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Differential effect of woody plant canopies on species composition and diversity of ground vegetation: a case study

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Abstract: We examined the effect of three woody plant canopies of contrasting characteristics on species composition and diversity of the ground vegetation. Understorey environment differed in terms of light intensity and soil factors between the three canopy types. NMS ordination, based on Importance Value Indices of the herbaceous species, resulted into three clusters corresponding to the three woody plant canopies. NMS axis-1 was related to light intensity and axis-2 was related to soil water holding capacity. Diversity parameters for the herbaceous vegetation, which were significantly different between canopy types, were also related to NMS axes. The canopy type exhibiting intermediate levels of light intensity, soil moisture and soil carbon, reflected the greatest herbaceous diversity. Mosaics of woody plant canopies can be used to maintain the diversity of ground vegetation in the Gangetic Plains.

Resumen: Examinamos el efecto de los doseles de tres especies leñosas con características contrastantes en la composición de especies y la diversidad de la vegetación del piso del bosque. El ambiente del sotobosque difirió entre los tres tipos de dosel en términos de la intensidad de luz y factores edáficos. Una ordenación de tipo NMS basada en los índices de valor de importancia de las especies herbáceas produjo tres conjuntos que se correspondieron con los tres doseles de plantas leñosas. El eje 1 del NMS estuvo relacionado con la intensidad de luz y el eje 2 estuvo relacionado con la capacidad de retención de agua. Los parámetros de diversidad para la vegetación herbácea, los cuales difirieron significativamente entre los tipos de dosel, también estuvieron relacionados con los ejes del NMS. El tipo de dosel que tuvo los niveles intermedios de intensidad luminosa, humedad edáfica y carbono del suelo, fue el que reflejó la mayor diversidad de plantas herbáceas. Los mosaicos de doseles de plantas leñosas pueden ser utilizados para mantener la diversidad de la vegetación del piso del bosque en las Planicies Gangeáticas.

Resumo: O efeito de três copas de plantas lenhosas de características contrastantes na composição e diversidade das espécies do solo foi examinado. O ambiente no subcoberto diferiu em termos de intensidade luminosa e factores edáficos entre os três tipos de copa. Uma ordenação NMS, baseada nos Valores dos Índices de Importância das espécies herbáceas, resultou em três clusters correspondentes às três copas das plantas lenhosas. O eixo 1 NMS encontrava-se relacionado com a intensidade luminosa e o eixo 2 relacionava-se com a capacidade de retenção da água no solo. Os parâmetros de diversidade para a vegetação herbácea, que eram significativamente diferentes entre tipos de copado, encontravam-se também relacionados com os eixos NMS. O tipo de copado exibindo níveis intermédios de intensidade luminosa, humidade e carbono do solo, reflectiram a maior diversidade herbácea. Mosaicos de copados de plantas lenhosas podem ser usados para manter a diversidade da vegetação no solo nas planícies do Ganges.

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Key words: Canopy types, gangetic plains, herbaceous diversity, India, light intensity.

Introduction

Woody plant canopies alter the micro-environment and physical and fertility conditions of soil (Weltzin & Coughenour 1990). Trees modify microenvironment in terms of reduced soil and air temperatures, wind speed and irradiation, resulting into reduced soil water evaporation and increased relative humidity (Jose *et al.* 2008; Rao *et al.* 1998). While trees and herbaceous plants usually compete directly for water, deep-rooted woody plants can benefit the understorey vegetation by transporting water from deeper soil layers to drier surface soils through hydraulic lift, particularly during dry periods (Burgess *et al.* 1998; Ong *et al.* 1999). Trees also acquire nutrients from deeper soil layers and redistribute them at the surface through litter fall which enhances soil carbon and nutrients, benefiting the understorey plants. Interception of solar radiation is a predominant factor influencing the understorey. In tropical forests, light reaches perpendicular to the ground, and decreases in a gradient from gap centre to edge to below-canopy locations (Chazdon 1986; Denslow 1987). Trees can either diminish or enlarge grass production by modifying the resource availability to ground flora (Vetaas 1992). Species differ in their response to shading. For example, Lin *et al.* (1999) found that shading reduced the mean dry weights of warm season grasses, but up to 50% shading did not reduce mean dry weights of cool season grasses. Woody plant canopies provide a more stable microhabitat for the understorey, probably because of the protection against direct irradiance and overheating (Lopez-Pintor *et al.* 2000); direct solar radiation supplies energy which increases evaporative demand and potential for moisture stress (Moro *et al.* 1997; Pausas & Austin 2001). The increase in radiation is often associated with a reduction in water availability, resulting into reduced species richness (Pausas & Austin 2001).

Plant community ecologists are concerned with patterns of species diversity in various environmental gradients. Species diversity studies in relation to resource availability suggested a humped-back curve (Grime 1973; Huston 1980; Tilman 1982). Wright (1992) found a positive relationship between soil fertility and herb richness, the latter tended to increase with radiation; however, this pattern is not universal probably due to interaction with other factors (Pausas & Austin 2001). Studies on the effect of tree canopies on herbaceous diversity in tropical forests (Denslow 1987; Gillet *et al.* 1999; Joshi *et al.* 2001; Rodriguez-Echeverria & Perez-Fernandez 2003; Zobel *et al.* 1994) have yielded equivocal results. Canopy patches beneath woody plants and the intercanopy patches experience heterogenous patterns of energy, water, and biogeochemistry (Breshears 2006), and the level of this heterogeneity should depend on the architecture of woody plant canopies. The presence of contrasting woody plant canopies can thus influence the diversity of ground vegetation. In the present study, we examine the floral composition and diversity of the ground vegetation under plantations of three tropical tree species having contrasting canopy characteristics.

Materials and methods

Study area

The study was conducted at nine plantation stands within the campus of the Banaras Hindu University (24^0 18' N and 83^0 03' E, and 129 m msl altitude), Varanasi, India, located in the middle Gangetic Plains, during February-March 2005. Three plantation stands belong to *Mangifera indica* Linn., labeled here as canopy-1, three to *Zizyphus jujuba* Lam., labeled as canopy-2 and the remaining three to *Dalbergia sissoo* Roxb., labeled as canopy-3. The tree species had contrasting canopy architecture: *Mangifera indica*, dense and oval; *Zizyphus jujuba*, spreading and bushy; *Dalbergia sissoo* porous and largely elliptical. *M. indica* trees were tallest followed by *D. sissoo* and *Z. jujuba*. In addition, *M. indica* is evergreen while the other two species are deciduous (Troup 1921).

These plantations were raised following abandoned cultivation around 20 yrs back.

The area experiences a seasonally dry tropical monsoon climate. The year is divisible into three seasons *viz.* a hot summer (April-June), a warm rainy season (July-September), and a cold winter (November-February). The months of March and October constitute transition periods, between winter and summer, and between rainy and winter seasons, respectively. Mean monthly minimum and maximum temperatures varied between 7.3-25.4^{0}C and 25.6-35.6^{0}C, respectively, and the mean annual rainfall was 932 mm (Annapurna & Singh 2003). The soil of the Banaras Hindu University campus has been characterized as Banaras Type III (Agrawal & Mehrotra 1952). The soil is pale brown, silty loam, inceptisol with neutral reaction. In general, the soil is alluvial, well drained and moderately fertile being low in available nitrogen and medium in available phosphorus and potassium (Singh & Singh 1994).

Sampling

A 10x10 m plot was established in the centre of each stand to avoid edge effect. At each plot, five quadrats, each 50 cm x 50 cm in size, were randomly placed, covering both beneath-canopy and intercanopy spaces. Thus, a total of 45 quadrats (3 canopies x 3 plots x 5 quadrats) were sampled. For each quadrat, number of individuals and their herbage cover were recorded by species. Cover was measured by gridding the quadrats into 5 cm × 5 cm cells and transferring the cover outlines on a graph paper.

Per cent sunlight incident 10 cm above the ground in each quadrat was measured by using a Lux Meter between 11 and 12 hrs on a cloud free day in February-March (Singh *et al.* 1997). A 80-100% sunlight corresponded to 1600-1720 μ mol $m^{-2}s^{-1}$ as measured by LCA-2 battery portable infrared carbon dioxide analyzer having PAR sensors (filtered Selenium photocells) (ADC Scinokem International, U.K.). These per cent sun light values are referred to as light intensity in this paper.

Soil samples (0-10 cm depth) were collected from each quadrat, using a 5 cm diameter corer. All fine roots were removed from the soil samples carefully. One part of each sample was weighed and oven dried at 105^{0}C to determine the gravimetric moisture content. Air dried soil samples, sieved through 2 mm mesh screen, were analyzed for water holding capacity and soil carbon.

Water holding capacity of soil was determined by using perforated circular brass boxes (Piper 1944). Soil organic carbon was analyzed by using dichromate oxidation and titration with ferrous ammonium sulphate (Walkley 1947).

Data analyses

Importance Value Index (IVI) of each herbaceous species for each plot (three plots for each canopy type) was calculated by summing the relative frequency, relative density and relative cover (Mueller-Dombois & Ellenberg 1974). The species having highest IVI was identified as dominant and that having the second highest IVI was defined as co-dominant species.

The α-diversity (H') and its components, i.e. species richness (number of species per plot) and evenness (E_w) were calculated for each plot. Following equations were used to calculate the diversity parameters:

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \quad \text{(Shannon \& Weaver 1949)}$$

Evenness (E_w) and β-diversity (β) were calculated using Whittaker index:

$$E_w = \frac{S}{\ln Ni - \ln Ns} \quad \text{(Whittaker 1972)}$$

$$\beta = \frac{Sc}{\bar{S}} \quad \text{(Whittaker 1972)}$$

In the above equations, p_i = proportion of importance value belonging to species '*i*', S = number of species, N_i = IVI of the most important species, N_s = IVI of the least important species, Sc = total number of species, $\bar{S}$ = mean number of species.

The canopy stands (plots) were ordinated by Non-metric Multidimensional Scaling (NMS) option in PC-ORD, using IVI of component species on each plot. NMS is particularly suited for the analysis of floristic data (McCune & Mefford 1999). Pearson's correlation coefficients were calculated to compare explanatory variables (light intensity, soil moisture, water holding capacity, soil carbon) and response variables (NMS axes scores, alpha diversity, species richness, evenness, beta diversity); using SPSS statistical software package (SPSS 1997).

Analysis of variance (ANOVA) procedure of SPSS package (1997) was used to see the effect of canopy types on species richness, evenness, α-diversity and β-diversity of ground vegetation, using three plots as replicates for each canopy type. A Tukey's HSD test was used to determine the significance of differences for mean number of species, evenness, alpha diversity and beta diversity between canopy types.

Results

The ground flora of canopy-3 received the greatest light intensity (53 % of sun light) followed by canopy-1 (36%) and canopy-2 (28%). Soil moisture and organic carbon contents were highest for the canopy-2 and lowest for the canopy-3. The water holding capacity was also higher for canopy-2 but was lower for canopy-1 (Table 1).

A total of 28 species, distributed in 14 families, was recorded from the study plots. Family Asteraceae had the maximum number of species (25% of the total species), while seven families were represented by a single species each (Table 2). Canopy-1 had 20 species and 14 families, canopy-2 had 14 species and 10 families and canopy-3 had 11 species and six families. Canopy-1 had the highest number of unique species (8) and canopy-2 had the minimum number of unique species (3) (Table 2). *Achyranthes aspera, Cynodon dactylon, Malvastrum coromandelianum* and *Sida acuta* were common to all canopy types and accounted for only 14% of total species (Table 2). *Cynodon dactylon* dominated the herbaceous flora in all the three canopy types but had the highest IVI in canopy-3. The canopy types, however, differed in co-dominant species. *Cyperus compressus, Imperata cylindrica*, and *Achyranthes aspera* co-dominated in canopy-1, 2 and 3, respectively. On the basis of the co-dominant and the third dominant species, canopy-1 represented *Cyperus compressus-Sida acuta* community; canopy-2, *Imperata cylindrica-Desmodium gangetium* community; and canopy-3, *Achyranthes aspera-Malvastrum coromandelianum* community (Table 2).

NMS ordination of the nine plots (stands) revealed three distinct clusters, one each for the three canopy types (Fig. 1). NMS axis-1 was related with light intensity (r = 0.67, P = 0.04) and the NMS axis-2 was related with soil water holding capacity (r = 0.75, P = 0.02) (Table 3). The significant relationships of diversity parameters to

Table 1. Light intensity and soil physico-chemical parameters under three woody plant canopies.

Environmental parameters	Canopy-1	Canopy-2	Canopy-3
Light intensity (% sun light)			
Range	5-70	15-69	27-75
Mean	36.2	28.2	53.5
±1SE	5.2	4.2	3.8
% Soil moisture			
Range	4.0-8.0	9.6-14.8	3.2-4.4
Mean	5.3	12.9	3.7
±1SE	1.3	1.7	0.4
% Water holding capacity			
Range	49-51	57-68	55-56
Mean	50.5	61.7	55.3
±1SE	0.4	3.2	0.5
% Soil carbon			
Range	1.9-2.7	2.2-4.7	1.5-2.1
Mean	2.4	3.6	1.7
±1SE	0.2	0.7	0.2

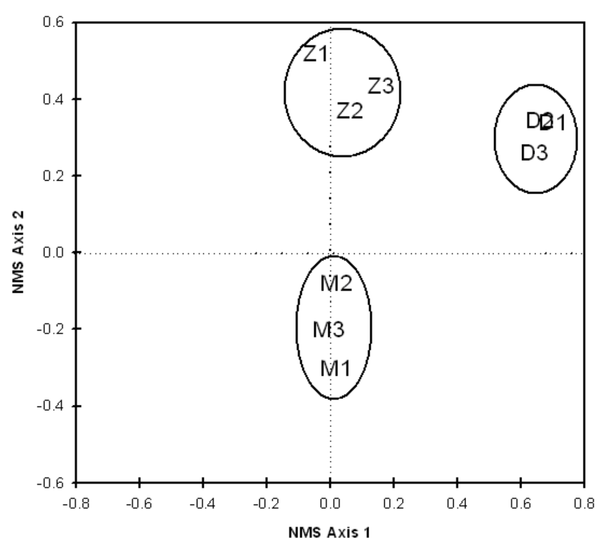

Fig 1. NMS ordination of nine sites based on Importance Value Indices of the herbaceous species under three woody plant canopies. M1, M2 and M3 represent three plots (stands) of canopy-1, Z1, Z2 and Z3 and D1, D2 and D3, respectively, for three plots each of canopy-2 and 3.

Table 2. Importance Value Index of herbaceous species under three woody plant canopies.

Species	Family	Canopy-1	Canopy-2	Canopy-3
Achyranthes aspera L.	Amaranthaceae	14.31	12.27	32.34
Ageratum conyzoides L.	Asteraceae	8.00	13.36	0.00
Alternanthera triandra Lamk.	Amaranthaceae	0.00	10.43	0.00
Blumea bifoliata (L) DC.	Asteraceae	5.04	0.00	18.35
Clerodendrum indicum (L.) Kuntze.	Verbenaceae	5.88	0.00	0.00
Clitoria ternatea L.	Papilionaceae	8.76	14.07	0.00
Cynodon dactylon Pers.	Poaceae	57.57	103.09	142.59
Cyperus compressus L.	Cyperaceae	30.27	0.00	0.00
Desmodium gangeticum (L.) DC.	Papilionaceae	9.90	25.31	0.00
Digitaria ciliaris Koel.	Poaceae	0.00	0.00	17.57
Eclipta alba (L.) Hassk.	Asteraceae	0.00	0.00	16.06
Evolvulus nummularius L.	Convolvulaceae	13.53	21.90	0.00
Imperata cylindrica L.	Cyperaceae	0.00	47.11	8.14
Launaea nudicaulis Auct.	Asteraceae	0.00	0.00	12.81
Ludwigia prostrata Roxb.	Onagraceae	5.64	0.00	0.00
Malvastrum coromandelianum L.	Malvaceae	12.51	15.11	19.97
Melochia corchorifolia L.	Sterculiaceae	4.78	0.00	0.00
Oplismenus compositus Beaub.	Poaceae	21.53	0.00	0.00
Parthenium hysterophorus L.	Asteraceae	0.00	0.00	14.46
Peristrophe bicalyculata Nees.	Acanthaceae	10.14	0.00	10.05
Phyllanthus urinaria L.	Euphorbiaceae	0.00	12.13	0.00
Rungia pectinata Nees.	Acanthaceae	25.54	9.72	0.00
Sida acuta Burm. f.	Malvaceae	26.07	7.62	7.70
Spilanthes iabadicensis H. Moore	Asteraceae	18.21	0.00	0.00
Triumfetta petandra A.Rich.	Tiliaceae	10.89	0.00	0.00
Tylophora macrantha Hook.f.	Asclepiadaceae	6.38	3.20	0.00
Urena lobata L.	Malvaceae	5.04	0.00	0.00
Xanthium strumarium L.	Asteraceae	0.00	4.67	0.00

NMS axis-1 and axis-2 scores (Table 3) indicated that diversity is an important factor in differentiating herbaceous communities. While diversity parameters were inter-related, they had no significant relationship with soil factors. Interestingly, soil moisture (r = - 0.69, P = 0.04) and soil carbon (r = - 0.77, P = 0.01) were inversely related to light intensity, indicating the drying effect of solar radiation.

Table 3. Pearson correlation coefficients between NMS axes scores and measured variables. Values in parentheses are significance levels.

Measured variables	NMS axes scores	
	Axis-1	Axis-2
Light intensity	0.67 (0.04)	0.01 (0.98)
% Soil moisture	-0.57 (0.11)	0.43 (0.25)
% Water holding capacity	0.06 (0.88)	0.75 (0.02)
% Soil carbon	-0.64 (0.06)	0.28 (0.46)
α-diversity	-0.70 (0.04)	-0.88 (0.00)
Species richness	-0.72 (0.03)	-0.88 (0.00)
Evenness	-0.58 (0.10)	-0.92 (0.00)
β-diversity	-0.08 (0.84)	-0.73 (0.02)

Analysis of variance revealed that the differences in species richness ($F_{2, 6}$ = 65, P = 0.00), evenness ($F_{2, 6}$ = 14, P = 0.01) and α-diversity ($F_{2, 6}$ = 18, P = 0.00) due to canopy type were significant, but differences in β-diversity (which ranged between 1.99 and 2.78 among the three canopies) due to canopy type was not significant ($F_{2, 6}$ = 03, P = 0.11). Values for α-diversity and its components were highest for canopy-1 and lowest for canopy-3. Tukey's test indicated that differences in species richness, evenness and α-diversity between canopy-1 and canopy-2, and between canopy-1 and canopy-3

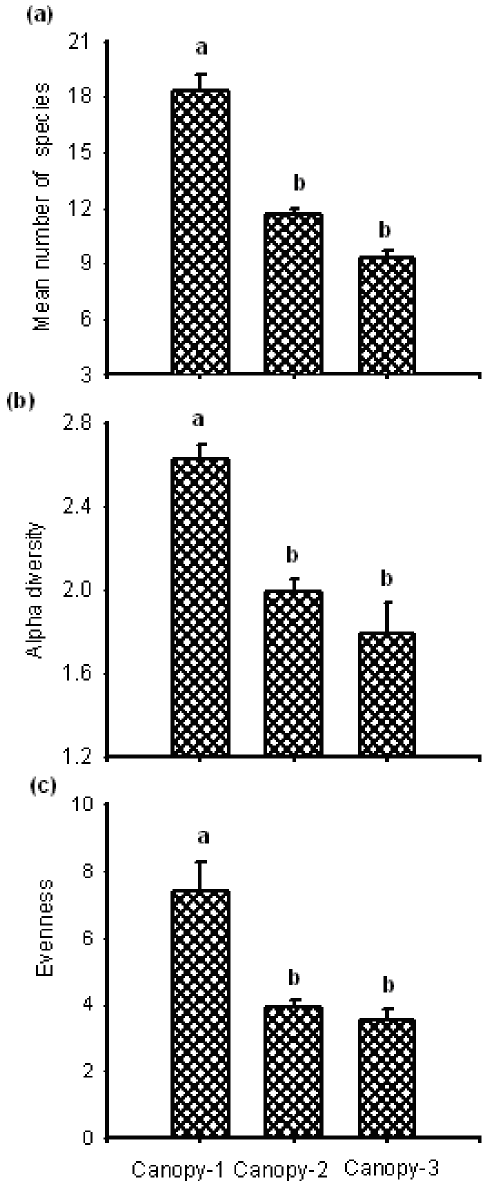

Fig. 2. Herbaceous species diversity under three woody plant canopies (a) mean number of species, (b) alpha diversity, and (c) species evenness. The bars within a diagram affixed with different letters are significantly different from each other at $P = < 0.05$.

were significant but those between canopy-2 and canopy-3 were not significant (Fig. 2).

Discussion

Light availability on the forest floor has been recognized as a key factor that influences intrinsic traits of inhabiting species (Jones *et al.* 1994; Walters & Reich 1996). One major process through which trees modify the sub-canopy environment is interception of direct solar radiation, which could also result in lower soil temperatures and evapotranspiration influencing the below-canopy soil moisture regimes (Vetaas 1992). Light interception would vary among species according to canopy architecture and the width and inclination of leaves. Canham *et al.* (1994) found that different species of canopy trees intercept different levels of light, so that tree species growing over saplings may influence the growth of these saplings. Dense shade creates a photosynthetically inactive light regime at the ground level (Fetcher *et al.* 1983; Turton & Duff 1992).

In this study, reduced light infiltration to ground in canopy-2, is reflected in lesser number of unique species and also lower species richness, evenness and alpha diversity compared to canopy-1. Below certain thresholds, light limitation alone can prevent herbaceous species survival regardless of other resource levels (Tilman 1982). On the other hand, greater irradiance on the ground in canopy-3 was inimical to the recruitment and diversity of herbaceous flora.

NMS ordination analysis indicated that the three canopy types harboured distinct herbaceous communities, each with a characteristic species composition. Significant relations of NMS axis-1 with light intensity, and NMS axis-2 with soil water holding capacity indicated that these explanatory variables had a substantial influence on the organization of herbaceous community. Significant relations between NMS axis scores and diversity parameters justify diversity as a measure of community organization.

The negative relationships of light intensity with soil carbon and soil moisture, and a positive relationship between these two soil characteristics suggested drying effect of solar radiation. Joshi *et al.* (2001) found more soil moisture and soil carbon in shaded area than in the open. Thus, light availability has been recognized as an important plant resource (Blankenship 2002; Maximov 1929) that may interact with other plant resources to affect plant performance (Cole 2003).

Other studies have also pointed out the impact of tree canopy on herbaceous diversity (e.g., Zobel *et al.* 1994). Tree shade in grasslands decreases light availability, which in turn reduces the quality and the quantity of herbage (Gillet *et al.* 1999; Zobel *et al*. 1994). Gillet *et al.* (1999) reported that the number of herbaceous species decreased under the tree crown as well as beyond a mean distance of 40 m to the nearest trees, whereas, an optimum was observed at ca. 30 m. Tree species have a significant impact on humus characteristics through the nature of their litter. The humus characteristics significantly explained the distribution of forest understorey species (Danielle *et al.* 2005). The tree leaf canopy alone is capable of preventing germination in a number of small seeded species (King 1975; Silvertown 1980; Taylorson & Borthwick 1969), due probably to a reduction in the ratio of red (R_{660}) to far red (FR_{730}) radiation. Cumming (1963) offered evidence that germination would be restricted on heavily shaded sites.

In our study, the physical and biological environment of canopy-1 (intermediate light intensity, soil moisture and soil carbon) provided a suitable habitat for high diversity of herbaceous species; this seems to partially support the equilibrium model of resource competition (Tilman 1999). According to Breshears (2006), "the physical and biological effects of woody plant canopies on the environment can create substantial heterogeneity in several ecological properties between canopy and inter canopy patches". Herbaceous species, in particular, take advantage of this heterogeneity and increase their diversity. The level of heterogeneity created, obviously, would depend on the height and architecture of the woody species.

Conclusions

Our study indicated that the patterns of herbaceous floral composition are controlled by the presence of woody plant canopies, and the intermediate levels of soil carbon, water, and shade, facilitated greater herbal diversity. The individual canopy types harboured 11-20 species, with only four species being common to all three canopy types, however, collectively they harboured 28 species. Thus diversity can be enhanced through plantation of heterogeneous canopy types rather than a homogeneous canopy type. Woody plant canopies can indeed be a tool for management of herbaceous diversity. However, studies involving a greater variety of woody plants and greater spatial coverage are needed.

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