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ECOTOPE CHARACTERISTICS OF COEXISTING *ERYTHRONEURA* LEAFHOPPERS (HOMOPTERA; CICADELLIDAE) ON SYCAMORE[1]

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Abstract. Eight species of leafhoppers (Homoptera: Cicadellidae) of the genus *Erythroneura* (maculata group) breed on the American sycamore, *Platanus occidentalis* L. Several occur sympatrically in many areas throughout the range of their host plant even though they have been shown to compete severely for the last 9 weeks of the season in Illinois. The species are *E. arta* Beamer, *E. bella* McAtee, *E. hymettana* Knull, *E. ingrata* Beamer, *E. lawsoni* Robinson, *E. morgani* (DeLong), *E. torella* Robinson, and *E. usitata* Beamer. Five of these are sibling species.

Ecotope characteristics (niche and habitat) were examined to determine the factors which permit coexistence in this leafhopper guild on sycamore. The five niche or intracommunity factors examined were temporal utilization, distribution within the canopy, occurrence on leaves of various sizes and ages, and location of feeding sites on the leaf. There were insufficient differences between species for all five niche parameters to explain coexistence in the guild by niche segregation. Three habitat or intercommunity parameters were examined: occurrence on trees along a moisture gradient, latitudinal distribution with respect to that of sycamore, and distribution within a given geographical locality. There were sufficient differences in the latter two parameters to explain coexistence by habitat segregation. The peak proportional abundances of seven of the eight species occurred in different latitudinal zones and the degree to which the distribution of each species was overlapped by those of all the other *Erythroneura* ranged from only 0.10 to 0.63 ($\bar{x} = 0.42$). Data indicate that species whose ranges overlapped substantially have apparently evolved differences in their manner of resource utilization, thus reducing competition through character displacement or through a shift in the adaptive mode of the population. There was a tendency for each species to become more unevenly distributed locally from its distributional center; this further reduced geographical overlap between species. Overall proportional similarities (*PS*), calculated for latitudinal and local distributions were low (*PS* range from 0.00 to 0.44; $\bar{x} = 0.17$ where $PS_{max} = 1.0$ and $PS_{min} = 0.0$). We infer that habitat segregation in the guild permits coexistence. Additional mechanisms which may permit coexistence are discussed.

Key words: Competition; dispersal; Erythroneura; *geographical distribution; habitat; Illinois; moisture gradient; niche; temporal utilization.*

INTRODUCTION

Eight species of leafhoppers (Homoptera: Cicadellidae) of the genus *Erythroneura* (maculata group) breed on the American sycamore, *Platanus occidentalis* L. In many areas throughout the range of their host plant several *Erythroneura* species occur sympatrically. They can also breed on the European sycamore, *Platanus acerifolia* Willdenow which is commonly planted in residential areas throughout Illinois. The group consists of *E. arta* Beamer, *E. bella* McAtee, *E. hymettana* Knull, *E. ingrata* Beamer, *E. lawsoni* Robinson, *E. morgani* (DeLong), *E. torella* Robinson, and *E. usitata* Beamer. Five of these are sibling species. Ross (1957, 1958) concluded that six of these species have identical niches apparently without competition among them (he did

not observe *E. hymettana* and *E. ingrata*). He offered this as evidence contradicting Gause's Law which states that no two species can occupy the same ecological niche at the same time. McClure and Price (1975) demonstrated that there is, in fact, severe competition in this sycamore leaf-feeding guild at population densities commonly observed throughout Illinois for a period of 9 weeks during the summer. Here we investigate those factors which maintain coexisting populations of these *Erythroneura*.

Each guild member was studied in 1973 and 1974 using five niche and three habitat parameters. Niche or intracommunity factors refer to local environmental variables including location within the tree canopy and on leaves, seasonal time, etc. Habitat or intercommunity variables are those with an extensive spatial component such as elevation, soil moisture from valley bottom to open slopes, community gradients, etc. The term ecotope is applied to the broader concept including both niche and habitat variables (Whittaker et al. 1973).

MATERIALS AND METHODS

Niche factors

The abundances of *Erythroneura* species were estimated on the following niche parameters: temporal utilization, distribution within the canopy, occurrence on leaves of various sizes and ages, and location of feeding sites with regard to the physical characteristics of the leaf. These niche parameters were shown by McClure (1974) to be of considerable importance in resource partitioning among *E. lawsoni* and four other species of leaf-sucking insects on sycamore.

An intense study was conducted at two sites in southern Illinois where seven of the eight species of *Erythroneura* occur sympatrically. *Erythroneura hymettana* could only be studied on certain parameters as its distribution is limited to more southern latitudes. One site was located in Johnson County near the intersection of Illinois Route 37 and the Cache River south of West Vienna; the other was in Pope County near Golconda where Illinois Highway 146 crosses Miller Creek. At each site, five sycamore trees were selected on a gradient from wet to dry bottomland habitats. A detailed description of these study sites and of the trees which were sampled was provided by McClure and Price (1975).

Adult leafhoppers were collected from individual leaves using an aspirator and were identified. Identifications were made using the original keys and descriptions provided by DeLong (1916), McAtee (1920), Robinson (1924*a*, 1924*b*), Beamer (1931, 1932*a*, 1932*b*, 1932*c*), and Knull (1949) and were checked by comparison with museum specimens provided by the Illinois Natural History Survey, Urbana and verified by Dr. Leon W. Hepner at Mississippi State University. Voucher specimens have been deposited in the Illinois Natural History Survey Collection, Urbana. A comprehensive, illustrated key for identifying these sycamore leafhoppers is now available (McClure 1975). For most of this study only male leafhoppers were used, as five of the eight species of *Erythroneura* are sibling species and are distinguishable only by characters of the male genitalia. Females of the three nonsibling species, *E. bella*, *E. hymettana*, and *E. morgani*, can be identified by external markings and were also used. The bulk of the sampling was restricted to the lower canopies, up to a height of ≈ 4 m due to mechanical limitations on collecting at higher levels. The upper portions were checked periodically with the help of ladders, pole pruners, and binoculars to estimate the evenness of leafhopper feeding throughout the canopy.

Leafhoppers were collected on 400 leaves from each of the five trees at both sites on seven dates throughout the season to determine the seasonal abundance of each species. Samples consisted of four subsamples of 100 leaves each taken from the north and south facing outer and inner portions of the lower canopy of each tree. This sampling procedure also enabled determination of species distributions in various portions of the sycamore canopy which afforded different microhabitat conditions. For a minimum of 115 male leafhoppers of each species, a record was made of the size and age of the leaf on which they occurred and the precise location of their feeding sites including their distance from main veins. The size categories were: leaves < 10 cm in width, 10 to 20 cm, and > 20 cm. The three leaf age classes—young, mature, and senescent —were determined by comparing leaf pubescence, flexibility, and coloration with previously marked leaves of known age. Leaf size and leaf age were found to be totally independent of one another. The distance of the feeding site of each leafhopper from main vains was recorded as < 2 mm, 2 to 4 mm, and > 4 mm.

Habitat factors

The relative abundances of *Erythroneura* species were determined on the following habitat parameters: occurrence on trees along a moisture gradient, latitudinal distribution with respect to that of sycamore, and distribution within a given geographical locality.

The proportion of each species collected from the five trees at both sites was calculated to determine species response to microclimatic conditions of the canopies. The relative moisture stress on residents of each tree was estimated by measuring the amount of water evaporated per 24-h period from six beakers per location. Groups of beakers were located in the north and south facing outer and inner portions of the canopy at a height of ≈ 2 m and on the ground on the north and south sides of the tree. On three dates in July and August, 400 ml of water was placed in each beaker and after 24 h, the amount which had evaporated was measured. An average number of milliliters of water evaporated per day for each tree and a mean for the three dates were calculated for both sites. The relative shelter from evaporation afforded by each tree remained constant throughout the summer. Psychrometer readings taken from the canopy of each tree were consistent with the evaporation data.

As an additional means of determining the relative shelter from evaporation afforded by each canopy, 400 leaves were removed from each of the north and south facing outer and inner portions of the canopy and the proportion of leaves in each of the three previously mentioned size classes was determined. This measure is of practical use as a disproportionately high number of large leaves in the canopy probably indicates greater shelter for leafhoppers.

FIG. 1. Distribution of 37 collecting sites from northern Illinois to the Smoky Mountains for *Erythroneura* leafhoppers (closed circles) and the geographical range of the host plant, sycamore (dashed line) in the eastern United States. Labeled sites indicate the center of sycamore distribution in the region of the Cumberland Mountains, Kentucky (CM) and the West Vienna (WV) and Golconda (G) study sites in southern Illinois. Latitude is given in degrees north.

Leafhoppers were collected at 37 sites from eight zones extending along a gradient from 35°N to 43°N latitude so the latitudinal distributions of the *Erythroneura* species with respect to that of sycamore could be determined (Fig. 1). The gradient extended from the northern limits of sycamore distribution in northern Illinois (Fowells 1965, Little 1971) to the region of the Cumberland and Smoky Mountains, the center of distribution of the mixed mesophytic forest, including sycamore, following the Pleistocene glaciations (Braun 1941, 1947). In this southern Appalachian region where the longest period of co-evolution between sycamore and its resident leaf-hoppers probably occurred, we expected to find the greatest leafhopper diversity with attenuation of species away from this distributional center. In each of the eight latitudinal zones, which were separated by ≈ 1° of latitude, four or five sites were chosen at a minimum of 8 km apart. The minimum numbers of male leafhoppers collected at each site and from each zone were 203 and 1,005 respectively. The time

taken to collect an adequate sample was recorded. The proportional abundances of each *Erythroneura* species among zones and among sites within a zone were calculated to determine its latitudinal distribution with respect to that of the host plant and the evenness of its distribution within a given geographical locality. Calculations were based on the number of males of each species collected per 15 h sampling time in each latitudinal zone so that data would be standardized.

The index used in determining the diversity of these leafhoppers on the latitudinal gradient was the diversity measure of Shannon and Weaver (1963):

$$H' = -\sum_{i=1}^{S} P_i \log_e P_i$$

where P_i is the proportion of the ith species in each sample for a total of S species. The maximum species diversity possible from this measure is given by $H_{max} = \log_e S$. The formula used to determine species equitability was H'/H_{max} (Pielou 1969).

TABLE 1. The proportion of the total number of ♂ ♂ of each *Erythroneura* species collected on seven dates throughout the 1973 season at the West Vienna (W.V.) and Golconda (G.) study sites. Proportional similarities are given in Table 4

| Species | | Collecting date | | | | | | | Total no. |
		6 Jun	28 Jun	13 Jul	2 Aug	17 Aug	17 Sep	7 Oct	
E. arta	W.V.	0.00	0.01	0.01	0.03	0.14	0.71	0.10	6082
	G.	0.00	0.15	0.12	0.05	0.20	0.27	0.21	467
E. bella	W.V.	----	----	----	----	----	----	----	0
	G.	0.00	0.04	0.16	0.05	0.05	0.38	0.32	75
E. ingrata	W.V.	0.00	0.01	0.02	0.07	0.07	0.73	0.10	298
	G.	----	----	----	----	----	----	----	0
E. lawsoni	W.V.	0.00	0.04	0.06	0.05	0.33	0.35	0.17	346
	G.	0.00	0.03	0.11	0.07	0.15	0.32	0.32	73
E. morgani	W.V.	0.00	0.03	0.04	0.15	0.21	0.47	0.10	133
	G.	0.00	0.12	0.12	0.23	0.15	0.23	0.15	40
E. torella	W.V.	0.00	0.01	0.01	0.01	0.22	0.63	0.12	149
	G.	0.00	0.00	0.00	0.00	0.25	0.42	0.33	24
E. usitata	W.V.	0.00	0.04	0.02	0.04	0.11	0.68	0.11	2159
	G.	0.00	0.08	0.23	0.04	0.08	0.37	0.20	119
$\bar{x}$	W.V.	0.00	0.02	0.03	0.06	0.18	0.59	0.12	9167
	G.	0.00	0.07	0.12	0.07	0.15	0.33	0.26	798

Proportional similarity

The proportional similarity measure used to determine the similarity of distribution of *Erythroneura* species with respect to the various niche and habitat parameters examined was:

$$PS_{x,y} = 1 - .5 \sum_{i=1}^{n} P_{x,i} - P_{y,i}$$

where $P_{x,i}$ and $P_{y,i}$ are the proportions of species x and y, respectively, found on the ith unit of the resource. Values of proportional similarity calculated from this formula range from $PS_{max} = 1.0$ to $PS_{min} = 0.0$. This index, which has been used by several authors including Schoener (1970) and Colwell and Futuyma (1971) is closely correlated with the index described by Horn (1966).

The similarity of *Erythroneura* distributions on several niche and habitat dimensions was calculated by taking the product of the separate proportional similarity values as described by Levins (1968) and used by Pianka (1969) and McClure (1974). This provides an overall estimate of ecological similarities between species in space and time and provides an index on the extent to which species are likely to encounter competition.

As is usual for niche studies, replicates were not taken at each sample point because sampling effort is so great. Thus sampling error could not be estimated. However, it is unlikely that proportional similarities of 1.0 can be observed in nature because of sampling error alone. Where products of several proportional similarity values are to be used, a very low overall proportional similarity value could be obtained even with a 10% sampling error. For example, in this study overall proportional similarity with three habitat parameters would be 0.73 and with five niche parameters it would be 0.59.

In addition small real differences in proportional similarity values are probably insufficient to permit coexistence. Various empirical or arbitrary ecological distances between species based on morphology have been derived ranging from 20–30% difference in order to permit coexistence (Hutchinson 1959, Schoener 1965, MacArthur and Levins 1967, MacArthur and Wilson 1967, May and MacArthur 1972, Hespenheide 1973). Again, when products of small and insignificant real differences are calculated, spurious conclusions are inevitable. The morphological differences needed to permit coexistence that have been established empirically probably lead to differences in patterns of resource exploitation. Reynoldson and Davies (1970) have applied the widely used estimates of morphological differences necessary for coexistence to differences in resource exploitation among lake-dwelling triclads. Root (1967) has documented the importance of morphological characteristics in niche exploitation patterns of the Blue-gray Gnatcatcher. Therefore, we assigned a 20% difference in proportional similarities as essential for permitting coexistence and a 10% sampling error estimate giving a minimum total difference of 30% (proportional similarity values of no more than 0.70) for each parameter as necessary to indicate resource partitioning in the *Erythroneura* guild on sycamore. This estimate coincides with the ecological distances which were measured empirically and discussed above.

TABLE 2. The proportion of the total number of ♂ ♂ of each *Erythroneura* species collected from various portions of the tree canopy at the West Vienna (W.V.) and Golconda (G.) study sites. Proportional similarities are given in Table 4

| Species | | Portion of canopy | | | | Total no. |
		North outer	North inner	South inner	South outer	
E. arta	W.V.	0.21	0.41	0.30	0.08	6082
	G.	0.28	0.20	0.29	0.23	467
E. bella	W.V.	----	----	----	----	0
	G.	0.40	0.13	0.28	0.19	75
E. ingrata	W.V.	0.21	0.42	0.32	0.05	298
	G.	----	----	----	----	0
E. lawsoni	W.V.	0.32	0.32	0.19	0.17	346
	G.	0.33	0.20	0.28	0.19	73
E. morgani	W.V.	0.28	0.27	0.17	0.28	133
	G.	0.30	0.13	0.27	0.30	40
E. torella	W.V.	0.21	0.38	0.20	0.21	149
	G.	0.52	0.10	0.00	0.38	24
E. usitata	W.V.	0.27	0.26	0.15	0.32	2159
	G.	0.45	0.17	0.12	0.26	119
$\bar{x}$	W.V.	0.22	0.37	0.25	0.16	9167
	G.	0.37	0.16	0.21	0.26	798

RESULTS

Niche factors

The seasonal abundances of all *Erythroneura* species were similar at both study sites (Table 1). At West Vienna, leafhopper abundance reached a peak in mid-September and then declined with the onset of leaf senescence and the subsequent movement of adults to overwintering sites in the leaf litter. At Golconda, trends were similar but due to the relatively low population levels achieved there, results were more variable. The leafhopper densities observed at West Vienna were shown by McClure and Price (1975) to be more representative of population levels at other sites throughout Illinois during the summer. All species occurred most often on the less insolated inner and north-facing portions of the sycamore canopy (Table 2). These areas of the tree probably provide greater protection from the desiccating southwest winds which prevail during the summer in Illinois. Differences between species in their seasonal abundances and canopy distributions were insignificant ($p > .05$ for both parameters by chi-square analysis).

All species were most abundant on mature rather than on young or senescent leaves (Table 3).

There were significant differences between some species in the size of leaves on which they occurred most often and between *E. morgani* and the rest of the guild in the distance of their feeding sites from main veins (Table 3). Usually *E. arta*, *E. lawsoni*, *E. morgani*, and *E. usitata* were found on larger leaves, *E. bella* and *E. ingrata* on smaller leaves, and *E. torella* on intermediate sized leaves ($p < .01$ for all comparisons of these three groups by chi-square analysis). The feeding sites of all species were located on the lower epidermal surface of the

TABLE 3. The proportion of the total number of ♂ ♂ of each *Erythroneura* species collected at various distances from the main veins of leaves, and on leaves of different size and age. Proportions for ♀ ♀ are given only for *E. bella* and *E. morgani* as the others are sibling species whose ♀ ♀ are indistinguishable. Proportional similarities are given in Table 4

| Species | | Width of leaf (cm) | | | Age of leaf | | | Distance from veins (mm) | | | Total no. |
		< 10	10–20	> 20	Young	Mature	Senescent	< 2	2–4	> 4	
E. arta	♂	0.31	0.26	0.43	0.03	0.94	0.03	0.83	0.05	0.12	174
E. bella	♂	0.53	0.35	0.12	0.03	0.93	0.04	0.84	0.00	0.16	118
	♀	0.58	0.27	0.15	0.04	0.90	0.06	0.88	0.01	0.11	130
E. ingrata	♂	0.56	0.20	0.24	0.04	0.90	0.06	0.83	0.02	0.15	119
E. lawsoni	♂	0.15	0.36	0.49	0.01	0.96	0.03	0.91	0.02	0.07	152
E. morgani	♂	0.11	0.28	0.61	0.03	0.94	0.03	0.27	0.00	0.73	119
	♀	0.13	0.29	0.58	0.05	0.90	0.05	0.52	0.02	0.46	125
E. torella	♂	0.18	0.58	0.24	0.02	0.94	0.04	0.93	0.02	0.05	125
E. usitata	♂	0.26	0.37	0.37	0.03	0.94	0.03	0.83	0.02	0.15	115
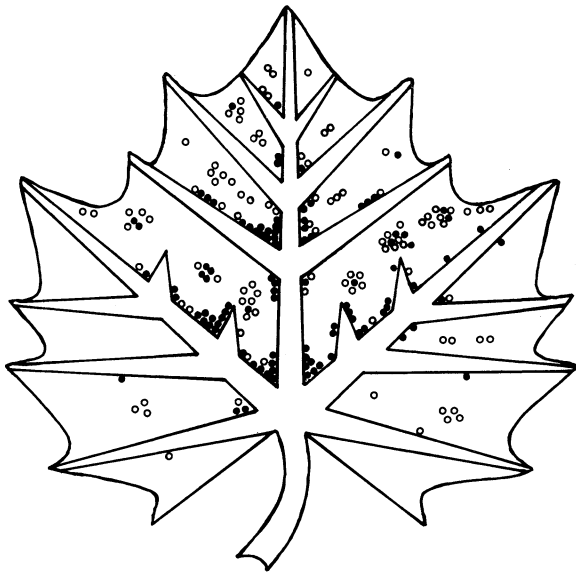
FIG. 2. Occurrence of *Erythroneura bella* ♂ ♂ (closed circles) and of *Erythroneura morgani* ♂ ♂ (open circles) on the lower epidermal surface of the sycamore leaf. Each dot represents 1% of the total distribution of each species. Data based on 118 observations for *E. bella* and 119 observations for *E. morgani*.

leaf blade and for six of the seven species of *Erythroneura* these sites were within 2 mm of the main veins. The distribution of feeding sites of *E. morgani*, generally at a distance > 4 mm from the main veins differed significantly from that of *E. bella*, typical

of the other guild species (by chi-square analysis $p < .0005$) (Fig. 2). The distributions of males and females of *E. morgani* differed significantly ($p < .0005$ by chi-square analysis); females were most often observed within 2 mm distance of the main veins. Females apparently divide time between feeding and oviposition activities and overlap other guild members on sites of oviposition along the main veins.

Proportional similarity.—For all 21 species comparisons of temporal utilization, canopy distributions, and occurrence on leaves of various age, proportional similarities (*PS*) were high and ranged from 0.60 to 0.94 ($\bar{x} = 0.77$), from 0.61 to 0.97 ($\bar{x} = 0.82$), and from 0.94 to 1.00 ($\bar{x} = 0.98$) for these three parameters respectively (Table 4). The relatively low similarity values between certain species in their occurrence on leaves of different size (Table 4) probably reflects differential species response to the microclimatic conditions afforded by these leaves (*PS* from 0.51 to 0.89; $\bar{x} = 0.72$). Larger leaves probably provide greater shelter from evaporation and thus a more humid microenvironment due to their umbrella-like physical characteristics.

Overall values of proportional similarity, calculated for the five niche parameters collectively, ranged from 0.25 to 0.59 ($\bar{x} = 0.43$) at Golconda and from 0.24 to 0.63 ($\bar{x} = 0.45$) at West Vienna for all 20 comparisons not involving *E. morgani* (Table 5). We consider that similarity values < 0.70 for each parameter (or $[0.70]^5 = 0.17$ for five parameters) are probably necessary for niche segregation, and

TABLE 4. Proportional similarity (*PS*) for all combinations of *Erythroneura* species for the niche or intracommunity parameters. W.V. and G. indicate data from the West Vienna and Golconda sites respectively. The *Erythroneura* species are: *E. arta* (a), *E. bella* (b), *E. ingrata* (i), *E. lawsoni* (l), *E. morgani* (m), *E. torella* (t), and *E. usitata* (u). Sample size as in Tables 1 and 3

| Species combina- tion	Temporal utilization		Distribution in canopy		Width of leaf	Age of leaf	Distance from veins	$\bar{x}$ across
	W.V.	G.	W.V.	G.				
a × b	----	0.74	----	0.88	0.69	0.99	0.95	0.85
a × i	0.93	0.64	0.97	0.60	0.75	0.96	0.97	0.83
a × l	0.64	0.82	0.80	0.95	0.84	0.98	0.92	0.85
a × m	0.71	0.82	0.73	0.91	0.80	1.00	0.39	0.77
a × t	0.90	0.68	0.87	0.61	0.68	0.99	0.90	0.80
a × u	0.94	0.79	0.70	0.80	0.89	1.00	0.97	0.87
b × i	----	0.62	----	0.65	0.85	0.98	0.98	0.82
b × l	----	0.88	----	0.93	0.62	0.97	0.91	0.86
b × m	----	0.64	----	0.89	0.51	1.00	0.37	0.68
b × t	----	0.75	----	0.69	0.65	0.99	0.89	0.79
b × u	----	0.86	----	0.84	0.73	0.99	0.98	0.88
i × l	0.60	0.72	0.77	0.65	0.59	0.94	0.92	0.74
i × m	0.69	0.53	0.70	0.55	0.55	0.96	0.42	0.63
i × t	0.83	0.83	0.84	0.62	0.62	0.96	0.90	0.80
i × u	0.92	0.53	0.67	0.74	0.70	0.96	1.00	0.79
l × m	0.73	0.74	0.84	0.89	0.88	0.98	0.34	0.77
l × t	0.72	0.79	0.89	0.62	0.75	0.98	0.98	0.82
l × u	0.67	0.79	0.85	0.81	0.88	0.98	0.92	0.84
m × t	0.81	0.63	0.86	0.75	0.63	0.99	0.32	0.71
m × u	0.73	0.70	0.96	0.81	0.76	1.00	0.42	0.77
t × u	0.88	0.67	0.83	0.81	0.79	0.99	0.90	0.84
$\bar{x}$ down	0.78	0.72	0.82	0.76	0.72	0.98	0.78	
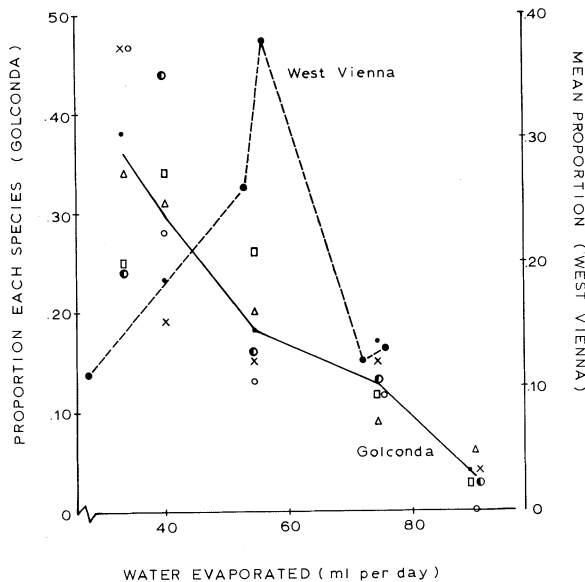
FIG. 3. Mean proportion of *Erythroneura* leafhoppers collected at Golconda (solid line) and at West Vienna (broken line) on five sycamore trees from which various amounts of H_2O were evaporated per day from beakers positioned throughout the canopies. For the Golconda site the proportions for each species are also given. Species are: *E. arta* (●), *E. bella* (○), *E. lawsoni* (×), *E. morgani* (△), *E. torella* (◐), and *E. usitata* (□). Sample size as in Table 1.

conclude that niches are similar enough so that competition is not reduced adequately to avoid competitive displacement. This competition has been shown to exist by McClure and Price (1975).

Habitat factors

There were no significant differences between species distributions on the five trees along the moisture gradient at either site in southern Illinois.

At Golconda, the highest proportion of each species occurred in those canopies from which the least amount of water was evaporated over a period of 24 h (Fig. 3). At West Vienna, the greatest mean proportions of leafhoppers were collected from canopies offering only intermediate degrees of shelter from evaporation. This discrepancy between trends at the two sites indicates a weakness in the estimate of moisture stress. It did not measure evaporation in the microsite occupied by the leafhoppers. When the second measure of evaporative stress, the proportion of large leaves in the canopy, was correlated with the mean proportion of leafhoppers collected from each tree highly significant product-moment correlation coefficients were obtained (Fig. 4) ($r = .886$, $p < .05$ at Golconda; $r = .921$, $p < .05$ at West Vienna). These data indicate that in a given locality the highest populations of *Erythroneura* species will occur together on those trees whose canopies provide the greatest shelter from desiccation. This has been observed during extensive collecting throughout Illinois, Kentucky, and Tennessee. Such a condition would further intensify the competitive interaction among coexisting species.

All eight species of *Erythroneura* occurred in the region of the Cumberland Mountains, Kentucky, while only three species were found at the northern limit of sycamore distribution (Fig. 5). This trend was expected as the guild is specific to sycamore. However, the highest value of species equitability was obtained in collections from southern Illinois where intensive studies were conducted.

The peak proportional abundances of the eight species of *Erythroneura* occurred in seven different latitudinal zones (Figs. 6 and 7). The greatest proportion of *E. torella* was collected toward the northern edge of sycamore distribution. To the south, the highest proportional abundances of *E.*

TABLE 5. Overall proportional similarity (*PS*) for all combinations of *Erythroneura* species for the niche or intra-community parameters studied at West Vienna and Golconda. Overall $PS > (0.70)^5$ or 0.17 reflect insufficient differences for niche segregation

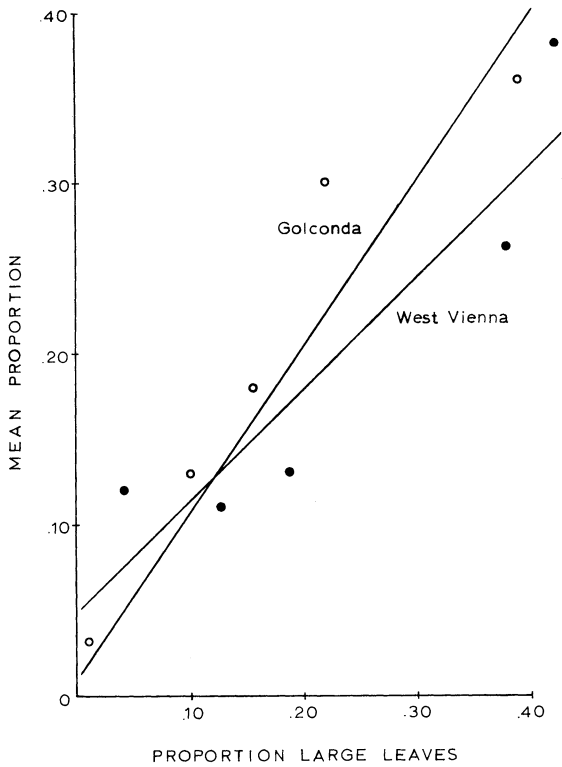|				WEST VIENNA					
	Species	*E. arta*	*E. bella*	*E. ingrata*	*E. lawsoni*	*E. morgani*	*E. torella*	*E. usitata*	$\bar{x}$
	E. arta		----	0.63	0.39	0.16	0.47	0.57	0.44
	E. bella	0.42		----	----	----	----	----	----
	E. ingrata	----	----		0.24	0.11	0.37	0.41	0.35
GOLCONDA	*E. lawsoni*	0.59	0.45	----		0.18	0.46	0.45	0.34
	E. morgani	0.23	0.11	----	0.19		0.14	0.22	0.16
	E. torella	0.25	0.30	----	0.35	0.09		0.51	0.39
	E. usitata	0.55	0.51	----	0.51	0.18	0.38		0.43
	$\bar{x}$	0.39	0.35	----	0.39	0.14	0.28	0.40	

FIG. 4. Mean proportion of total *Erythroneura* leafhoppers collected at Golconda (open circles) and at West Vienna (closed circles) on five sycamore trees whose canopies contain various proportions of large leaves (> 20 cm in width). The regression lines are described by the formula $Y = .008 + .975X$ ($r = .886$; $p < .05$) at Golconda and by $Y = .046 + .666X$ ($r = .921$; $p < .05$) at West Vienna. Sample size as in Table 1.

lawsoni, E. morgani, E. usitata, E. ingrata, E. bella, and *E. hymettana* occurred in that order, each separated by one degree on the latitudinal gradient. The only species showing a bimodal distribution pattern was *E. arta.*
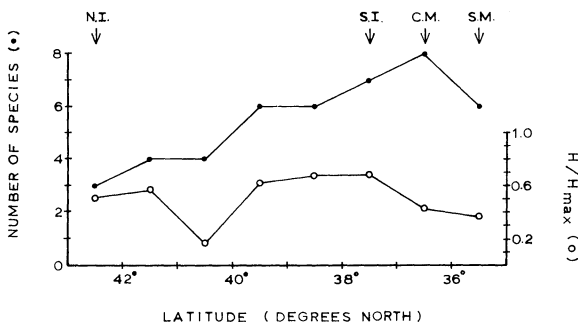
FIG. 5. Number (closed circles) and equitability (open circles) of *Erythroneura* species in eight zones along the latitudinal gradient. Labeled points locate latitudes of study sites in northern Illinois (NI), southern Illinois (SI), and in the Cumberland (CM), and Smoky Mountains (SM).
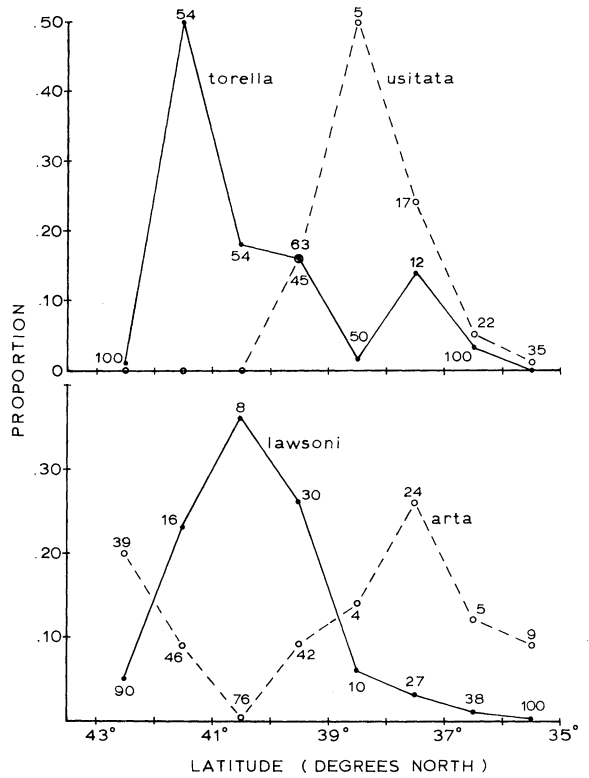

FIG. 6. Proportion of the total number of individuals of four *Erythroneura* species collected from eight zones along the latitudinal gradient for *E. torella* ($N = 255$), *E. usitata* ($N = 1330$), *E. lawsoni* ($N = 3838$), and *E. arta* ($N = 4007$). The number at each point gives the range of percent abundances among sites within each latitudinal zone for each species. A value of 100 indicates that all individuals collected from a given zone occurred at a single site showing very uneven local distribution; a value of 0 indicates that equal numbers occurred at each site showing even distribution. Samples consisted of a minimum of 205 leafhopper ♂ ♂ from each site and of 1005 from each zone.

There was a tendency for the *Erythroneura* species to become more unevenly distributed away from distributional centers (Figs. 6 and 7). This indicates that species interaction in a zone of geographical overlap may be substantially less than would have been predicted on the basis of their latitudinal distributions alone.

Proportional similarity.—Values of proportional similarity calculated for all combinations of the eight *Erythroneura* species for the two habitat or intercommunity parameters related to geographical distribution indicate that there are sufficient differences to explain coexistence in the guild in terms of habitat segregation (Table 6). However, for the third habitat parameter, distribution on trees along a moisture gradient, similarity values were high (*PS* from 0.70 to 0.93; $\bar{x} = 0.83$) for all 21 species comparisons.
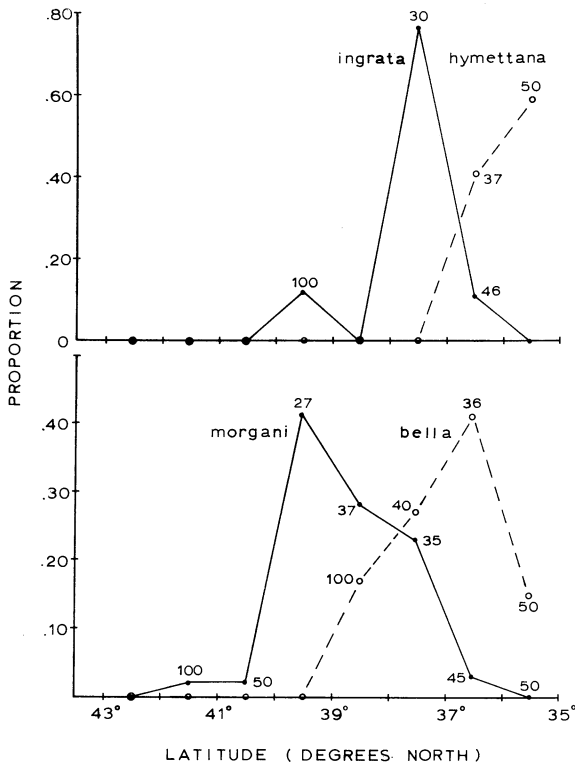
FIG. 7. Proportion of the total number of individuals of four *Erythroneura* species collected from eight zones along the latitudinal gradient for *E. ingrata* (*N* = 66), *E. hymettana* (*N* = 57), *E. morgani* (*N* = 191), and *E. bella* (*N* = 184). The number at each point gives the range of percent abundances among sites within each latitudinal zone for each species. Sample size as in Fig. 6.

TABLE 6. Proportional similarity (*PS*) for all combinations of *Erythroneura* species for the habitat or inter-community parameters. W.V. and G. give the data for the West Vienna and Golconda sites respectively. The *Erythroneura* species are: *E. arta* (a), *E. bella* (b), *E. hymettana* (h), *E. ingrata* (i), *E. lawsoni* (l), *E. morgani* (m), *E. torella* (t), and *E. usitata* (u). Sample size as in Table 1 (for humidity) and in Figs. 6 and 7 (for distribution)

Species combina-tion	Canopy humidity		Distribution		$\bar{x}$ across
	W.V.	G.	Lati-tudinal	Local	
a × b	----	0.86	0.61	0.47	0.65
a × h	----	----	0.20	0.54	0.37
a × i	0.82	----	0.41	0.63	0.62
a × l	0.78	0.91	0.35	0.48	0.63
a × m	0.82	0.88	0.52	0.55	0.69
a × t	0.74	0.79	0.35	0.46	0.58
a × u	0.85	0.81	0.53	0.83	0.76
b × h	----	----	0.56	0.44	0.50
b × i	----	----	0.38	0.43	0.40
b × l	----	0.91	0.10	0.47	0.49
b × m	----	0.84	0.43	0.61	0.63
b × t	----	0.77	0.17	0.46	0.47
b × u	----	0.78	0.48	0.53	0.60
h × i	----	----	0.11	0.75	0.43
h × l	----	----	0.01	0.39	0.20
h × m	----	----	0.03	0.28	0.15
h × t	----	----	0.01	0.13	0.07
h × u	----	----	0.06	0.46	0.26
i × l	0.72	----	0.16	0.48	0.45
i × m	0.70	----	0.43	0.39	0.51
i × t	0.75	----	0.27	0.42	0.48
i × u	0.76	----	0.41	0.47	0.55
l × m	0.88	0.81	0.40	0.50	0.65
l × t	0.89	0.74	0.64	0.41	0.67
l × u	0.93	0.74	0.26	0.56	0.62
m × t	0.84	0.83	0.36	0.48	0.63
m × u	0.91	0.83	0.71	0.60	0.76
t × u	0.85	0.89	0.33	0.52	0.65
$\bar{x}$ down	0.82	0.84	0.33	0.49	

For the latitudinal distributions of the guild proportional similarity values < 0.70 were obtained for 27 of 28 species comparisons and a mean value of only 0.33 for all species combinations. The degree to which the latitudinal distributions of each species were overlapped by those of all other species were as follows: *E. arta* 0.51, *E. bella* 0.40, *E. hymettana* 0.10, *E. ingrata* 0.38, *E. lawsoni* 0.36, *E. morgani* 0.51, *E. torella* 0.63, and *E. usitata* 0.46. For 28 comparisons of the local distributions of species, proportional similarity values ranged from 0.13 to 0.83 ($\bar{x}$ = 0.49). For 26 of these comparisons local distributions were less than 0.70 similar. Overall proportional similarities calculated for latitudinal and local distributions were considerably lower than 0.49 (or [0.70]²) for 26 of 28 species comparisons (range from 0.00 to 0.29; $\bar{x}$ = 0.15) and suggest habitat segregation in the guild (Table 7). The highest geographical overlaps were obtained for *E. usitata* and *E. arta* (0.44) and for *E. usitata* and *E. morgani* (0.42). Overlap values obtained for *E. hymettana* with *E. lawsoni* and with *E. torella* indicate complete habitat segregation (*PS* = 0.00).

Competition

McClure and Price (1975) reported that for each *Erythroneura* species there was an increase in the number of progeny produced under mixed species as compared to single species rearing conditions. This was expected because individuals of the same species are likely to compete more severely than are individuals of different species. We tested the significance of these observed increases in progeny production in mixed rearings for all 16 comparisons (eight mixed species rearing pairs) by Student's *t*-test. For each species in some rearing pairs, such as *E. usitata* with *E. morgani* (Fig. 8), the increases were significant (*t*-values > 2.9; *p* < .01) whereas for others, such as *E. lawsoni* with *E. usitata*, increases were insignificant (*t*-values < 1.9; *p* > .05). We concluded that some species (those with significant *t*-values) differed in their manners of resource utilization which permitted larger numbers of progeny to survive because of reduced competition.

There was a strong correlation between the degree to which the geographical distributions of certain of

TABLE 7. Overall proportional similarity (*PS*) for all combinations of *Erythroneura* species for the habitat or inter-community parameters (latitudinal × local distribution). Overall *PS* < (0.70)² or 0.49 reflect sufficient differences for habitat segregation

Species	E. arta	E. bella	E. hymettana	E. ingrata	E. lawsoni	E. morgani	E. torella	E. usitata
E. bella	0.28							
E. hymettana	0.11	0.25						
E. ingrata	0.26	0.15	0.08					
E. lawsoni	0.17	0.05	0.00	0.08				
E. morgani	0.29	0.26	0.01	0.17	0.20			
E. torella	0.16	0.08	0.00	0.11	0.26	0.17		
E. usitata	0.44	0.25	0.07	0.19	0.15	0.42	0.17	
x̄	0.24	0.19	0.07	0.13	0.13	0.22	0.14	0.24

the *Erythroneura* species overlap and the severity of competitive interaction between these same species as estimated in mixed species rearings by McClure and Price (1975). A significant product-moment correlation coefficient was obtained ($r = 0.932$; $p < .001$). Those species whose patterns of resource utilization were found to be insignificantly different were also found to have the least similar latitudinal distributions (Fig. 8). Conversely, those species which showed significant differences in their utilization of resources were found to have the most similar latitudinal distributions.
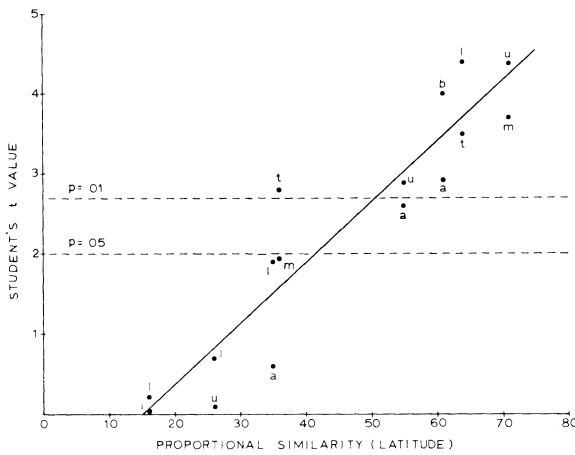

FIG. 8. Relationship between proportional similarity (*PS*) of the latitudinal distributions of eight pairs of *Erythroneura* species (e.g., points u and a at *PS* = 0.53) and the Student's *t*-value calculated from analysis of the differences in the mean number of progeny reared under single species versus mixed species conditions for those same species pairs. Thus high *t*-values indicate significant differences between species in their utilization of re-sources; low values show insignificant differences in re-source utilization. Values for *t* are from McClure and Price (1975). The regression line is $Y = -1.13 + 7.56\,X$ ($r = .932$; $p < .001$). Dotted lines give significance levels for *t* at $p < .05$ and $p < .01$. Species are: *E. arta* (a), *E. bella* (b), *E. ingrata* (i), *E. lawsoni* (l), *E. morgani* (m), *E. torella* (t), and *E. usitata* (u).

DISCUSSION

There were insufficient differences between species for all five niche parameters to account for coexistence in the leafhopper guild on sycamore. The relatively low similarity between certain species in their occurrence on leaves of different sizes is probably of minimal importance in reducing interspecific competition. McClure and Price (1975) have shown that leaf damage from feeding leafhoppers reached an average > 94% for all leaf sizes before either nymphal or adult peak abundance at West Vienna. The differences between the location of feeding sites of *E. morgani* and the other species (Table 4) (*PS* from 0.32 to 0.42; x̄ = 0.38) are also probably of little importance in reducing competition, as *E. morgani* competed as severely in mixed species rearings in the field as did the other species of *Erythroneura* (McClure and Price 1975). On the basis of niche analysis alone one might have inaccurately predicted that competition would be effectively reduced by the apparent segregation of feeding niches. These findings emphasize the importance of combining both ecotope analysis with competition studies to verify inferences drawn from proportional similarity values.

There were sufficient differences between species for the two habitat factors related to latitudinal distribution to explain coexistence in the guild by habitat segregation. Each *Erythroneura* species had its peak abundance in a different latitudinal zone. Thus geographical overlap was reduced and interspecific competition lessened. There is evidence that the latitudinal distributions of the sycamore leafhoppers have remained fairly stable in time. Our determination of *Erythroneura* distributions throughout Illinois is remarkably similar to that of Ross (1957) from 20 years ago! Five of the six species for which comparisons were possible (*E. arta, E. bella, E. lawsoni, E. morgani,* and *E. usitata*) were most abundant in the same latitudinal zone in both studies. In the sixth species (*E. torella*) distribution remained the same but estimates of relative abundance differed.

Unfortunately only rough comparisons could be made as only rank in abundance rather than actual abundance was available from Ross (1957).

The strong correlation between the degree to which *Erythroneura* geographical distributions overlap and the severity of interspecific competition (Fig. 8) suggests that species whose ranges overlap substantially have evolved slight differences in the manner in which they utilize resources, thus reducing competition somewhat where they occur sympatrically. These slight differences in resource utilization are not sufficient to allow coexistence in the guild (McClure and Price 1975) but possibly indicate a current evolutionary trend towards reducing competition between some species through character displacement or through a shift in the adaptive mode of the population.

Ross (1957) reported that both temperature and precipitation have profound effects on population levels of *Erythroneura* leafhoppers on sycamore in Illinois. These factors affect leaf succulence, evapotranspiration of the foliage which in turn affects the humidity of the canopy and the microhabitats of small species restricted within the boundary layer of a leaf, and the humidity of a general region which has a profound influence on the drying potential of winds. Considerable differences in temperature and precipitation have been reported between northern and southern Illinois which are separated by about five degrees of latitude. Average summer and winter temperatures differ by 2.8°C and 6.6°C, respectively, and annual precipitation by 36 cm (Page 1949, Ross 1957). These climatic differences and their subsequent effect on the community, including the phenology of the host plant, may explain the differential occupation by the guild members of particular latitudinal zones throughout the sycamore range.

There is some evidence, though not conclusive, that a species has superior competitive ability in the latitudinal zone where it occurs most abundantly. In competition experiments conducted thus far in east central Illinois where *E. lawsoni* is dominant, that species has shown consistent, although not significant, competitive superiority in all four mixed rearings tested. When reared with *E. ingrata*, *E. usitata*, *E. arta*, and *E. torella*, *E. lawsoni* produced a proportionately greater number of offspring (indicated by higher Student's *t*-values) than did its competitor in each case (Fig. 8). If increases in progeny were proportionately equal, then *t*-values for each species in the pair would also be equal. Thus, the higher *t*-value for *E. lawsoni* as compared with its competitor indicated possible competitive ability. The striking similarity between our determination of *Erythroneura* distributions and that of Ross (1957) also indicates that the seasonal conditions of a particular latitudinal zone may favor the continuous occupation by a given species.

McClure and Price (1975) reported that competitive ability in the *Erythroneura* guild on sycamore may be frequency-dependent since at high densities each species adversely affected its own fitness more than it did that of its competitor in mixed species rearings. Gause (1934) and Ayala (1971) have provided models based on the population growth equations which predict a stable coexistence among competing species where fitness is inversely related to density. Because densities of the sycamore leafhoppers are sufficiently high at their distributional centers to be limited by density-dependent fitness, a stable coexistence among species can be achieved by this type of interaction alone. However, further rearing experiments with these leafhoppers are needed to determine with certainty the applicability of these models to coexistence in the sycamore guild.

The dispersal capability of *Erythroneura* and other leafhoppers has been well documented by Johnson (1935), Medler (1962), Chiykowski and Chapman (1965), Cook (1967), Johnson (1969), and DeLong (1971).

Several authors have described situations in which competing species can coexist in a nonequilibrium state when dispersal is important. Skellam (1951) and Hutchinson (1953, 1965) have postulated that, with certain local migration and extinction rates, competitors may coexist without achieving a stable equilibrium. From theoretical considerations, Skellam (1951) hypothesized that if species with lower reproductive rates also have higher dispersal rates, then coexistence can be maintained. Hutchinson (1953) suggested that if there is a tendency for competitively weaker species (fugitive species) to disperse more easily, then coexistence is possible where catastrophic events continually destroy previously occupied habitats while creating empty sites available for colonization. Models based on differential equations have been proposed by Levins and Culver (1971), Horn and MacArthur (1972), and Slatkin (1974) to predict conditions in which competing species can coexist in nonequilibrium. Horn and MacArthur (1972) predict that coexistence is possible even over a region of similar habitable patches since a balance of local extinction and colonization would leave some patches unoccupied. As long as there are unoccupied patches in a given environment there is no limit to the number of competing species which can coexist (MacArthur 1968, Horn and MacArthur 1972). Coexistence among the sycamore leafhoppers in less favorable areas of the sycamore range may, in part, be explained by these various non-equilibrium models.

On the basis of our findings to date, the following hypotheses on coexistence among *Erythroneura* leaf-

hoppers are suggested for consideration in future studies:

1) Optimal adaptation of each species to the particular set of conditions at a different latitude. This feature would not, in itself, lead to coexistence as competitive exclusion could run to completion, with the result that each species would occupy exclusive and adjacent ranges. This is so particularly during a favorable series of years when density-dependent factors become important early in each breeding season.

2) Frequency-dependent competitive fitness (McClure and Price 1975) such that the less well adapted species can coexist at low densities with the optimally adapted species. This situation could lead to a stable coexistence during favorable conditions for the species out of their optimal ranges.

3) The ability of species to disperse and colonize unoccupied sites at sub-optimal parts of the sycamore range could lead to non-equilibrium coexistence of species.

Further competition experiments at each latitude and involving several successive generations of these leafhoppers are needed to test our hypotheses that each *Erythroneura* species is optimally adapted to the environmental conditions of a different part of the sycamore range and that fitness is density-dependent. The relative abilities of the *Erythroneura* species to disperse and to colonize sites throughout the sycamore range should also be examined to test the relevance of non-equilibrium models to co-existence among these multivoltine organisms. Indeed the adaptive nature of dispersal and the intrinsic controls on dispersal might be better understood through the further study of these species. This guild offers great potential for gaining further understanding of the ways in which short-lived organisms coexist.

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