

1002

ARBOREAL ARTHROPOD COMMUNITY STRUCTURE IN AN EARLY SUCCESSIONAL CONIFEROUS FOREST ECOSYSTEM IN WESTERN OREGON

T. D. Schowalter¹, S. G. Stafford², and R. L. Slagle²

ABSTRACT.—This study was designed to characterize arboreal arthropod community structure in an early successional coniferous ecosystem. We sampled six-year-old snowbrush (*Ceanothus velutinus* Dougl. ex Hook) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) at the H. J. Andrews Experimental Forest in western Oregon during 1982. The arthropod fauna was dominated in terms of densities by psyllids and aphids on snowbrush and by adelgids and cecidomyiids on Douglas-fir. Significant associations among taxa, e.g., positive correlation between aphids and ants, indicated trophic interactions or similar responses to host conditions. Significant seasonality was observed for individual taxa and for the community, reflecting the integration of individual life-history patterns. Significant spatial pattern (patchiness) in the arthropod community may reflect the influence of faunas on individual plants within neighborhoods and/or the influence of ant foraging patterns.

Patterns in terrestrial arthropod community structure remain poorly understood, largely because of their taxonomic complexity. Most community-level studies have reduced this complexity to indices of diversity or have examined only subsets (guilds) of the community (Price 1984). Unfortunately, such restriction likely masks patterns that could be useful in identifying community responses to changes in environmental conditions (e.g., Lawton 1984, Thompson 1985). Changes in community structure may promote or limit pest population growth (Dixon 1985, Schowalter 1986, Strong et al. 1984, Tilman 1978) and may control temporal and spatial patterns in ecosystem nutrient cycling and succession (e.g., Mattson and Addy 1975, Schowalter 1985, Seastedt and Crossley 1984). At the same time, community structure reflects the integration of population responses to environmental conditions (Lawton 1983, 1984, Schowalter 1985, Schowalter and Crossley 1987, Strong et al. 1984).

Our purpose in this study was to describe the pattern(s) of arboreal arthropod community structure in an early successional coniferous ecosystem in western Oregon. We tested the hypothesis that the integration of patterns at the species level results in distinct temporal and spatial patterns, rather than unintelligible overlap, at the community level (Lawton 1984, Thompson 1985). Multivariate statisti-

cal techniques were used to examine the effect of seasonality and spatial position of host plants on arthropod community patterns as well as on individual arthropod taxa.

MATERIALS AND METHODS

The study was conducted during 1982 on Watershed (WS) 6 at the H. J. Andrews Experimental Forest Long Term Ecological Research (LTER) Site in the western Cascades, 65 km east of Eugene, Oregon. The Andrews Forest is administered jointly by the Pacific Northwest Forest and Range Experiment Station, the Willamette National Forest, and Oregon State University.

The climate of Andrews Forest is maritime with wet, relatively mild winters and dry, cool summers. Mean annual temperature is 8.5 C, and mean annual precipitation is 2,300 mm, with more than 75% falling as rain between October and March. The Andrews Forest is dominated by old-growth (>200-yr-old) Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn) (Grier and Logan 1977).

WS 6 is a south-facing, 13-ha watershed at 1,000–1,100 m elevation, with an average slope of 35%. The watershed was clearcut in 1974, broadcast burned and planted to Douglas-fir at 3 × 3-m spacing in 1975. The six-yr-old vegetation in 1982 was dominated by

¹Department of Entomology, Oregon State University, Corvallis, Oregon 97331.
²Department of Forest Science, Oregon State University, Corvallis, Oregon 97331.

evergreen snowbrush (*Ceanothus velutinus* Dougl. ex. Hook) and Douglas-fir with a canopy height of 1–2 m.

A belt transect 50×4 m was established strategically across the middle of the watershed to represent vegetation diversity and spatial heterogeneity. Because other community studies have indicated that the various arthropod taxa are distributed largely independently (Schowalter et al. 1981, Strong et al. 1984), we considered our sampling of a plot designed to maximize intersection of habitat patches to sufficiently represent the arthropod community in this relatively simple system. This design maximized sampling efficiency and safety on the steep, debris-strewn slope. Furthermore, unlike random sampling across the watershed, this design permitted evaluation of potentially important effects of plant position on insect demographics (Schowalter 1986, Thompson 1985, Tilman 1978).

The 40 snowbrush and 20 Douglas-fir within this transect were mapped to explore spatial patterns and were sampled eight times at 3–4 week intervals, between 19 May (Julian date 139) and 10 November (Julian date 314) 1982 to address temporal patterns. Sampling consisted of quickly enclosing a single, randomly selected branch, bearing 2–5 g dry wt. foliage (or 1–3% of the foliage mass), from each plant in a large plastic bag, clipping the sample, and sealing the bag for return to the laboratory. Samples were chilled at 5 C until processed. This sampling procedure was designed to represent arthropod intensity (#/g foliage) through time on a spatially discrete set of host plants. Chemical or other changes in host quality brought about by periodic removal of small foliage samples (Schultz and Baldwin 1982) were assumed to have a negligible effect on successive samples. Sample bias may exist due to selection of healthy, foliage-bearing plant parts and to the underrepresentation or absence of active species that leap, fly, or drop when motion or contact in their vicinity occurred during sample collection. (Note: Care was taken to minimize disturbance during sampling.)

Samples were sorted into foliage and arthropod components. Foliage material was dried at 45 C to constant weight. Arthropods were tabulated by taxon.

Trends in arthropod intensities (#/g foliage) and community structure were analyzed sta-

tistically using the SAS statistical software package (SAS Institute, Inc. 1982). The square-root transformation was used to normalize the intensity data in the analyses. Degrees of freedom were adjusted to account for autocorrelation arising from the sampling procedure (Milliken and Johnson 1984) in the analysis of variance for each of 18 taxa. Correlation analysis, principal component analysis, cluster analysis, stepwise discriminant analysis, and Spearman's rank correlation (Lawton 1984, Steel and Torrie 1960) were used to explore interactions and temporal and spatial patterns among the 18 taxa.

RESULTS

Mean intensities of arthropods on WS 6 during 1982 are summarized in Table 1. Principal component analysis using the covariance matrix verified the obvious importance of the sap-sucking Homoptera, especially woolly aphids (*Adelges cooleyi* [Gillette]) and psyllids (*Arytaina robusta* Crawford, some *Craspedolepta* sp.). Overall, these two principal components explained 95% of the total variance.

Correlation analysis revealed significant ($P < .05$) interactions that we believe indicate trophic relationships or similar responses to host conditions. As expected (Dixon 1985, Fritz 1983, Schowalter et al. 1981, Strong et al. 1984), aphids and ants were positively correlated ($r = 0.31$, $df = 480$, $P < .0001$), reflecting ant (*Camponotus modoc* Wheeler) tending of *Aphis ceanothi* Clark on snowbrush and *Cinara pseudotaxifoliae* Palmer on Douglas-fir. Positive correlation between psyllids and leaf-mining gelechiid larvae ($r = 0.31$, $df = 480$, $P < .0001$) suggested similar responses to host conditions. Surprisingly, significant negative correlations ($P < .05$) were found only between taxa restricted in occurrence to different hosts.

Statistically significant ($P < .05$) temporal trends were found for aphids, psyllids, aleyrodids, pollen-feeding thrips, defoliating tortricid larvae, gelechiid larvae, and ants on snowbrush (ANOVA, $F > 4$; $df = 7, 44$; $P < .01$) (Fig. 1) and for adelgids on Douglas-fir (ANOVA, $F = 12$; $df = 7, 21$; $P < .01$; (Fig. 2). Aphids, aleyrodids, thrips, and tortricid larvae were most abundant May–August. Psyllids and gelechiid larvae were most abundant September–November. Woolly aphids showed peaks in spring and fall on Douglas-fir.

TABLE 1. Mean (\pm SEM) arthropod intensities (number/kg foliage) and percent of total arboreal arthropods on six-yr-old snowbrush (*Ceanothus velutinus*, N = 40) and Douglas-fir (*Pseudotsuga menziesii*, N = 20) on WS 6 at the H. J. Andrews Experimental Forest, Oregon, during 1982.

Taxon	Snowbrush		Douglas-fir	
	Number/kg	Percent of total	Number/kg	Percent of total
Sap-sucking phytophages				
Woolly aphid (<i>Adelges cooleyi</i>)	0	0	17,000 (1700)	99
Aphids				
<i>Aphis ceanothi</i>	388 (220)	4.8	0	0
<i>Cinara pseudotaxifoliae</i>	0	0	34 (19)	0.2
Cicadellids (3–4 spp.)	48 (7)	0.6	16 (8)	0.1
Aleyrodid (1 sp.)	40 (6)	0.5	0	0
Psyllids (<i>Arytaina robusta</i> and <i>Craspedolepta</i> sp.)	7,300 (520)	91	2 (2)	0
Mirid (<i>Psallus</i> sp.)	5 (2)	0	0	0
Thrips (2 spp.)	64 (10)	0.8	8 (4)	0
Chewing phytophages				
Geometrid (1 sp.)	15 (14)	0.2	0	0
Tortricid (1 sp.)	17 (4)	0.2	0	0
Gelechiid (1 sp.)	37 (7)	0.5	0	0
Chrysomelid (<i>Scelolyperus varipes</i>)	6 (2)	0.1	8 (8)	0
Gall-formers				
Cecidomyiid (<i>Contarinia</i> sp.)	1 (1)	0	0	0
Omnivores				
Formicid (<i>Camponotus modoc</i>)	9 (3)	0.1	13 (10)	0.1
Predators				
Parasitic Hymenoptera (5–6 spp.)	5 (2)	0.1	14 (6)	0.1
Spiders (2 spp.)	29 (5)	0.4	62 (15)	0.4
Miscellaneous arthropods*	43 (7)	0.5	71 (23)	0.4

*Primarily nonfeeding adult midges.

The temporal dynamics of the various taxa produced a distinct seasonality in community structure. Cluster analysis on faunal similarity among plants separated 93% of snowbrush samples collected May–August (season 1) from 97% of snowbrush samples collected September–November (season 2) but failed to separate samples by time for the Douglas-fir fauna.

Cluster analysis was used to explore spatial patterns in community organization. We derived four geometric clusters (patches) of plants from coordinate geometry of nearest neighbors within the plot. Spearman's rank correlation was used to compare these clusters to four faunal clusters derived from faunal similarity among these plants. Each plant species was analyzed for each of the two seasons. Significant ($P < .05$) patch effects on arthropod community structure were found during both seasons for Douglas-fir (Spearman's r_s for season 1 and 2 = 0.48 and 0.71, $t = 2.3$ and 4.3, $df = 18$, respectively). The snowbrush

fauna was relatively homogenous during season 1, with 36 plants supporting a common fauna; the remaining four plants, distributed in three vegetation patches, supported three distinct faunas. The four patches became faunally distinct during season 2 (Spearman's $r_s = 0.91$, $t = 13$, $df = 38$), suggesting that the four plants distinguished during season 1 constituted centers for subsequent development of arthropod communities at the patch level.

Stepwise discriminant analysis was used to identify taxa constituting the groups identified by cluster analysis. Mirid adults, thrips ($P < .05$), cicadellids ($P = .07$), and ants ($P = .13$) contributed to the spatial pattern for snowbrush during season 1, and psyllids and cicadellids ($P < .05$) for snowbrush during season 2. Woolly aphids ($P = .06$), chrysomelid adults ($P = .08$), and cicadellids ($P = .13$) contributed to the spatial pattern for Douglas-fir during season 1, and aphids ($P = .15$) for Douglas-fir during season 2.

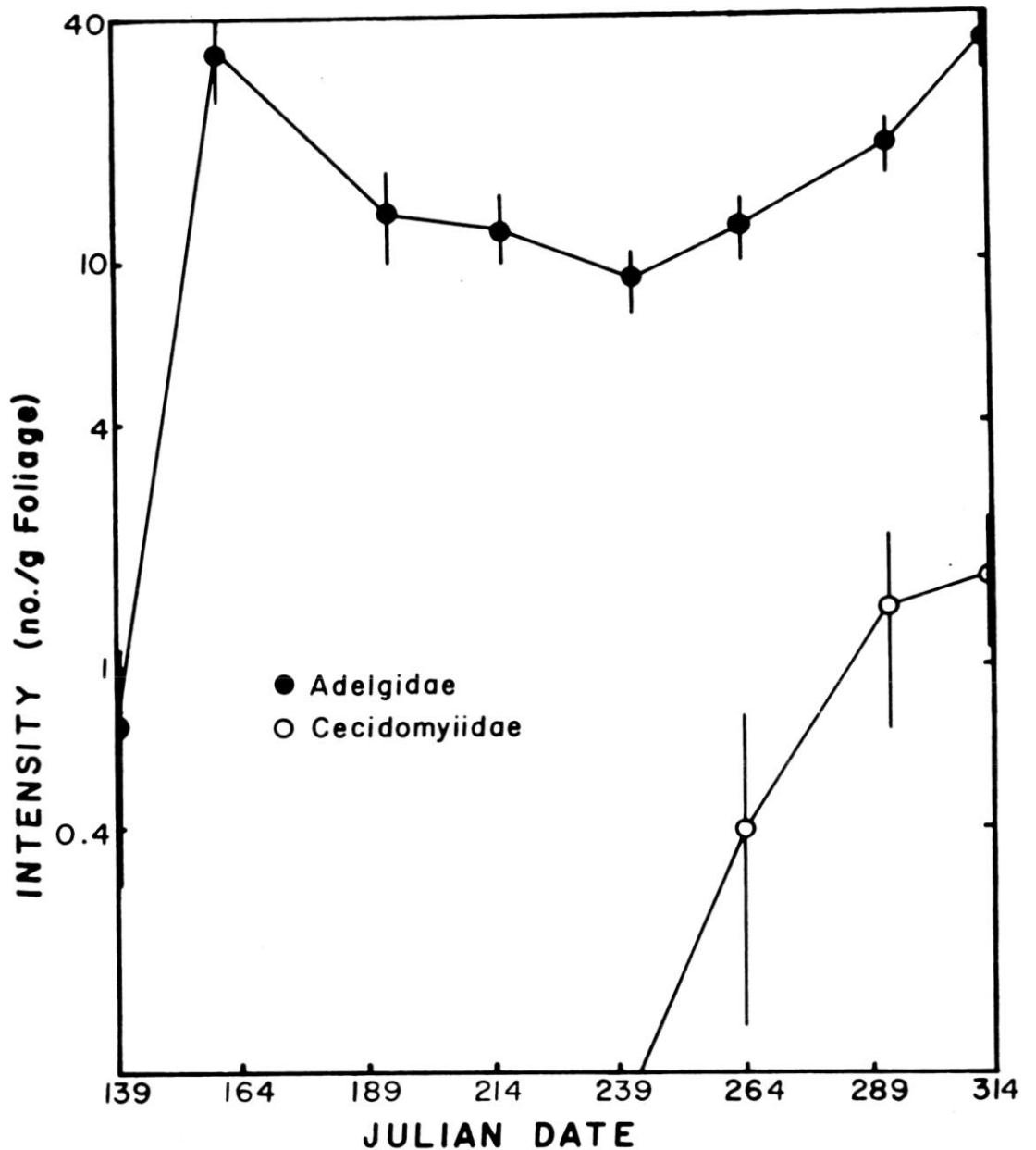


Fig. 1. Mean (± 1 SEM) intensities of arthropods showing significant ($P < .05$) temporal trends on young snowbrush (*Ceanothus velutinus*) from May 19 (Julian date 139) to November 10 (Julian date 314) 1982.

DISCUSSION

Four species of Homoptera (one woolly aphid, one aphid, and two psyllids), all small phloem-sucking insects, characterized the arthropod community in this early successional ecosystem. Other species occurred at low population levels but showed some

evidence of interaction with the dominating Homoptera.

This arthropod community structure is functionally similar to the aphid-dominated community of an early successional hardwood forest at Coweeta (Schowalter and Crossley 1987), but distinct from the

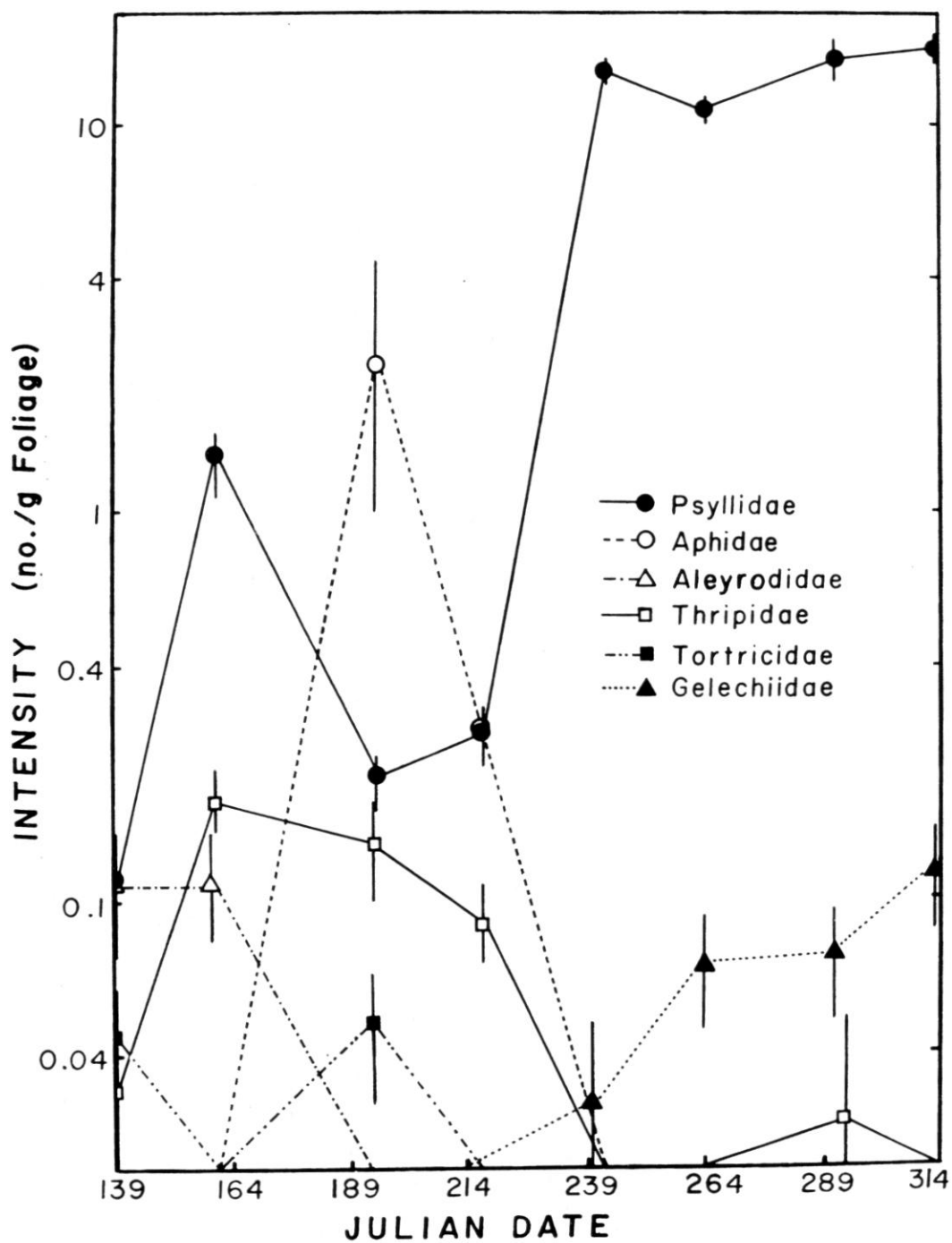


Fig. 2. Mean (± 1 SEM) intensities of woolly aphids (*Adelges cooleyi*) on young Douglas-fir (*Pseudotsuga menziesii*) from May 19 (Julian date 139) to November 10 (Julian date 314) 1982.

defoliator-dominated communities characterizing mature forests at both sites (Schowalter and Crossley 1987, Schowalter, unpublished data). In particular, the faunal association on snowbrush, a symbiotic N-fixer, is functionally identical to that on the ecologically equivalent black locust, *Robinia pseudoacacia* L., a symbiotic N-fixer at Coweeta that was dominated by aphids, *Aphis craccivora* Koch, and ants, *Formica* sp. (Schowalter and Crossley 1987). Thus, although these forest communities were taxonomically distinct, they were functionally similar in the dominance of phloem-sucking Homoptera at similar stages of forest development. These data support the hypothesis that arthropod communities are not randomly organized but rather reflect functional interactions (Lawton 1984, Schowalter 1986).

The faunal structure on Douglas-fir also was similar to the faunal structure on 20-year-old Douglas-fir studied by Mispagel and Rose (1978). *Adelges cooleyi* constituted a much higher proportion of arthropods on Douglas-fir in our study (96% vs. 58%). This may reflect a successional trend or may be due to our inclusion of immatures. Species richness on Douglas-fir was much lower in our study (11 vs. 75 taxa of equivalent rank) as expected if species richness increases with increasing habitat complexity (Schowalter et al. 1986, Strong et al. 1984).

Temporal trends in community structure observed in this study reflected the life history patterns of the constituent species. For example, the appearance of adult psyllids on nonhost Douglas-fir in August was the result of dispersal of winged adults; subsequent reproduction on snowbrush was evident in the rapid increase in intensity (of nymphs) during late summer and fall. The seasonal structure of the community suggests a greater suitability of environmental conditions in spring and fall, relative to summer.

Spatial heterogeneity on a scale of meters in arboreal arthropod community structure has not been reported previously. Our data are consistent with the scale of heterogeneity reported for terrestrial plant (Pickett and White 1985), litter arthropod (Santos et al. 1978, Seastedt and Crossley 1981), stream arthropod (Reice 1985), and marine intertidal communities (Sousa 1985). Such patch patterns underlie the demography of outbreaks and

patterns of herbivory (Schowalter 1985) but would be masked by random sampling.

Our data suggest that individual plants supporting distinct arthropod communities early in the growing season could have constituted centers for the development of faunal patches later in the growing season. The patch pattern in arthropod community structure could have reflected the effect of environmental gradients or of foraging patterns of keystone species such as ants, as suggested by our stepwise discriminant analysis. Ants are attracted to particular plants by floral or extrafloral nectary production and by honeydew-producing Homoptera (Dixon 1985, Fritz 1983, Schowalter and Crossley 1987, Tilman 1978). Ants patrolling these plants remove nonmyrmecophilous herbivores and predators, thereby promoting homopteran-dominated communities. The spatial distribution of ant foraging could produce a patch pattern of homopteran- and nonhomopteran-dominated communities (e.g., Tilman 1978).

In conclusion, the results of this study indicate that arthropod community structure in this early successional coniferous forest ecosystem was dominated by Homoptera. This dominance may reflect the influence of plant architecture interacting with ant foraging pattern in young forests. Spatial and temporal trends in these factors may contribute to patchiness in arthropod community structure. The similarity of canopy arthropod community structure between this western coniferous ecosystem and an eastern deciduous ecosystem suggests that arthropod communities are not organized randomly but rather are based on functional interactions common to taxonomically distinct ecosystems.

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