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## THE SPATIAL PATTERN AND REPRODUCTIVE CONSEQUENCES OF OUTBREAK DEFOLIATION IN *QUARARIBEA ASTEROLEPIS*, A TROPICAL TREE

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### SUMMARY

(1) *Quararibea asterolepis* (Bombacaceae), a common canopy tree in the old forest on Barro Colorado Island, Panama, was the only species defoliated during an outbreak of *Eulepidotis* (Noctuidae) larvae in May and June 1985.

(2) The level of defoliation among 460 potentially reproductive trees ( $\geq 16$  cm dbh) over a 50-ha plot was related to local conspecific density and to the severity of defoliation of the three nearest neighbours.

(3) Young leaves suffered greater damage than mature leaves in the same *Quararibea* crown. Trees with mostly young leaves before the outbreak suffered heavier defoliation than those with mostly mature leaves. Trees that escaped defoliation had either all or mostly mature leaves.

(4) When sapling pairs were matched with respect to leaf age, saplings near an infested adult suffered heavier defoliation than distant saplings. The distance effect was reversed, however, when near saplings had mature leaves and far saplings had young leaves.

(5) Heavily defoliated crowns of large ( $\geq 64$  cm dbh) *Quararibea* trees produced significantly fewer flowers and fruits than lightly defoliated crowns. Flowering also occurred later and was less synchronized for heavily defoliated trees. This difference in reproductive output did not persist beyond the outbreak year.

### INTRODUCTION

The supposition that insect outbreaks do not occur in complex, species-rich tropical forests (Voute 1946; Kalshoven 1951; Elton 1958; Fittkau & Klinge 1973) has been challenged by recent observations of severe insect defoliation in various species of tropical forest plants (Wolda & Foster 1978; Janzen 1981, 1984, 1985). The biology of outbreaks occurring in species-poor temperate forest is well known and has been intensively studied because defoliated tree species are often commercially important. There are few quantitative data about the geographic extent and severity of outbreaks in species-rich tropical forests, however, and even less about the consequences of defoliation for reproduction and survivorship of tropical trees.

This study reports a recent outbreak of lepidopteran larvae that defoliated *Quararibea asterolepis* Pitt. (Bombacaceae), a canopy tree species common in old forest on Barro Colorado Island, Panama. The effects of density and distance of conspecific plants on the severity of defoliation were tested. The effect of leaf age was also examined because the larvae of many lepidopteran species depend on young foliage to complete their development (Feeney 1970; Scriber & Feeney 1979; Futuyama & Wasserman 1980). The reproductive consequences of defoliation were evaluated by comparing flower and fruit production of lightly and heavily defoliated trees before, during and after the outbreak.

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## STUDY AREA AND SPECIES

The study was conducted in the 50-ha forest dynamics plot on Barro Colorado Island (BCI), Panama (9° 10'N, 79° 50'W). The semideciduous vegetation on BCI is classified as tropical moist forest (Holdridge & Budowski 1956). Less than 10% of the 2600 mm of annual total precipitation falls in the dry season, which usually begins in December and ends in April. Median rainfall for the first thirteen weeks of the calendar year is just 88 mm (Leigh & Wright, in press). In the open, average annual temperature is 27 °C with an average diurnal temperature range of 9 °C (Dietrich, Windsor & Dunmore 1982). The forest in the 50-ha plot is more than 500 years old (Piperno, in press). All trees, saplings and shrubs with stem diameters greater than 1 cm at breast height (dbh) have been individually tagged, identified to species, and mapped to the nearest metre.

*Quararibea asterolepis* is one of two species in the genus on BCI and is the second most common species among trees  $\geq 20$  cm dbh in the 50-ha plot (Hubbell & Foster 1983). The other species, *Q. pterocalyx* Hemsl., does not occur in the 50-ha plot and *Quararibea* hereafter only refers to *Q. asterolepis*. Occasional individuals rise above the canopy but crowns of *Quararibea* usually form part of the canopy. Individuals with their crowns in the canopy exchange leaves early in the wet season, and a second leaf exchange may occur in late December or early January (D. Windsor and S. J. Wright, unpublished data). *Quararibea* saplings also show two peaks in leaf production, a sharp peak in May, shortly after the start of the rainy season, and a second, broader peak between November and January (Rundel & Becker 1987).

The smallest tree observed with flowers was 16 cm dbh. The hermaphroditic flowers (Robyns 1964) open in June and July and fruits mature from August to November (Croat 1978). Some individuals flower a second time in December and January, but few fruits result (S. J. Wright, unpublished data). Little is known about the pollination biology of *Quararibea* but the genetic structure of populations examined on BCI suggests that *Quararibea* is an out-crossing species (Loveless & Hamrick 1986).

In late May and early June 1985, *Quararibea* was defoliated by the larvae of two unidentified noctuid moth species of the genus *Eulepidotis*. During the outbreak, thousands of *Eulepidotis* caterpillars descended on silk threads from defoliated crowns, making it difficult and unpleasant to move through the understorey near *Quararibea* trees. By 5 June, few caterpillars were seen and pupae were found in great numbers loosely attached to the moist underside of fallen leaves in the vicinity of defoliated trees. The two species of *Eulepidotis* appeared to feed exclusively on *Quararibea*. Crowns of other tree species adjacent to heavily defoliated *Quararibea* crowns showed no signs of caterpillar feeding damage. There was no indication of a subsequent generation of *Eulepidotis*. Defoliated trees remained leafless for 5–6 weeks and started to flush new leaves in mid-July. The replacement leaf crop developed to maturity without suffering damage.

## METHODS

*Pattern of defoliation**Defoliation in individual crowns*

Between 10 and 18 June, when only pupae of *Eulepidotis* were present, 460 potentially reproductive *Quararibea* trees ( $\geq 16$  cm dbh) within the 50-ha plot were scored for defoliation. Twenty-three additional trees were excluded from the census and analyses because their crowns were partially or completely hidden by other vegetation. Crown defoliation was estimated by eye as follows. The percentage of defoliated branches in each

quarter section of the crown was estimated to the nearest 20% and then averaged. Defoliation scores are thus recorded at intervals of 5%. Four defoliated trees inadvertently scored twice received the same scores each time, showing that this method was replicable. Branches denuded by *Eulepidotis* were readily distinguished from deciduous branches because caterpillars consumed the leaf blade but not the petiole. Defoliated branches were also often covered with glistening tangles of silk.

Leaves present in crowns were classified as mature (dark green) or young (light green). The proportion of each leaf age-class in the crown was estimated with the method described for defoliation. Leaves remaining in the crowns were not always intact and the level of damage caused by caterpillars in most of the leaves within each age-class was visually scored as low ( $\geq 20\%$  of lamina gone), medium (21–80% of lamina gone), or high ( $> 80\%$  of lamina gone).

### *Spatial effects*

To test the null hypothesis that defoliation was independent of the local density of *Quararibea*, contiguous circular plots with radii of 50, 62.5, 75 and 83 m were superimposed in a regular grid over the 50-ha plot. The independent variable for least-squares regression analysis was the number of *Quararibea*  $\geq 16$  cm dbh in each circular plot. The dependent variable was the average percentage defoliation of those trees.

The severity of defoliation of a tree may depend on the level of defoliation of its neighbours rather than their density. This possibility was tested at two spatial scales. The first test was on the scale of the three nearest neighbours of a focal tree. Least-squares regression was used to test the null hypothesis that percentage defoliation of a focal tree is independent of percentage defoliation of its three nearest neighbours. Focal trees were chosen at random. To ensure independent observations, potential observations were excluded if the focal tree or any one of its three nearest neighbours had occurred in a previous observation. The algorithm that chose focal trees continued until 100 consecutive observations failed to meet this criterion.

The second test was on the scale of hectares and was based on similarity in the extent of defoliation among neighbouring hectares. The average percentage defoliation of *Quararibea*  $\geq 16$  cm dbh was calculated for each of the fifty mapped hectares. If defoliation occurred at random at this spatial scale, then hectares where mean percentage defoliation was above the median would be randomly intermixed with hectares at or below the median. The metric chosen to test this null hypothesis was the number of vertical and horizontal contacts between hectares above and at or below the median. A Monte Carlo distribution of the test metric was obtained by randomly assigning the forty-five observed averages to the forty-five hectares with one or more trees  $\geq 16$  cm dbh. The observed locations of the five hectares with no trees  $\geq 16$  cm dbh were always preserved. This procedure was repeated ninety-nine times.

### *Effect of leaf age*

Three analyses were conducted to determine if leaf age had an effect on the level of herbivore damage in *Quararibea*. First, the level of feeding damage for young and mature leaves was compared for seventy-three crowns with both young and mature leaves. The level of defoliation was then examined for fifteen trees with known leaf phenology before the outbreak. Leaf age and the presence of reproductive structures have been censused bi-weekly for these fifteen trees since 1981. Finally, leaf-age composition was examined for crowns that escaped defoliation.

*Defoliation in saplings*

To test the effect of distance from infested adults on the level of defoliation in saplings (1–4 cm dbh), seventeen heavily defoliated trees that were the nearest conspecific adult to one near (< 10 m) and one far (> 20 m) sapling were located. Saplings within 10 m of adults were designated as near because this distance represents the maximum crown radius encountered in the *Quararibea* crowns included in the flower and fruit census (see below). The severity of defoliation in each sapling was determined by averaging the individual defoliation scores of all branches. For each branch, the proportion of petioles without lamina was visually estimated to the nearest 5%. Leaf age composition was also noted.

*Consequences of defoliation on reproduction*

Flower and fruit production were quantified for fourteen heavily defoliated (median=97.5%, range=80–100%) and fourteen lightly defoliated (median=5%, range=0–30%) trees >64 cm dbh. The diameters of heavily defoliated trees (median=89.8 cm, range=70–105.2 cm) did not differ significantly ( $P=0.613$ , Mann–Whitney  $U$ -test) from those of lightly defoliated trees (median=90.4 cm, range=67.9–158.0 cm) included in this census. Trees included were dispersed over the 50-ha plot and were selected on the basis of their proximity to established trails so as to minimize the damage of frequent foot-traffic on understorey vegetation. A stratified random design was used to place twelve 0.11-m<sup>2</sup> traps beneath each crown, with three traps in each quarter section of the crown. Traps were emptied weekly from 11 July until 11 December 1985 and the contents were sorted into buds, flowers, and immature and ripe fruits. The count of ripe fruits is the sum of the number of intact fruits plus a conservative estimate of whole fruits based on the greater of the number of loose capsules or the number of loose seeds divided by two (most fruits contain two seeds). The weekly means (e.g. number of flowers trap<sup>-1</sup>) of the different reproductive items for each tree were summed over the study period to provide a relative measure of reproductive output for the season. The weekly census of reproductive activity was repeated in 1986 from 30 May until 19 November to assess reproductive performance beyond the outbreak year.

The reproductive output of nine trees included in the above flower and fruit census has been monitored in a standardized manner since 1981. Three of these trees were lightly defoliated in 1985 (<20%) and six were heavily defoliated (>80%). The reproductive output of these trees between 1981 and 1984 was used to determine whether or not differences in reproduction during the outbreak year reflected pre-existing intrinsic differences. The dependence of the data among years precludes rigorous application of inferential statistics for more than one year. Bearing this in mind, the Mann–Whitney  $U$ -test was used to formalize qualitative comparisons of reproductive performance between the lightly and heavily defoliated trees.

## RESULTS

*Pattern of defoliation**Defoliation of individual crowns*

The severity of defoliation varied between zero and 100% and its frequency distribution was bimodal (Fig. 1). Tree diameters (range=16–220 cm) explained <6% of the variation in percentage defoliation ( $n=460$ ,  $r=0.241$ ,  $P<0.001$ ). The statistical significance of this relationship depends on the large sample size. As sample size increases, the

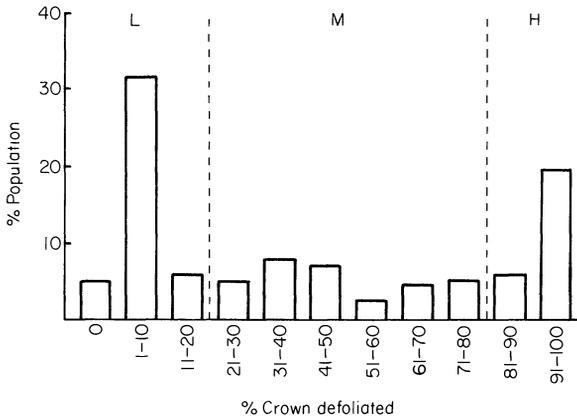


FIG. 1. Frequency distribution of percentage defoliation in 460 *Quararibea asterolepis* trees with dbh  $\geq 16$  cm on Barro Colorado Island, Panama. L: lightly defoliated, M: moderately defoliated, H: heavily defoliated.

power of an analysis approaches one (Berkson's paradox). In this situation, it is appropriate to subsample to determine whether or not there is a biologically meaningful relationship (Sokal & Rohlf 1981). The relationship between percentage defoliation and tree diameter was not significant for random subsamples of eighty trees.

#### *Spatial effects*

Heavily and lightly defoliated trees were frequently nearest neighbours (Fig. 2a). Nevertheless, the average percentage defoliation of the three nearest neighbours explained 16% of the variation in the percentage defoliation of a tree ( $n=67$ ,  $r=0.402$ ,  $P<0.001$ ). Moreover, there was a strong neighbourhood effect at the scale of hectares. With the exception of two hectares in the north-west corner of the 50-ha plot, hectares where the average percent defoliation was greater than the median (50%) were contiguous (Fig. 2b;  $P<0.01$ , Monte Carlo simulation). Finally, conspecific density explained 24% of the variation in average percentage defoliation of the trees for circular plots with radii of 75 m ( $r=0.49$ ,  $P<0.05$ ). The relation was not significant for radii of 50, 62 and 83 m.

#### *Effect of leaf age*

Young leaves suffered higher levels of caterpillar damage than old leaves in fifty-six of seventy-three crowns with both young and old leaves (Sign test,  $P<0.001$ ). For the fifteen trees whose leaf phenologies were known before the *Eulepidotis* outbreak, ten had young leaves and were more heavily defoliated (median = 92.5%, range = 80–100%) than five which had only mature leaves (median = 17.0%, range = 5–50%;  $P=0.002$ , Mann-Whitney *U*-test). Fifteen of the twenty-three trees that escaped defoliation had only mature leaves while six of the eight others had crowns with mostly mature leaves (> 60%).

#### *Defoliation in saplings*

The sapling near the heavily defoliated adult suffered heavier defoliation than the far sapling in nine of ten pairs in which both saplings had leaves of the same age (Sign test,  $P=0.01$ ). However, near saplings with mature leaves suffered lower levels of feeding damage than far saplings with young leaves in six of seven pairs (Sign test,  $P=0.03$ ).

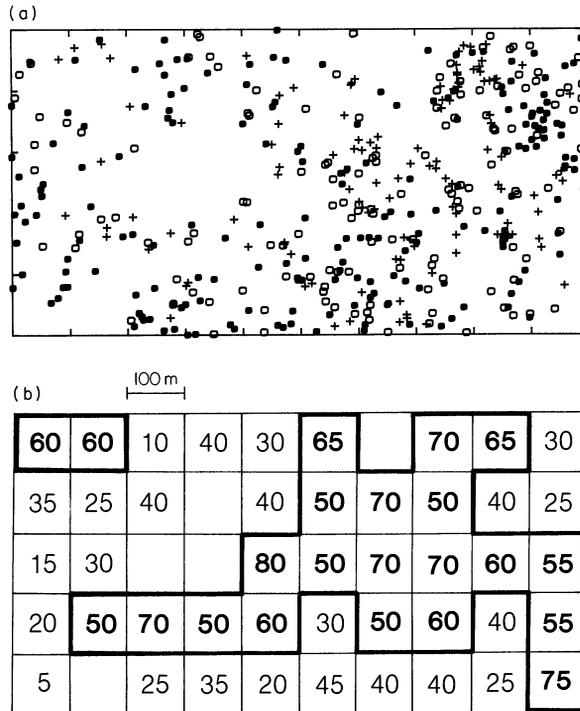


FIG. 2. (a) Spatial pattern of defoliation in *Quararibea asterolepis* trees with dbh  $\geq 16$  cm on Barro Colorado Island, Panama. Trees are assigned to three levels of defoliation: light (0–20%, ●), moderate (21–80%, ○), and heavy (81–100%, +). (b) The average percentage defoliation of *Quararibea asterolepis* trees ( $\geq 16$  cm dbh) in each hectare of the 50-ha plot. Hectares with bold numbers are at or above the median (= 50). Empty hectares had no individuals  $\geq 16$  cm dbh.

#### Effect of defoliation on reproduction

Heavy defoliation reduced reproductive output in *Quararibea*. Heavily defoliated trees produced significantly fewer flowers than did lightly defoliated trees (medians 0.6 and 81.1, respectively; ranges 0–23.6 and 0.1–198.4, respectively;  $P < 0.001$ , Mann–Whitney *U*-test) and significantly fewer fruits (medians 0.0 and 1.0, respectively; ranges 0–15.5 and 0–17.0, respectively;  $P = 0.03$ ; Mann–Whitney *U*-test). One heavily defoliated tree failed to flower. Five heavily defoliated and one lightly defoliated trees failed to fruit after flowering.

Besides flowering less, heavily defoliated trees also flowered later than lightly defoliated trees. Using the week of peak flower production as a phenological marker, the week of maximum flower production in 1985 occurred later and was less synchronous for heavily defoliated than lightly defoliated crowns (Table 1). Peak flowering occurred earlier and more synchronously during 1982 and 1986, two non-outbreak years with substantial reproductive activity (Table 1).

The differences in reproductive output between lightly and heavily defoliated trees in 1985 were not present in non-outbreak years. There was no difference between the lightly and heavily defoliated trees in the year following the outbreak in the production of flowers (medians 88.0 and 79.0, respectively; ranges 0.7–576.8 and 8.6–229.3, respectively;

TABLE 1. Synchrony of flowering in lightly and heavily defoliated crowns of *Quararibea asterolepis* on Barro Colorado Island for the years 1982, 1985 and 1986. Trees were censused weekly.

Year	Percentage defoliation in 1985	n	Number of trees at peak flowering activity week <sup>-1</sup>													
			June			July				August			September			
			1	2	3	4	1	2	3	4	5	1	2	3	4	
1982	< 30	3		1	1		1									
	> 80	6			6											
1985	< 30	14					6	5	1			1				
	> 80	14					1	1		4	1		1	1	2	1
1986	< 30	14		2			10	2								
	> 80	14			3		10					1				

TABLE 2. Trees of *Quararibea asterolepis* for which reproductive data were collected before 1985 by the Environmental Science Program on Barro Colorado Island. Numbers represent sum of weekly means for each year.

Tree number	% Crown defoliated in 1985	Flowers collected in			Fruits collected in			
		1982	1983	1984	1981	1982	1983	1984
705	10	436.3	0.0	39.3	19.7	4.3	0.0	3.0
4208	5	252.3	0.0	0.0	0.0	6.7	0.0	0.0
6056	5	110.0	1.0	7.0	15.0	3.0	0.0	2.7
1733	95	430.0	0.0	17.4	8.7	18.3	0.0	2.7
3191	100	215.0	0.0	2.0	1.0	10.3	0.0	0.0
3195	80	227.7	0.0	19.0	0.7	4.3	0.0	0.0
3196	80	212.7	0.0	0.0	0.0	4.0	0.0	0.0
3563	90	126.6	0.0	0.0	0.0	6.3	0.0	0.0
4577	100	120.7	0.0	10.3	0.0	2.3	0.0	0.7
P*		0.606	0.157	0.793	0.599	0.897	—	0.279

\*Mann-Whitney *U*-test (performed to formalize qualitative comparisons).

$P=0.613$ , Mann-Whitney *U*-test) and fruits (medians 4.5 and 6.9, respectively; ranges 0.2–28.8 and 1.6–44.2, respectively;  $P=0.646$ , Mann-Whitney *U*-test). Nor were there any pre-existing differences. Trees that differed in severity of defoliation in 1985 did not differ in reproductive output during 1981–84 (Table 2).

## DISCUSSION

### *Pattern of defoliation*

Previous studies in species-poor agricultural settings and temperate-zone habitats indicate that herbivore abundance and associated feeding damage are strongly influenced by host-plant density (Dethier 1959; Pimentel 1961; Jones 1977; Thompson 1978; Root & Kareiva 1984). Given the heterogenous nature of tropical rain forests, it was not clear that patterns of herbivory due to simple density or distance effects would emerge. Natural populations of tropical tree species such as *Quararibea asterolepis* show great individual variation, almost never occur in even-aged stands, and are normally intermixed with trees of many other species.

Foliage age is one important variable. Seven species of *Eulepidotis* larvae reared at Santa Rosa National Park, Costa Rica, feed exclusively on young foliage (D. Janzen, personal communication). On BCI, Coley (1980, 1983) found that young *Quararibea* leaves are more nutritious and digestible and are also grazed more heavily than mature leaves. During an outbreak of *Eulepidotis*, we found that the percentage defoliation of a *Quararibea* crown is strongly influenced by the abundance of newly emerged leaves at the time of the outbreak. The frequent occurrence of lightly defoliated *Quararibea* crowns adjacent to heavily defoliated conspecifics (Fig. 2a) may be explained by preferential defoliation of young leaves among trees that varied in the timing and intensity of leaf flush.

The level of defoliation was clearly affected by the local density of *Quararibea* and by the percentage defoliation of conspecific neighbours. It is not clear why. Adult *Eulepidotis* may have preferentially oviposited in dense patches of *Quararibea*. Or, caterpillars may have congregated in dense patches of *Quararibea*. Caterpillars moved readily from defoliated *Quararibea* to neighbouring conspecifics. It seems likely that proximity to many individuals infested with caterpillars increased the chance of discovery, but because of the caterpillars' preference for young leaves, the eventual level of crown damage was determined by the amount of young foliage present. Plant populations tightly synchronized in timing and intensity of leaf flush would more likely manifest strong responses to spatial effects in herbivore damage during an outbreak of young-leaf specialists.

For many species of tropical trees, juveniles distant from adults have higher survival rates than juveniles close to adults (Janzen 1971; Connell 1971; Clark & Clark 1984). One explanation is that near juveniles are more likely to be attacked by predators attracted to adults than are far juveniles (Janzen 1970; Connell 1971). This possible explanation has rarely been demonstrated especially for effects of herbivores on young plants (Clark & Clark 1984). *Quararibea* saplings near heavily defoliated adults suffered higher levels of feeding damage than did distant saplings when sapling pairs had matching leaf phenology. The distance effect was reversed, however, when near saplings had mature leaves and far saplings had young leaves.

#### *Effect of defoliation on reproduction*

Plant reproductive responses to defoliation include reduced fruit quality (Ramasamy 1980), and reduced seed production (Rockwood 1973; Ramasamy 1980; Marquis 1984; Edwards 1985). The magnitude and manner of response depend on the severity of defoliation (Stickler & Pauli 1961; Guene & Minnick 1967), the timing of defoliation in relation to the reproductive phenology of the plant (Rockwood 1973; Janzen 1976), and the availability of stored reserves for leaf replacement and for reproductive activities.

Defoliation clearly reduced reproductive output in *Quararibea*, and caused a mobilization of general reserves to supplement local production of photosynthate for flower and fruit production. Defoliated branches as well as totally defoliated crowns produced flowers before leaf replacement was completed. The reduction in flower and fruit production among heavily defoliated trees indicates, however, that reserves were insufficient to sustain both leaf replacement and normal levels of reproductive activity.

Limited reserves may not be the only explanation for low fruit production during an outbreak year. Compared to a non-outbreak year, the decrease and asynchrony in flowering subsequent to defoliation must greatly reduce the number of suitable reproductive partners, and thus fruit set for *Quararibea*, an out-crossing species (Loveless & Hamrich 1986). Analogously, the small number of fruits produced by the few trees

flowering a second time in December 1986 (S. J. Wright, unpublished data) may be attributable to low mate density.

The effects of defoliation on reproduction were confined to the outbreak year because there were no differences in reproductive output between the two groups in the following year. It is possible that in smaller trees, where reserves are likely to be lower, severe defoliation may continue to depress reproductive output beyond the outbreak year.

*Eulepidotis* pupae occurred in very low density in the litter beneath *Quararibea* crowns in June 1986 and June 1987. We do not know what provokes the infrequent outbreaks of this lepidopteran. Our study suggests, however, that when an outbreak of young-leaf specialists does occur, between-crown asynchrony in leaf flush modifies the pattern of defoliation ordinarily attributable to proximity of infested conspecifics or to density effects.

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