Latitudinal effects on treehopper species richness (Homoptera: Membracidae)

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ABSTRACT. 1. Membracid species richness declines with increasing latitude in the Western hemisphere but begins to increase again in temperate regions. In northern latitudes this transition occurs in the highlands of Mexico and is the result of the emergence of a new tribe and greater host specialization.

2. The relationship between number of species per genus and latitude is parabolic.

3. We suggest the low number of species per genus in tropical regions may be due to the lack of host specialization and reduced coordination of life history with host phenology.

Key words. Membracidae, species richness, latitudinal gradients, species per genus, host specialization.

Introduction

Membracids are phytophagous insects which range from solitary species to those with highly developed parental care (Wood, 1974, 1976a, b, 1977, 1978, 1979). Four factors: predation, ant mutualism, host specialization and geographic constraints are the most likely major selective factors moulding membracid life history patterns (Wood, 1982). The seemingly high diversity of membracid species in the tropics suggests to taxonomists that the family Membracidae is of tropical origin (Funkhouser, 1951). Membracids are distributed in the Western Hemisphere throughout South America to southern Canada. With few exceptions, there is no overlap between New and Old World faunas.

Collecting in both the New World tropics and North temperate regions suggested to T.K.W. that species richness might not be

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greatest in the tropics. To answer this question and determine the relative importance of the four proposed selective factors on life histories, we began a biogeographic analysis of Western Hemisphere species.

Methods

Metcalf & Wade (1965) catalogued the Western Hemisphere species by country and state. Their locality records and additional lists were used for the initial analysis (Kopp & Yonke, 1973a, b, c, 1974; Dennis, 1965, 1970; Hinton, 1977; Wood, unpublished). Regions we selected were those sampled by membracid taxonomists during the last 60 years.

We used the classification system of Deitz (1975) for the subfamily and tribe. Synonomy of species followed that of Metcalf & Wade (1965). We determined the following for each region: (a) area in square miles; (b) median latitude; and (c) the number of subfamilies, tribes, genera and species present (Table 1).

TABLE 1. The number of membracid subfamilies, tribes, genera, and species for each region. Area, median latitude, and mean number of species per genus are also given.

Region	Area (in miles^2)	Mid latitude	No. of subfamilies	No. of tribes	No. of genera	No. of species	H′	J′	$\bar{X}$ species per genus
Argentina and Chile	1,370,516	38.5°S	5	13	32	86	1.36	0.90	2.69 ± 2.44
Peru	496,222	8.57°S	5	17	63	169	1.65	0.91	2.68 ± 2.50
Ecuador	104,510	1.5°S	6	20	75	253	1.71	0.91	3.37 ± 3.36
The Guianas	175,275	4.7°N	7	19	59	181	1.61	0.91	3.07 ± 3.07
Colombia	439,828	4.0°N	6	19	84	342	1.75	0.91	4.07 ± 4.34
Venezuela	352,143	6.5°N	5	18	40	94	1.50	0.93	2.35 ± 1.85
Panama	28,575	8.25°N	6	20	63	137	1.69	0.94	2.17 ± 1.75
Costa Rica	19,238	9.5°N	6	21	63	134	1.69	0.94	2.13 ± 1.70
Guatemala	42,042	16.0°N	6	18	62	146	1.66	0.92	2.35 ± 2.20
Mexico	761,530	23.5°N	7	22	85	274	1.75	0.90	3.22 ± 3.44
Mexico divided:									
(1) South	Unknown	18.25°N	6	19	72	185	–	–	2.57 ± 2.47
(2) North	Unknown	27.0°N	6	13	21	27	–	–	1.29 ± 0.72
Florida	58,560	28°N	4	9	29	63	1.33	0.91	2.17 ± 1.95
Alabama, Georgia and Mississippi	158,141	32.5°N	2	9	22	51	1.17	0.87	2.34 ± 2.75
Arizona	113,909	34.5°N	5	12	41	76	1.51	0.93	1.85 ± 1.47
Oklahoma	69,919	35.0°N	3	9	23	67	1.15	0.84	2.91 ± 3.60
North Carolina	52,712	35.0°N	3	9	26	71	1.28	0.90	2.73 ± 2.41
Missouri	69,674	38.25°N	3	9	28	100	1.25	0.86	3.57 ± 4.08
Kansas	82,276	38.5°N	3	8	25	68	1.26	0.90	2.72 ± 2.60
Ohio	41,222	40.25°N	3	9	24	112	1.13	0.81	4.67 ± 6.47
New York	49,576	43.0°N	3	9	26	116	1.17	0.82	4.46 ± 6.02
Wisconsin	56,154	44.0°N	2	8	22	74	1.14	0.85	3.36 ± 3.80

To determine relationships among the above variables we used standard linear and quadratic regression analyses. To examine diversity and evenness, we used the Shannon-Weaver diversity index by substituting genera for species, and species for individuals (Brower & Zar, 1977).

Results

A linear regression indicated no significant correlation between the number of species and area or with log area (Table 2). A stepwise regression indicated that area does not contribute to species richness with or without transforming the data (see Table 2). The number of species or log species do negatively correlate with median latitude (Table 2) suggesting decreasing species richness with increasing latitude. However, examination of the data points (Fig. 1) suggested the linear regression was not the only fit to the data. A quadratic regression provided an equally good fit ($P < 0.01$) to the data (Table 2). The point representing Mexico appeared to be aberrant

due to the number of species common to both the tropics and North America. Exclusion of Mexico improved the parabolic fit (Table 2). To further verify this quadratic relationship we arbitrarily divided Mexico (14.5–22.0°N and 22.1–32.0°N). Using Metcalf & Wade (1965) we examined the literature cited there for exact localities. We could find exact localities for 202 of the 274 species listed. Of these 202 species, 185 were recorded from southern latitudes and twenty-seven from northern latitudes. Only ten species were common to both regions. When the number of species for two latitudes were added in linear and quadratic fits the quadratic explained 62.7% of the variation in species richness while the linear model explained only 50% (see Table 2).

The basis for this relationship appears to be the different numbers of species per genus at higher taxonomic levels. The regression of diversity (H') ($Y = 1.77 - 0.0133X'$, $R^2 = 0.75$, $r = 0.87$, $P < 0.01$, $n = 20$) and evenness (J') ($Y = 0.94 - 0.0017X'$, $R^2 = 0.47$, $r = 0.69$, $P < 0.01$, $n = 20$) with median latitude showed a significant decrease with increasing latitude.

TABLE 2. The effect of area, log area, and median latitude on the number of treehopper species (N.S. = Not significant).

| Regression	Equation	
Number of species v. area	$Y = 117 + 0.0001 X$	$(R^2 = 0.065, r = 0.255, F = 1.251, \text{N.S.}, n = 20)$
Number of species v. log area	$Y = -166 + 58.8 X$	$(R^2 = 0.140, r = 0.374, F = 2.926, \text{N.S.}, n = 20)$
Log number of species v. log area	$Y = 1.37 + 0.136 X$	$(R^2 = 0.088, r = 0.297, F = 1.731, \text{N.S.}, n = 20)$
Log number of species v. median latitude	$Y = 2.31 - 0.0104 X$	$(R^2 = 0.471, r = 0.686, F = 15.99, P = 0.0008, n = 20)$
Linear: Number of species v. median latitude	$Y = 212 - 3.35 X$	$(R^2 = 0.421, r = 0.649, F = 13.09, P = 0.002, n = 20)$
Quadratic: Number of species v. median latitude	$Y = 242 - 8.02 X + 0.104 X^2$	$(R^2 = 0.451, F = 6.990, P = 0.0061, n = 20)$
Linear (excluding Mexico):		
Number of species v. median latitude	$Y = 205 - 3.32 X$	$(R^2 = 0.505, r = 0.711, F = 17.35, P = 0.0006, n = 19)$
Quadratic (excluding Mexico):		
Number of species v. median latitude	$Y = 270 - 14.2 X + 0.241 X^2$	$(R^2 = 0.674, F = 16.52, P = 0.0001, n = 19)$
Linear (Mexico divided):		
Number of species v. median latitude	$Y = 205 - 3.42 X$	$(R^2 = 0.479, r = 0.629, F = 17.48, P = 0.0005, n = 21)$
Quadratic (Mexico divided):		
Number of species v. median latitude	$Y = 267.31 - 12.93 X + 0.2099 X^2$	$(R^2 = 0.626, F = 15.10, P = 0.0001, n = 21)$
$\bar{X}$ number of species v. median latitude	$Y = 2.65 + 0.012 X$	$(R^2 = 0.054, r = 0.232, F = 1.027, \text{N.S.}, n = 20)$
Quadratic: $\bar{X}$ number of species v. median latitude	$Y = 3.69 - 0.152 X + 0.0036 X^2$	$(R^2 = 0.429, F = 6.396, P = 0.0085, n = 20)$
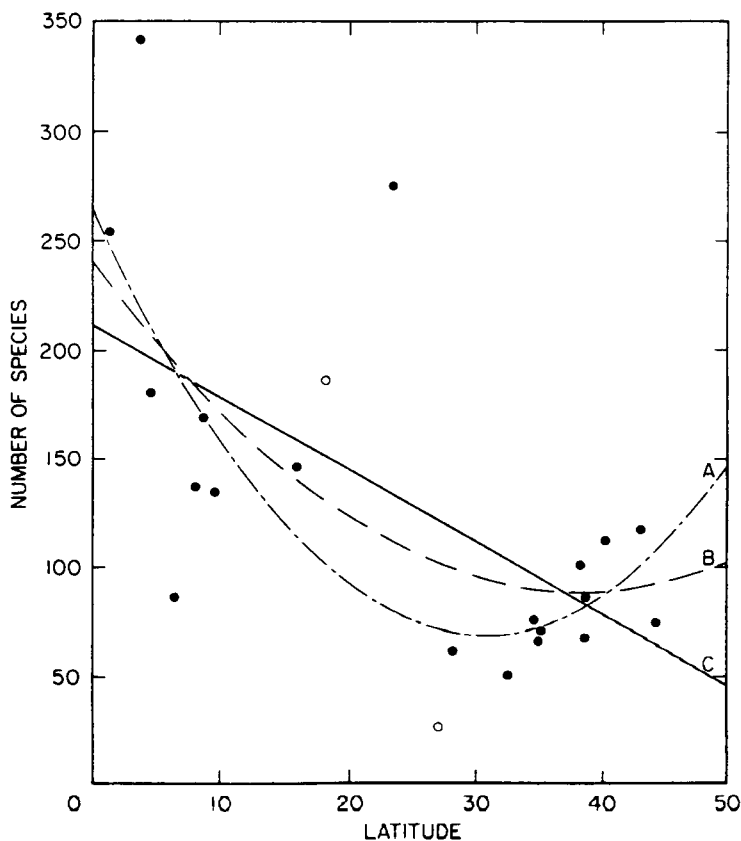
FIG. 1. The number of treehopper species with increasing latitude. Line A represents the quadratic fit to the data with Mexico divided into two areas. Line B is the quadratic fit to the data with Mexico as one area. Line C is the linear fit to the data. North or South designations were not given for each latitude. Open circles are for northern and southern Mexico. Regression equations are in Table 2.

There is a significant decrease in the number of genera with increasing latitude ($Y = 73.7 - 1.19X'$, $R^2 = 0.66$, $r = 0.81$, $P \leqslant 0.01$, $n = 20$). These relationships indicate large numbers of tropical genera contain few species while North temperate genera have many (Fig. 2).

The number of tribes decreases with increasing latitude (Table 1). Tropical regions have seventeen to twenty-two tribes while higher latitudes have six to eleven. The number of subfamilies drops from five to seven in the tropics to two or three at higher northern latitudes.

Discussion

The increase in the number of species in Mexico and North America is the result of greater generic diversity and speciation in the tribe Smiliini. Only one of the twenty-two (*Antianthe*) genera in this tribe is both tropical and temperate in its distribution. The remaining twenty-one genera are temperate with the first northern records from the highlands of Guatemala and Mexico. However, the greatest diversification of genera and species occurs in North America; 46.2% of the 307 species north of Mexico are members of the Smiliini. Host plant records (Ball. 1931, 1932, 1933; Bray & Triplehorn, 1953; Dennis, 1952; Funkhouser, 1917; Goding, 1893; Leonard, 1928; Plummer, 1936, 1938, 1945; Wood, personal collection; Woodruff, 1924) of 106 of the 156 species of Smiliini (excluding *Antianthe*, which is found on solanaceous plants) indicate they are only found on *Quercus* (oak) and must be regarded as specialists. Only twenty of the
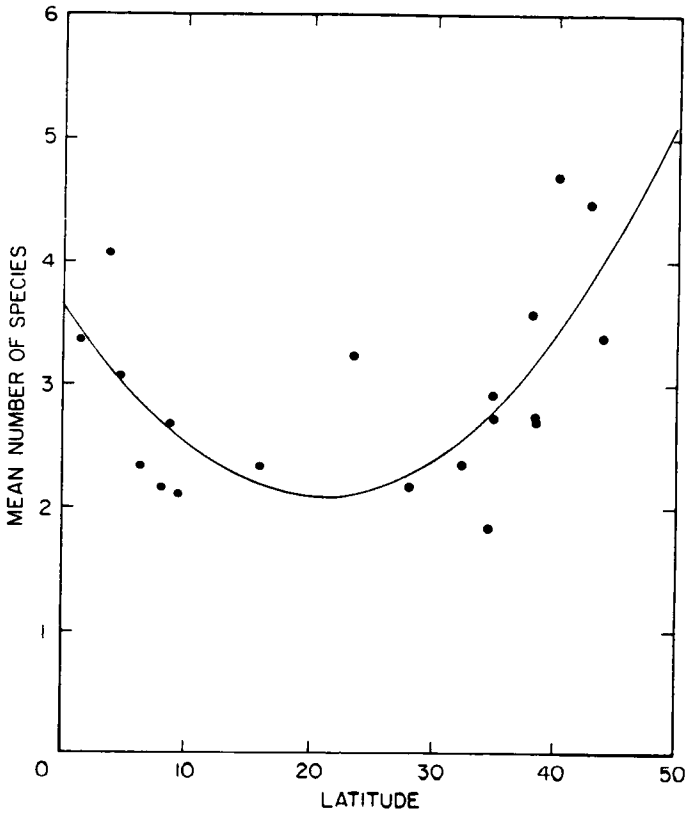
FIG. 2. The mean number of species per genus with increasing latitude. The best fit to the data was the quadratic ($Y = 3.69 - 0.152\,X + 0.0036\,X^2$, $R^2 = 0.429$, $F = 6.396$, $P = 0.0085$, $n = 20$).

156 are recorded from other hosts. We postulate that a Smiliini progenitor became a specialist on *Quercus* in the highlands of Mexico which is the centre of oak diversity (Trelease, 1924). In Costa Rica, many tree-hopper species appear to be multivoltine and 46% of sixty-eight species are polyphagous (utilize two or more genera of hosts) in lowland wet forests while at higher elevations (lower montane) 83% of twenty-nine appear to be monophagous (Wood, in preparation). Similar trends are found in lowland areas of the Old World tropics. For example, for the thirty-seven species from southern India, 46% utilize two or more genera of host plants (Ananthasubramanian & Ananthakrishnan, 1975). In the New World north temperate areas (e.g. Ohio), species are univoltine with few exceptions (Funkhouser, 1917) and a majority are monophagous (utilize one genus of host), for example 84% of 112 species in Ohio are monophagous (Wood, in preparation). The overall reduction in the number of generations in a year appears to be the result of greater seasonality and the physiology of *Quercus*. Eggs of the Smiliini at higher latitudes hatch at bud break with nymphs maturing 4–5 weeks later. Adults mate, oviposit and die in late June and early July (Wood, personal observation). This life cycle correlates with the phenology of *Quercus* and the availability of nutrients from the host to these phloem feeding insects (Longman & Coutts, 1974). Host plant records at present are not sufficiently detailed to permit us to determine if members of the Smiliini are specific to *Quercus* species. There is considerable variation in phenology among species of *Quercus* which may promote host specialization below the generic level. If host special-

ization is found then speciation may have occurred in a similar way as the *Enchenopa binotata* Say complex (Wood, 1980; Guttman *et al.*, 1981; Wood & Guttman, 1981, 1982).

The relationships reported here and for *Enchenopa* argue that host specialization has been a major factor in membracid speciation in North temperate regions. We suggest the apparent low number of species per genus in lowland tropical regions appears to correlate with reduced host specialization, multivoltine life histories, and lack of coordination of life history with host phenology in the absence of severe seasonality.

The large number of species in Colombia and Ecuador may be the result of elevational effects. It seems logical to propose higher elevations should promote univoltine life histories and a trend toward host specialization. Richter (1954) suggests that species in Colombia above 2000 m tend to be restricted to a single host species. Thus high elevations in the New World tropics may promote speciation in a way that is similar to latitudinal effects.

Acknowledgments

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