover of 20–70%), even though no single plant functional group dominated species richness. We did not find savanna vegetation cover and species richness to be dominated by forbs as has been reported in other oak savannas (Leach and Givnish 1999). Rather, it appears that species richness was maximized in savannas and woodlands because intermediate canopy cover conditions allowed large numbers of grass, forb, and woody species to coexist in a spatially heterogeneous, fine-scale mosaic. Mean quadrat species richness was highest on partially shaded sites and community heterogeneity ($\beta$ diversity) was maximized in savannas and woodlands with intermediate tree canopy cover.

Savannas and woodlands feature high community heterogeneity as plant community composition varies across fine scale environmental gradients associated with spatial variability in tree canopy cover (Vetaas 1992; Scholes and Archer 1997). At Cedar Creek, soil nitrogen cycling rates, surface soil moisture, plant functional group cover, and aboveground net primary productivity all vary with tree canopy cover (Peterson 1998; Reich et al. 2001; Dijkstra et al. 2006; Peterson et al. 2007), which is in turn correlated with fire frequency (Peterson and Reich 2001). Therefore, tree canopy cover represents a complex ecological gradient, across which disturbance frequency, plant resource availability, plant functional group cover, and aboveground productivity all vary. Community heterogeneity may therefore be high in savannas and woodlands because spatial variability in tree canopy cover and associated resources is high, particularly where tree spatial patterns are aggregated. This would be consistent with the resource heterogeneity hypothesis.

We found that tree canopy cover was associated with species richness for all three plant functional groups, but the underlying mechanisms probably vary. Grass and forb species richness appears to be sensitive to light availability, declining with increasing tree canopy cover as shading from both overstory trees and understory woody plants increases. The $C_4$ grasses and prairie forbs may be particularly sensitive to shading, including that from herbaceous litter (Peterson et al. 2007). The increase in woody species richness with increasing tree canopy cover may reflect a positive response to increased availability of soil resources, reduced competition from grasses and forbs, and positive feedbacks of tree leaf litter on nutrient cycling rates (Davis et al. 1999; Reich et al. 2001). However, higher tree canopy cover is also associated with lower fire frequencies and reduced direct fire effects on woody species. Therefore, support for the intermediate resource hypothesis is somewhat ambiguous. Some grassland and savanna studies have concluded that high grass cover and productivity reduces forb species richness in high light environments through shading and competition for soil resources (Collins et al. 1995; Collins and Steinauer 1998). We found little evidence for this at Cedar Creek, perhaps because the sandy, relatively infertile soils at Cedar Creek reduce the productivity and competitive ability of the grasses.

In summary, plant species richness in oak savannas and woodlands within the forest-grassland biome transition zone appears to be related to both fire frequency and overstory stand structure. High fire frequencies reduce the competitive dominance of overstory trees and understory woody plants (particularly on sandy soils), which would otherwise suppress and competitively displace many of the native prairie grasses and forbs. At the same time, an intermediate abundance of overstory trees reduces the competitive dominance of $C_4$ grasses and creates spatial heterogeneity in plant resource availability that promotes high species richness by promoting high community heterogeneity. For oak savanna restoration, our study suggests that high plant species diversity is likely to be achieved if prescribed fire frequencies are high enough to maintain intermediate and spatially variable levels of tree canopy cover and suppress dominance of understory woody plants, but not so high as to unduly reduce woody plant species richness. Although biennial fire frequencies promoted high species richness and community heterogeneity in this study, fire frequency effects may vary with local site factors—like soil fertility, topography, and species pools—that influence vegetation productivity, competitive interactions, and fire resiliency.

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