Biodiversity of Tropical Homoptera, with the First Data from Africa

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MEASURING BIODIVERSITY PROVIDES THE base-line information on distribution, richness, and relative abundance of taxa that is needed for conservation decisions, studies of ecosystem ecology, and cladistic biogeography. Considering the immense contribution of insects to the world's biota, any general explanations of diversity should account for patterns of insects. The advantage of working with hyperdiverse taxa is that there are surely many repeated patterns, which are the clues to processes. The richness also presents a challenge: in most habitats the true richness of major taxa can never be observed, so estimating species richness requires quantitative sampling. The purpose of this article is to review past quantitative studies of Homoptera, principally Auchenorrhyncha, in tropical forests and to describe the first such study in Africa, which examines the altitudinal patterns of homopteran species richness and composition compared to that of the plant community.

Homoptera and Biodiversity

Hemiptera (Heteroptera plus Homoptera) is the fifth most speciose order of insects, after beetles, flies, wasps, and moths (Wilson 1992). The suborder Homoptera, and, particularly, the infraorder Auchenorrhyncha, accounts for most of these, with about 50,000 known species. Homoptera is abundant in individuals as well as species, especially in the tropics. In surveys of an Amazonian Terre Firme forest, Homoptera was the third most numerous group and even ranked high in biomass (Adis et al. 1984). However measured, homopterans constitute a significant portion of the world's biota.

There is growing evidence that Homoptera is paraphyletic with respect to Heteroptera (van Dohlen and Moran 1995, Sorensen et al. 1995). Nevertheless, these paraphyletic lineages share several unique, plesiomorphic, homologous features that functionally unite their species in ecosystems

Fig.1. In the central mountains of Puerto Rico, an adult (near top) and nymph (near bottom) of *Nessorhinus gibberulus* Stål coincidentally feed on the same branch of a blackberry bush, *Rubus* (*Eubatus*) sp. Like this solitary treehopper, nearly all homopterans share the same or similar niche as adults and immatures.

and, thereby, lend these higher taxa relevance in the context of biodiversity.

Immatures and adults of nearly all species of Homoptera are herbivorous sap-suckers (a few are fungivorous). This is greater ecological uniformity than found in any other insect taxon of comparable richness. The herbivorous habit is interesting for several reasons: (a) herbivores are the first het-

erotrophic tier in an ecosystem and are, therefore, especially important in energy transfer; (b) homopterans completely rely on their host plants throughout development, in similar niches, so floristic diversity may affect many species in similar ways; and (c) many homopterans are vectors of plant pathogens and, thus, have an amplified effect on the patchiness and quality of the entire ecosystem.

Homopterans are paurometabolous. More speciose taxa are holometabolous, which is thought to have contributed to their diversity because adults and immatures, usually having non-overlapping niches, are under separate selection pressures. In contrast, adults and nymphs of homopterans usually share one niche (Fig. 1), so there are probably fewer complex ecological processes producing and maintaining their diversity. If this is true, it could be easier to understand the causes of their richness and distribution—one aim of biodiversity studies.

Previous Surveys of Tropical Forest Homoptera

Of the quantitative surveys that have looked at patterns of species, genera, families, or superfamilies of tropical forest Homoptera (Table 1), most have differed in focal group, geographic region, and sampling methods. Unfortunately, because there have been few studies, local site differences cannot yet be separated from regional differences.

Species Abundance. Larger samplings usually have captured more species because most species are rare. Novotny (1992) found even more singleton species (abundance = 1) than predicted by the log series model, which adequately describes the

Table 1. Quantitative surveys of tropical forest Homoptera that have treated Auchenorrhyncha and Psylloidea at the level of superfamily or below

Focal Taxon	Region	Sampling Method	Reference
Arthropoda	Borneo	canopy fogging	Stork 1987, 1991
Insecta	Panama, Brunei, Sulawesi Papua New Guinea	light-traps	Sutton 1983, Sutton et al. 1983
Hemiptera	Sulawesi	light- and suction traps	Rees 1983
Hemiptera	Sulawesi	light-traps, malaise traps, flight-interception traps, yellow-pan traps, sweep netting, hand searching	Hodkinson and Casson 1991
Homoptera	Papua New Guinea	malaise traps	Springate and Basset 1996
Homoptera	Venezuela	sweep netting	Janzen et al. 1976
Auchenorrhyncha	Vietnam	sweep netting	Novotny 1992, 1993
Auchenorrhyncha	Panama	canopy fogging, light-traps	Wolda 1977; 1978a,b; 1979; 1980a; 1983a,b,c; 1987
Cicadoidea	Peru	light-traps, visual search	Pogue 1996
Membracoidea	West Amazonia	canopy fogging (SI/ANTSE), light-traps	McKamey 1994

relative abundance patterns of many organisms, from insects to fungi (Magurran 1988). In Pogue's (1996) multiyear sampling of cicadas in Peru, although species richness generally tracked the abundance of specimens, at both sites the greatest number of species were not obtained by the largest sample. This may be explained largely by a combination of yearly variation in richness of particular sites and in effectiveness of light-trapping due to environmental conditions.

Light-trap Biases. Light-trap catches result from a combination of distribution, relative abundance, differential activity and attraction of each taxon, and the variable response of each taxon to environmental factors. The last factor was studied by Rees (1983) in Sulawesi, where total catches were correlated negatively with the moon phase but correlated positively with rainfall, except for delphacids. Springate and Basset (1996) quantified the activity biases of different homopteran superfamilies in Papua New Guinea using unlit flight interception traps, which can help determine the extent to which light-trap data are a function of activity rather than the other aforementioned factors. With further work along these lines, it may be possible to obtain some measure of richness and relative abundance from light-trap samples.

Vertical Distribution. Canopy samples capture more homopteran individuals per unit effort than do understory samples (Sutton and Hudson 1980, Sutton 1983, Sutton et al. 1983, Rees 1983, Wolda 1987). This is expected because most species feed preferentially through meristematic plant tissue. Surprisingly, however, Wolda (1987) found more species in the understory than in the canopy (Note, in his Fig. 2, that his text reveals that his figure legend is transposed).

Host-plant Specialization. In Panama, the numbers of individuals and species of Homoptera collected by pyrethrum-fogging were correlated significantly with the number of vines in the target canopy (Wolda 1979), suggesting host-plant specialization. In contrast, in a pyrethrum-fogging study in Borneo (Stork 1987), species overlap between samples was explained more by the proximity of trees than by their taxonomic similarity, suggesting low host specificity.

Altitudinal Richness Gradients. There are no definitively concordant results about homopteran species richness peaks along altitudinal gradients. In Panama, Wolda (1987) found that richness decreased gradually with altitude. In Sulawesi, maximum richness occurred between 600 and 1,000 m (Hodkinson and Casson 1991). In disturbed Venezuelan habitats, the highest homopteran richness was detected at 1,600 m (Janzen et al. 1976). (Note, however, that because Janzen et al. did not sample between 200 m and 1,600 m, their results are compatible with a 600–1,000 m peak.) Different regions may not have parallel patterns. Nevertheless, some divergence of results probably was due to the different sets of sampling methods used in each study (see Table 1).

Community Complementarity. Within western Amazonia, homopteran communities are fairly uniform on a regional scale. Pogue (1996) studied the cicadas at two sites approximately 215 km distant and found a 50% similarity in the fauna. Another study (McKamey 1994) used the measure of complementarity (C, of Colwell and Coddington 1994; see definition and discussion below) and compared small samples of membracid morphospecies from lowland rainforests of western Amazonia that had been collected by different methods (canopy-fogging vs. light-trapping). Although small samples generally inflate C values (see below), small samples of membracids showed 81% C across 660 km (about 30% of the Tambopata, Peru, species occurred in Rondonia, Brazil, samples), and 91% C across 1550 km (10% of the Tambopata species occurred in Napo, Ecuador, samples). Thus, many species of Cicadoidea and Membracoidea tend to be widespread across continuously forested lowland areas. Silva and Coddington (1996) found spider communities in adjacent lowland forests of Peru to have even lower complementarity, from 65%–85%.

Tanzanian Homoptera

The floral richness of a region is relevant to the richness patterns of herbivores, as the variety of exploitable resources often is cited as a factor affecting the number of species than can coexist (e.g., Futuyma 1979, Huffaker and Rabb 1984). To investigate the extent to which plant diversity and altitude drive animal diversity, the Homoptera, principally Auchenorrhyncha and Psylloidea, were sampled across altitudes and compared to the changes in the plant community.

Table 2. Summary of sampling per elevation, site, season, and plot in the Usambara Mountains, Tanzania, by insecticidal fogging of the understory and canopy

Elevation (in meters)	Site	No. of Plots	
		2 Jul–26 Jul 1995	31 Oct–8 Dec 1995
1,650–1,730	Mazumbai 1 4°48.90′S, 38°29.46′E	5	4
1,650–1,730	Mazumbai 2 4°49.42′S, 38°29.16′E	0	2
1,370–1,435	Mazumbai 3 4°48.78′S, 38°30.86′E	0	2
825	Kwamgumi 1 4°57.27′S, 38°44.92′E	0	1
430	Kwamgumi 2 4°57.22′S, 38°44.76′E	0	1
170–220	Kwamgumi 3 4°57.27′S, 38°44.16′E	6	7
210	Segoma 4°58.77′S, 38°44.22′E	0	1

Fig. 2. One fogging plot from Mazumbai Forest, Tanzania. The suspended, open tetrahedral sampler nets create an almost continuous collecting surface.

Study Sites

The Eastern Arc mountain chain is a previously neglected but unique biotic region. It extends from Mozambique to Kenya and its forests are thought to have persisted for perhaps 30 million years, since Africa attained its present position (Lovett and Wasser 1993). The Eastern Arc increasingly has become isolated from the large Guineo-Congolian rainforest since the Miocene, with the uplift of the Central African Plateau, while the individual mountains have remained separated from each other by open, dry, savannah habitat—a major barrier to dispersal for many organisms. The age of the Eastern Arc forests, their isolation from each other and from the West African forests, and their high insolation and rainfall have combined to produce among the highest levels of animal and plant endemism in Africa, much higher than that found in adjacent mountains of recent, volcanic origin, such as Kilimanjaro. Scharff (1992) found greater than 80% endemism in linyphiid spiders on individual mountains of the Eastern Arc. The Usambaras, of the Eastern Arc in NE Tanzania, have been recognized as being among the sites of highest priority for biological inventory and conservation by the U.S. National Research Council and World Wide Fund for Nature (WWF), yet little entomological work had been conducted there (Scharff 1992).

All sites of this study receive on average at least 100 mm rain each month and a mean maximum of 2,000 mm per year, with bimodal rainfall peaks: a long wet season from February to May or June, and a short wet season from October to November or mid-December. The Usambaras are coldest in June and July. Samples were collected in July and October–December in 1995, an unusually dry year, from 170–825 m altitude in Kwamgumi and

Segoma Forest Reserves (lowland to submontane rainforest), of the East Usambaras, and from 1,370–1,730 m in Mazumbai Forest Reserve (submontane to montane rainforest), of the West Usambaras, 30 km NW of the Kwamgumi plots. A total of 29 plots were sampled across 7 sites at 5 altitudes (Table 2), yielding over 2,600 samples. Sampling was concentrated at two sites representing the altitudinal extremes: Mazumbai 1 (1,650–1,730 m) and Kwamgumi 3 (170–220 m). Interplot distance within an elevation varied from 0.01 to 2.0 km. Most sites have suffered historically from selective logging.

Materials and Methods

Arthropods were sampled by applying a PulsFog K-10 Standard thermal fogger to the canopy and, usually, understory vegetation of mixed-tree plots. Plots were chosen subjectively for good canopy cover. The fogger was operated from the ground except in one plot, where it was suspended in the canopy from a pulley arranged using a crossbow set with a fishing reel and weighted, blunt arrowheads. When possible, fogging was conducted at dawn, when the 30°C fog could rise the highest and drift the least. In Mazumbai, some plots could be fogged only in the afternoon or early evening.

The insecticide was 2.0 L of 0.8% active ingredient, water-based solution of refined natural pyrethrum (25% active ingredient), piperonyl butoxide as a synergist, and a nonionic combination of cetosteryl and cetoniagrol as an emulsifier, prepared by Monsoor Daya Chemical Co. in Dar es Salaam, Tanzania. Similar fogging programs use oil-based pyrethrum solutions, which produce a hotter fog and are considered to be more effective. Nevertheless, the water-based solution was able to capture cicadas and other strong fliers, such as large apids, tabanids, and syrphids.

Falling arthropods were captured in 88 to 91 tetrahedral, nylon, fine-mesh nets, each net measuring one square meter, suspended among parallel lines strung across the plot in an even array that produced an almost continuous collecting surface (Fig. 2). After a 2-hr drop time, specimens were tumbled to the center of the nets, tied off, and transported to camp, where they were sealed in 70–75% ethanol using a tabletop plastic seamsealer. Usambara insects also were sampled using canopy-level 'black' UV-traps and timed visual searches off chest-level 'white' [= superactinic] UV sheets. All specimens were retained and will be made available for systematic and biodiversity studies by the Zoological Museum, University of Copenhagen. Contact Søren Langemark (solang@zmuc.ku.dk) for further information.

Auchenorrhyncha and Psylloidea adults were identified to morphospecies by comparison to a reference collection extracted from the samples. Data were managed using the L1.5 pre-release version of the Biota biodiversity database program (Colwell 1996a).

There is a variety of methods for estimating species richness (Colwell and Coddington 1994, Chazdon et al. 1998). Species censuses are unattainable for nearly all animals. Fitting species abundance curves to parametric models, such as the log-normal curve (see Magurran 1988), generally are impractical for insects because a large proportion of the species tends to be rare, regardless of sample size. A species accumulation curve can be made by counting cumulative species as successive samples are pooled and then be used to estimate richness by fitting various parametric models. But for insects, because the sampling usually is far from sufficient, the resultant estimates depend more on the models used than on the number of species actually present.

Another class of estimators is nonparametric, which deals better with collections containing numerous rare entities. Some of these were reviewed by Colwell and Coddington (1994). There are two main classes of nonparametric estimators: those based on incidence (presence or absence) and those based on abundance (relative abundance) of species. Although these models are newer and are being tested for reliability for biological data (Coddington et al. 1996, Silva and Coddington 1996, Chazdon et al. 1998), as a class they are more appropriate for arthropod richness studies.

Estimates 4.2 (Colwell 1996b) was used to estimate total homopteran species richness (S) for each plot, each site, and each elevation across seasons using a variety of nonparametric estimators, including the Abundance-based Coverage Estimator (ACE) and Incidence-based Coverage Estimator (ICE). ACE and ICE were developed by Chao and colleagues (Chao et al. 1993, Lee and Chao 1994) to augment her earlier estimators (Chao 1984, 1987) that were termed Chao 1 and Chao 2 by Colwell and Coddington (1994). Chazdon et al. (1998) discuss the performance of these estimators for real and simulated biological data. The bias-correction terms in ACE and ICE are based only on the rarer species—in my study, species that were represented by 10 or fewer individuals (ACE) or present in 10 or fewer samples (ICE).

The aforementioned measure of distinctness, complementarity (C, of Colwell and Coddington 1994), was used to compare plots within and among elevations. As a straightforward measure of the degree that two samples are complementary, C is the proportion of the pooled species richness (S_{jk}, in samples j and k) that is unique to either sample (U_{jk}). That is,

$$C = U_{jk}/S_{jk} \qquad (1)$$

So, for example, two samples of 75 species that have 50 shared and 50 unique (25 unique in each sample) will have a complementarity of 0.5. C varies from 0, when samples are identical ($U_{jk} = 0$), to 1, when the samples are completely complementary ($U_{jk} = S_{jk}$), and can be expressed as a percentage. As with many simple measures of overlap, C is affected strongly by sample size.

I used a new, ad hoc adjustment to C that kept the formula simple while attempting to give the measure more biological meaning when samples vary in size and capture different numbers of species, as they tend to do in field studies.

There are two ways sample size can inflate C. First, C based on two samples with different numbers of species has a lower bound greater than the theoretical minimum of zero because some species in the larger sample must be unique, even if both samples are drawn from the same species pool. The theoretical minimum number of unique species (U_{min}) occurs at maximum overlap [i.e., when the species-poorer sample (S_j) is a subset of the other (S_k), richer sample (S_{max})]. Even if no real sample is actually a subset of another, the theoretical C_{min} can be calculated for all pairwise sample comparisons:

$$C_{min} = U_{min}/S_{jk}$$
$$= |S_j\text{-}S_k|/S_{max} \qquad (2)$$

The minimum C can be subtracted from the observed C but is insufficient by itself to adjust for sample size.

A second influential factor is the number of sampled species (obs S_{jk}) relative to the number of species that are truly available (S). Smaller samples will find fewer species, underestimate ranges, and thus overestimate C (Colwell and Coddington 1994). This factor is more difficult to account for because 'small' is meaningful only when compared to the total species richness (S), which is usually unknown. As a rough correction, I divided the observed richness of two pooled plot samples (obs S_{jk}) by the highest richness estimate for any single site in the study (max S_{est}) or by the obs S_{jk} for that comparison, whichever was higher, because this was the best available estimate of S.

To account roughly for both factors, then,

$$C_{adj}= (C_{obs} - C_{min})(\text{obs } S_{jk}/\text{max } S_{est}), \text{ hence}$$
$$= [(U_{jk}/S_{jk}) - (|S_j\text{-}S_k|/S_{max})](\text{obs } S_{jk}/\text{max } S_{est}) \qquad (3)$$

Table 3. Observed (S_{obs}) and ACE-estimated (S_{est}) species richness and observed complementarity (C), from text equation 1, of Auchenorrhyncha and Psylloidea in the Usambara mountains, based on adults obtained by insecticidal fogging of the understory and canopy[a]

Altitude, No. of fogs	per plot		per altitude		
	S_{obs}	S_{est}	S_{obs}	S_{es}	C(%)
1,650–1,730 m, 11	17–36	30–91	124	169	65–93
1,370–1,435 m, 2	46–48	88–111	82	149	78
825 m, 1	20	51	20	51	n/a
430 m, 1	39	108	39	108	n/a
170–220 m, 13	11–63	16–112	176	250	65–93

[a]In each fogged plot, falling arthropods collected in 88 to 91 nets of 1 m² collecting area.
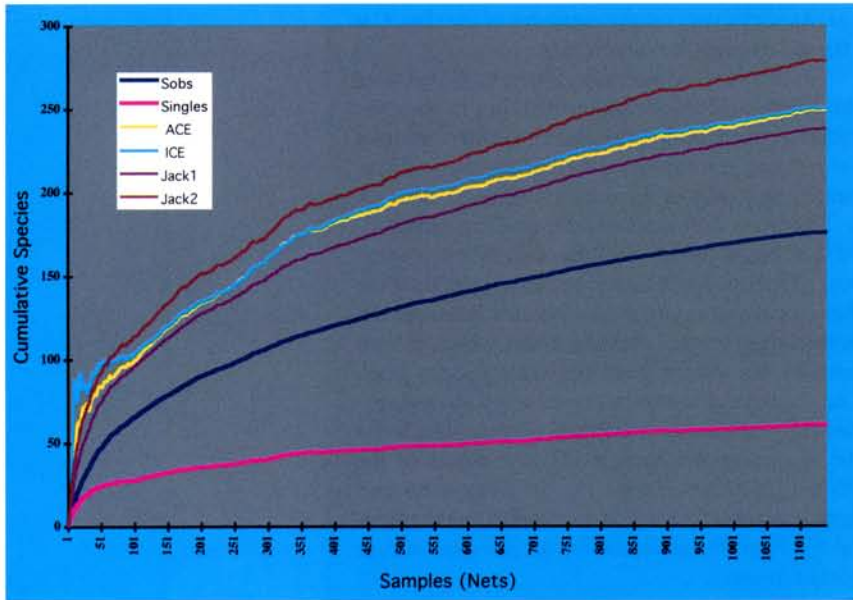
Fig. 3. Curves for an abundance-based richness estimator (ACE), incidence-based estimators (ICE, First-order Jackknife [Jack1], second-order Jackknife [Jack2]), the observed species-accumulation curve (Sobs), and the singleton curve (Singles) for lowland rainforest, 170-220 m, Kwamgumi and Segoma Forest Reserves, Tanzania. 1,148 samples, 20 randomizations.
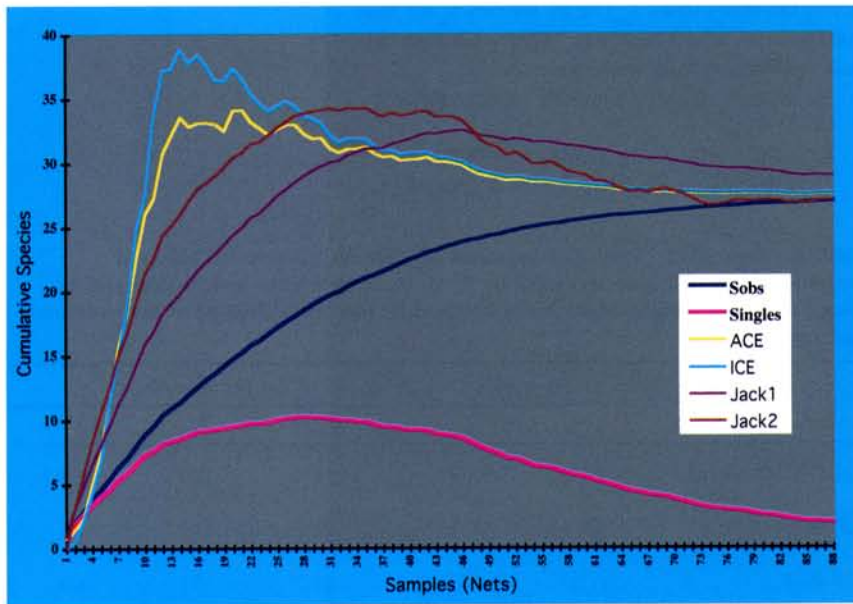

Fig. 4. Richness estimators, species-accumulation curve, and singleton curve for Fog #29 (montane forest), Mazumbai Forest Reserve, Tanzania. 100 randomizations. See text for explanation. See Figure 3 for meanings of acronyms.

The first result of this adjustment factor is to decrease the C of two samples of different sizes, which normally would have inflated distinctness values because of a minimum difference that must be observed. The second result is to decrease the C value for two samples of small but equal size, which normally would have inflated distinctness values because neither is expected to capture many of the same species. When the numbers of species in each sample approach equality and both approach the estimated total richness, C_{adj} approaches C_{obs}. Like C_{obs}, C_{adj} varies from 0, when samples are identical ($U_{jk} = 0$, $S_j = S_k = S_{jk}$), to 1, when samples are completely complementary ($U_{jk} = S_{jk}$), equal in size ($S_j = S_k$), and obs S_{jk} = max S_{est}. The adjustment is conservative because the total species richness usually is underestimated. Nevertheless, it should be remembered that this adjustment is an ad hoc method to add realism to C values, not a logically deduced statistic.

A statistically sound method of reducing sampling bias in complementarity metrics was published recently by Chen et al. (1995) but, so far, only in Chinese; an informal translation in English is available at R. K. Colwell's web site: http://viceroy.eeb.uconn.edu/EstimateS.

Results and Discussion

Species Richness. Species richness results are given in Table 3. Nets are used as the unit of effort in the species accumulation curves even though they were clumped in fogging events. In all but one case, sample size was still limiting, as shown for the lowland site (Fig. 3). Larger samples yielded more observed species and more estimated species because the fraction of singletons and doubletons remained high after all samples had been examined (e.g., Fig. 3 Singles curve, toward the right of the graph). None of the site- or elevation-species accumulation curves, or the estimator curves stabilized, meaning that sample size was insufficient to estimate their absolute richness reliably.

In only one of the 29 plots did the species accumulation curve stabilize (Fig. 4). In this plot, all estimators predicted that the observed richness was the 'true' richness (those species at that site and time, and susceptible to that method), except Jack1, the first-order Jackknife, an incidence-based estimator, which predicted that there were a few undiscovered species. Asymptotic species accumulation curves are rare in surveys of tropical invertebrates. Perhaps the curve leveled off in this plot due to a combination of low richness and the nonaggregated distribution of the rarer species.

All the nonparametric richness estimators depend to some extent on the fraction of observed species that occur as singletons or doubletons (abundance = 1 or 2) or in one or two samples (incidence = 1 or 2). This is shown in Figure 4: all estimators rose sharply when few samples were combined (Fig. 4, toward the left of the graph) because the proportion of rare species was high.

Additional specimens of those species were discovered as more samples were combined so the singleton curve declined (Fig. 4, toward the right). Most of the estimators behaved appropriately with this plot, rising quickly to a stable estimation of richness.

The abundance- and incidence-based estimator pairs ACE and ICE rose and fell simultaneously, yielding similar estimates at all points along the randomized sample accumulation curve. Chazdon et al. (1998) found in simulations that such coincident behavior is indicative of little spatial patterning. However, there was less coincident behavior of ACE and ICE in the randomized accumulation curve for the same number of samples from the entire lowland site (Fig. 5), suggesting some spatial patterning. Comparing Figures 4 and 5, this study may provide an empirical example of the importance of scale; there was little aggregation within the plot (approximately 10 m × 10 m), but singletons in one plot generally remained singletons in one site (approximately 1 km × 1 km), suggesting that species might be clumped at this larger scale.

Altitudinal Richness Gradients. Although the absolute species richness at each elevation could not be estimated, the two extremes can be compared to each other. The two most densely sampled elevations (170–220 m and 1,650–1,730 m) had approximately equal sampling effort, as measured by sample area coverage (m²), and in both seasons the lowland site had approximately 50% more species observed and estimated (Table 3). This is compatible with Wolda's results for Homoptera in Panama, showing a gradual decline of richness with increasing altitude (unadjusted for area—see Rahbek 1995). This result is also compatible with a mid-elevation peak, as found by Janzen, although in the Usambaras such a peak would have to be lower than 1,600 m.

For numbers of individuals per superfamily, psylloids were dominant in the montane forest (65% of all adults), fulgoroids in the submontane forest (40%), and membracoids, principally cicadellids, in the lowland forest (63%; Fig. 6). Cercopoids were most abundant in the lower montane forest but even there represented only 4% of the individuals; cicadoids were collected infrequently during the foggings. In terms of species richness, however, the three major superfamilies constituted nearly constant proportions of the sampled homopteran fauna at all five elevations: Psylloidea 15–20%, Fulgoroidea 15–28%, and Mem- bracoidea 48–57%. The reasons for this regularity are unknown.

Community Complementarity. Complementarity among plots *within* each elevation varied from 65–93% (Table 3), suggesting similar proportionate levels of species turnover within all elevations. If the rates of species turnover *across* elevations are similar, the community distinctness should be directly proportional to difference in altitude. When all data from each elevation were pooled (Table 4), observed complementarity among
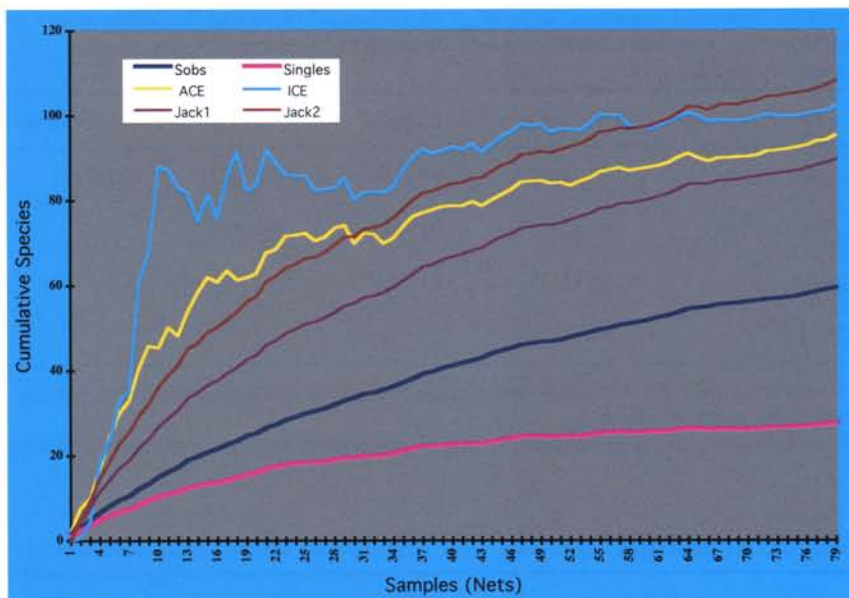

Fig. 5. Richness estimators, species-accumulation curve, and singleton curve for the first 79 samples of the lowland curve presented in Figure 3. See text for explanation. See Figure 3 for meanings of acronyms.

Fig. 6. Representing Membracoidea, the homopteran superfamily dominant in the lowlands, a treehopper (*Anchon* sp.) feeds on an understory herb in Kwamgumi Forest, Tanzania. Most membracoids are leafhoppers (Cicadellidae).

Table 4. Observed complementarity (C_{obs}) of Auchenorrhyncha and Psylloidea species in the Usambara mountains, based on adults obtained by insecticidal fogging of the understory and canopy[a, b]

	170–220 m	430 m	825 m	1,370–1,435 m
1,650–1,730 m	90 (274)	94 (154)	96 (139)	73 (162)
1,370–1,435 m	91 (237)	93 (113)	96 (98)	
825 m	96 (189)	93 (55)		
430 m	84 (187)			

[a] Complementarity (C, of Colwell and Coddington 1994) measures distinctness, varying from 0, for identical sets, to 1.

[b] Cell values are %C (text equation 1) and, in parentheses, total observed species richness (S_{jk}).

Table 5. Complementarity values from Table 4 adjusted for sample size in two ways[a, b, c, d]

	170–220 m	430 m	825 m	1,370–1,435 m	1,650–1,730 m
1,650–1,730 m	60.5	25.5	12.1	39.1	
1,370–1,435 m	37.6	40.6	20.4		25.4
825 m	7.4	44.2	—	8.0	6.7
430 m	6.2		9.7	18.3	15.7
170–220 m		4.6	5.6	35.6	60.5

[a] Above diagonal, values adjusted for differences in numbers of species captured ($C_{obs} - C_{min}$; see text equation 2).

[b] Below diagonal, values adjusted for former factor *and* for absolute sample size, relative to estimated sampling universe (text equation 3).

[c] Bold-faced values above diagonal are those most likely inflated because sample sizes approximately equal but small, so overlapping species were unlikely to be encountered.

[d] Bold-faced values below diagonal are the corresponding values, after adjusting for absolute sample size (text equation 3).
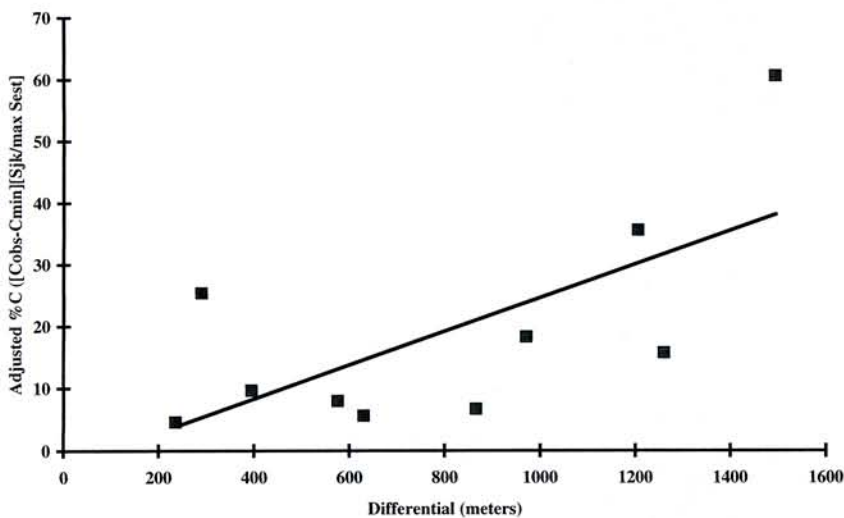

Fig. 7. Adjusted complementarity across elevational difference (from Table 5, below the diagonal). The median of each altitudinal range was used to calculate the differentials between sites. r² = 0.67. The unadjusted complementarity (not shown) was less correlated with elevational difference (r² = 0.41).

elevations varied from 73–96%, but was not correlated with altitudinal difference ($r^2 = 0.41$). This may be an artifact of sample size; the highest values are associated with the smallest sample (825 m). When the minimum complementarity was subtracted from C_{obs} (Table 5, above the diagonal), the correlation with altitudinal difference was changed little: $r^2 = 0.45$. However, C_{adj} (Table 5, below the diagonal) showed an increased correlation ($r^2 = 0.67$, Fig. 7) between increasing complementarity and increasing altitudinal difference. Considering the crudeness of the adjustment and the variation of the fogging technique in the field, obtaining this much correlation suggests that there is indeed a gradual species turnover across altitude from 170 to 1,730 m in the Usambaras as was found for the tree community (Lovett 1996).

Host-plant Specialization. Lovett (1996) analyzed the diversity of tree species of the West Usambaras, which were more continuously forested at lower altitudes when his data were collected than they are at present. Although there was a gradual species turnover with altitude, there was not a change in number of tree species. Although there is also some evidence that there is a gradual turnover in homopteran species with altitude (Fig. 7), the lowland fauna of homopterans is about 50% greater than the montane fauna. Thus, the richness of homopterans varies somewhat independently of the tree diversity. The reasons for this lack of parallel changes are unknown. Although it is possible that the homopterans are highly host-specific and track a subset of tree taxa, or that lianas and epiphytes consititute a major host resource for homopterans, the simpler explanation at this time is that factors other than host-specificity play an important role in determining the richness of the Usambara homopteran community.

Acknowledgments

gional Development Office, Muheza District Commisioner Office, and the Tanzanian Commission for Science and Technology, which granted permission to conduct the research. Rob Colwell (University of Connecticut, Storrs, CT) generously provided his then-unpublished data management and analysis tools, Biota and EstimateS, and helpful discussion and comments on the manuscript. The manuscript was further improved through suggestions from J. A. Coddington (Entomology Department, Smithsonian Institution, Washington, D.C.), M. G. Pogue (USDA Systematic Entomology Laboratory, Beltsville, MD), and an anonymous reviewer.

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