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Notes on the faunistic complexity of cicadas (Homoptera; Cicadidae) in northern Costa Rica

by

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Abstract: The geographical, habitat, and seasonal distributions of neotropical cicadas were studied at twelve localities on a northeast-southwest transect across northern Costa Rica. Geographical regions sampled are: lowland tropical rain forest, montane wet forest, and seasonal forest (highland and lowland). Habitat associations (primary, secondary, and forest remnants; cultivated lands) are where cicada nymphal casts are found. There are about 23 species with highest faunal complexity (genera and species) in lowland tropical rain forest. Faunas of the Caribbean and Pacific slopes of the Cordillera Central are very distinct. The present-day fauna of the Meseta Central is similar to that of wet regions, with infiltration of a few seasonal forest species. In lowland dry forest, the fauna is greatly impoverished, probably due to past destruction of the original vegetation cover. Small pockets of persisting forest here support cicadas not found in disturbed habitats (pastures). The original fauna of the Meseta Central very likely contained more of the species found today in wet regions, but these became extinct when the vegetation was cleared. Faunal complexity here remains high owing to several species thriving in small forest refugia along streams, coupled with some living in cultivated habitats. High impoverishment occurs in a montane region of secondary forest. Faunal complexity of montane primary wet forest is only slightly lower than that of lowland rain forest, presumably as a result of increased climatic instability and other factors. Throughout Costa Rica, many species emerge during the dry season, and timing of emergences during both seasons correlates well with seasonality of rainfall. The geographical complexity of Costa Rica, regional climatic and vegetation variations over short distances, and the existence of many secondary forests and cultivated lands, are the major determinants of the faunal diversity of cicadas. As more lowland tropical rain forest is cleared for cultivation and lumbering, many species of cicadas will likely become extinct, especially if no forest refugia are left behind.

Although the American tropics are faunistically complex, as especially determined for vertebrates (e.g., L. C. Stuart in West, 1964), there are very little

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data on geographical patterns of insect families. This paper summarizes the geographical distribution patterns of several genera and species of cicadas (Homoptera: Cicadidae) across northern Costa Rica. With the exception of early records on collection of cicada species, and some recent ecological studies in certain localities **(Young,** 1972, 1974, 1975), nothing has been published on the distributional patterns of cicadas in Costa Rica or elsewhere in the American tropics. This survey revealed changes in both faunal complexity (local number of species) and geographic displacement or replacement of genera and species amongst several regions that vary in elevation, climate, and vegetation.

GEOGRAPHICAL REGIONS, LOCALITIES AND METHODS

Twelve localities were sampled in Costa Rica over the past five years. These are located in approximately northeast-to-southwest line (V-line), including both mountainous and lowland regions (Fig. 1). These localities were selected on these criteria: distinctness in elevation; distinctness in vegetation-type; and, accessibility. Most localities are located close to a major road (within 1-8 km). The range in elevation sampled is 30 meters ("Puntarenas") to 1600 meters (mountains surrounding the Meseta Central). Three different vegetational regions, characteristic of Central America **(West.** 1964) are included within these localities: (1) lowland tropical rain forest; (2) montane wet forest; (3) seasonal (semi-decidious) forest.

The tropical rain forest locality studied is "Tirimbina" near La Virgen de Sarapiqui (Heredia Province) where it is hot and rainy (about 2000 mm per year) throughout the year, with a brief but irregular dry period usually between January and March. This locality is the lowest in elevation (170 m) sampled in the Caribbean coastal lowlands, and it is representative of the Central American rain forests extending from the Gulf of Honduras to northern South America along the Caribbean side of the isthmus. Two montane wet forest localities, "Cariblanco" (Heredia Province) and "Bajo la Hondura" (San Jose Province) are about 1500 m, consisting of rugged ravines within the Caribbean side of the Cordillera Central, the terminating point of the volcanic axis of Central America. Within the central plateau, the Meseta Central, two other montane forest, but semi-deciduous, localities, "Alajuela" and "San Rafael de Ojo de Agua" are cultivated areas sampled (about 1300 m). Following to the northwest, three localities ("Rosario de Grecia", "Naranjo", and "San Ramon") form an increasing elevational gradient of sample sites (1300-2200 m) in the Pacific semi-deciduous mountains of the Central Cordillera. These localities fall within the seasonal forest series although they are less seasonal and wetter than three other localities sampled further northwest ("Esparta", "Puntarenas", and "Taboga"). As with the Meseta Central, the ascending slopes of the Pacific side of the Cordillera Central are highly cultivated; cicada samples are taken in coffee farms and adjacent strips of forest remnants (usually along streams). The "Esparta" locality, on the descending slope of the Pacific zone of the Cordillera Central (about 600 m), is a rugged, steep ravine. The "Puntarenas" and "Taboga" localities represent Pacific lowland tropical dry forest (seasonal forest series) where the dry season is most severe, usually lasting six months. Many trees are deciduous here–far more so than at other localities sampled. At "Puntarenas" cicadas were studied in highly disturbed habitats while at "Taboga" they are studied in persisting pieces of dry forest on slopes and along a stream. An atypical locality of this general region is the "Barranca site" below

Miramar; this is a small piece of semi-deciduous wet forest generally lush throughout the year.

Other localities in the lowland dry forest zone studied for cicadas are: "below Monteverde", "Playas del Coco", and "Santa Rosa National Park". The locations of these sites are not shown in Fig. 1 since only adult records were obtained rather than populations censuses. At each of these three localities, the major habitat studied was remnant primary forest.

Cicadas at each of the above localities were taken during wet and dry seasons over a five-year period. This was done in two ways: (1) collection of a series of adult specimens (usually 3-10 specimens per species) at each locality, and (2) census of final instar nymphal casts left behind when at eclosion. On the latter method, quadrats were established to monitor emergences of cicadas throughout the year for several years, in order to study the population biology of these insects (Young, in preparation). Casts are collected from quadrats at regular intervals. The juvenile cicada lives in the soil and tunnels to the surface for the final molt. Casts are very useful indicators of species as they differ greatly between species and genera in terms of color, size, and abdominal tergal plates. Adults are located either through general observation or tracking singing males. Tape recordings of the majority of the species sampled were taken by Dr. Thomas E. Moore (University of Michigan).

At several localities, cicadas were sampled in secondary habitats since primary forest was often absent, having been removed for agricultural purposes. At localities where both primary and secondary habitats were present, additional information was gathered on habitat associations of cicada species. Association for a given habitat was made on the basis of where nymphal casts were found.

RESULTS

Nine genera and 23 species of cicadas occur along the geographical transect, although the number of taxa varies considerably at each locality (Table 1). For example, the greatest numbers of genera and species occur in lowland tropical rain forest (e.g., "Tirimbina") and the least numbers in secondary montane wet forest ("Bajo la Hondura") There are six localities in which the next largest number of species occurs in the lowland seasonal (dry) forest ("Puntarenas").

Collectively, the various localities in the mountains surrounding the Meseta Central support a rich diversity of cicadas (Table 1), with considerable differences (regional non-overlap) between the Caribbean and Pacific slopes. Of considerable interest for the zoogeography of insects in the tropics is regional overlap of fauna. Here, overlap between lowland tropical rain forest and lowland seasonal dry forest is three genera. There are probably only three or four species in common between these regions.

Of related interest is the question of taxonomic complexity within single genera. For example, the greatest number of congeneric species (5-possibly 6) occur in *Fidicina* in lowland tropical rain forest, and there are three mono-specific genera in Costa Rica: *Quesada* in montane and lowland wet forests, and *Conibosa* in montane wet forest and montane seasonal forest; and *Diceroprocta* in lowland seasonal forest (Table 1). The greatest range in body sizes occurs in lowland tropical rain forest, ranging from about 39 mm for *Quesada gigas* to about 11 mm for *Carineta indecora.*

TABLE 1

*Geographical distribution (faunal complexity) and habitat association of neotropical cicadas (Homoptera: Cicadidae) across Costa Rica**

Locality	Region	No. Genera	Genera	No. Species	Species	Habitat Association
"Tirimbina"	NE lowland rain forest	5	*Fidicina*	6	*mannifera*	prim.
			F.		*sericans*	prim.
			F.		*amoena*	prim.
			F.		*spinocosta*	sec.
			F.		*pronoe*	sec.
			F.		*fumea*	prim.
			Zammara	1	*smaragdina*	prim., sec.
			Quesada	1	*gigas*	sec.
			Carineta	2	*indecora*	prim.
			C.		sp.	sec.
			Proarna	1	*sallei*	sec.
			Majeorona	1	*bovilla*	prim.
"Cariblanco"	NE montane wet forest	3	*Fidicina*	4	*mannifera*	prim.
			F.		*sericans*	prim.
			F.		*"variegata"*	sec.
			F.		sp.	prim.
			Zammara	1	*tympanium*	prim.
			Carineta	3	*postica*	prim.
			C.		sp.	prim.
			C.		sp.	prim.
"Bajo la Hondura"	SE montane wet forest	2	*Procollina*	1	*biolleyi*	sec.
			Carineta	1	*postica*	sec.
"Alajuela"	Meseta Central	3	*Fidicina*	2	*amoena*	remnant prim.
			F.		*"coffea"*	coffee
			Zammara	1	*smaragdula*	coffee
			Quesada	1	*gigas*	coffee
"San Rafael de Ojo de Agua"	Meseta Central	4	*Fidicina*	2	*amoena*	remnant prim.
			F.		*pronoe*	coffee
			Zammara	1	*smaragdula*	remnant prim.
			Conibosa	1	sp.	coffee
			Quesada	1	*gigas*	remnant prim. cultiv. land
"Rosario de Grecia"	NW Pacific escarpment	4	*Fidicina*	2	*sericans*	coffee, sec.
			F.		*amoena*	coffee, sec.
			Zammara	1	*smaragdula*	coffee, sec.
			Quesada	1	*gigas*	coffee
			Conibosa	1	sp.	coffee
"Naranjo"	NW Pacific escarpment	4	*Fidicina*	3	*amoena*	remnant prim.
			F.		*"coffea"*	coffee
			F.		*"guayabana"*	coffee
			Zammara	1	*smaragdula*	coffee
			Quesada	1	*gigas*	coffee
			Conibosa	1	sp.	coffee
"San Ramon"	NW Pacific escarpment	4	same as "Naranjo"			
"Esparta"	NW Pacific escarpment	4	*Fidicina*	4	*mannifera*	remnant prim.
			F.		*amoena*	remnant prim.
			F.		*pronoe*	sec.
			F.		*spinocosta*	sec.
			Zammara	1	*smaragdula*	remnant prim.
			Quesada	1	*gigas*	remnant prim.
			Pacarina	1	sp.	sec.
"Puntarenas"	Pacific dry lowland	4	*Zammara*	1	*smaragdula*	remnant prim.
			Diceroprocta	1	*bicosta*	remnant prim.
			Proarna	2	*sallei*	sec.
			P.		sp.	sec.
			Pacarina	2	sp.	sec., pasture
			P.		sp.	sec., pasture
"Barranca site"	NW Pacific dry lowlands	3	*Fidicina*	1	*mannifera*	prim.
			Zammara	1	*smaragdula*	prim.
			Pacarina	2	sp.	sec., pasture
					sp.	sec., pasture

Locality	Region	No. Genera	Genera	No. Species	Species	Habitat Association
"Taboga"	NW Pacific dry lowlands	3	*Zammara*	1	*smaragdula*	prim.
			Diceroprocta	1	*bicosta*	prim.
			Pacarina	2	sp.	sec.
			P.		sp.	sec.
"below Monte-verde"	NW Pacific dry lowlands		*Fidicina*	2	*amoena*	remnant prim.
			F.		*pronoe*	remnant prim.
			Quesada	1	*gigas*	remannt prim.
			Pacarina	1	sp.	sec., pasture
"Playas del Coco"	NW Pacific dry lowlands		*Diceroprocta*	1	*bicosta*	remnant prim.
			Proarna	1	sp.	sec.
			Pacarina	1	sp.	sec.
"Santa Rosa National Park"	NW Pacific dry lowlands		*Fidicina*	3	*mannifera*	remnant prim.
			F.		*amoena*	remnant prim.
			F.		*pronoe*	remnant prim.
			Zammara	1	*smaragdula*	remnant prim.
			Proarna	1	sp.	sec.
			Pacarina	2	sp.	sec.
			P.		sp.	sec.

* See Figure 1 for a geographical representation of the localities sampled. The order given for localities in the table is the sequence of sample sites from the northeastern wet lowlands, through the central mountains (Cordillera Central), to the Pacific dry lowlands. One locality in the latter region, the "Barranca site", is atypical in that it is a piece of semi-deciduous forest that remains lush throughout the year; see the text for further comment.

In different regions of Costa Rica, cicadas exhibit associations with different habitats (Table 1). For example, in lowland tropical rain forest ("Tirimbina") there are four strictly primary forest species, while five species are strictly secondary forest species. One species, *Zammara smaragdina,* is associated with both primary and secondary forests (Table 1). *Fidicina spinocosta* and *F. pronoe* are associated with early stages of secondary succession, where woody seedlings are intermingled with dense vines. Others such as *Proarna sallei* and *Quesada gigas* are found in more advanced stages of secondary forest. At "Cariblanco", montane wet forest, most cicadas are found in primary forest, although *F. "variegata",* is found in ridge-top old secondary forest.

The montane wet forest at "Bajo la Hondura", is old secondary, the original forest having been cleared about 80 years ago for dairy cattle grazing. The paucity of cicada species here (2) could be related to this early extensive cutback, with slow replacement (invasion) of cicadas. For the Meseta Central, a region of Costa Rica where past forest clearing for cultivation has been so thorough that original forest is scarce, cicadas are found in forest remnants along streams and with leguminous trees, *(Inga* spp.) used to shade coffee plants, and others (e.g., *Cassia* sp.) scattered in fields. However, note that several cicadas of wet forest regions, such as *Fidicina mannifera, F. sericans, F. spinocosta* and *Proarna sallei,* are absent from the Meseta Central.

In the Pacific highlands, cicadas are associated with forest remnants along streams and coffee shade trees. The fauna here includes *Pacarina* which is absent from wet regions, and which probably represents an invasion from the seasonal dry environment into the Meseta Central. A different species of *Zammara (smaragdula)* is also prevalent here, and while *Z. smaragdina* is endemic to lowland wet regions, the former is associated with more seasonal regions, including the Meseta Central. Some species of *Fidicina,* such as *"coffea"* and *"guayabana"* are strictly associated with shade trees of coffee in the central highlands. Others of wetter regions, such as *Fidicina mannifera* and *F. sericans* reappear at "Esparta" on the Pacific slopes of

TABLE 2

The seasonal distribution of cicada emergences in different regions of Costa Rica

Species	Dry Season only	Wet Season only	Both Seasons	Sometimes transitional*
		I Northeastern wet lowlands		
Zammara smaragdina		X		X
Fidicina mannifera			X	
F. sericans	X			X
F. spinocosta		X		
F. pronoe	X			
F. amoena	X			
F. fumea	X	X		
Quesada gigas	X			
Carineta indecora			X	
Carineta sp.			X	
Proarna sallei			X	
Majeorona bovilla			X	
		II Northwestern dry lowlands		
Zammara smaragdula		X		
Fidicina mannifera		X		
F. amoena	X			
F. pronoe	X			
Quesada gigas	X			
Proarna sp.	X			
Diceroprocta bicosta	X			X
Proarna sallei		X		
Pacarina sp.	X			
Pacarina sp.		X		
		III Highlands around Meseta Central**		
Fidicina mannifera		X		X
F. "variegata"	X			
F. "coffea"	X			
F. guayabana	X			
F. amoena	X			
F. sericans	X			X
Zammara smaragdula		X		X
Z. tympanium			X	
Quesada gigas	X			
Carineta postica			X	
C. sp.	X			X
C. sp.			X	
Pacarina sp.		X		
Conibosa sp.		X		
		IV Meseta Central		
Zammara smaragdula		X		
Fidicina amoena	X			
F. pronoe	X			
F. "coffea"	X			
Quesada gigas	X			X
Conibosa sp.		X		

* This category refers to the emergence of cicadas during the transition from dry to wet seasons.

** This category includes eastern (Caribbean) and western (Pacific) slopes of the Central Cordillera.

the Cordillera Central, but they are strictly confined to small moist pockets of primary forest; *F. mannifera* extends to the moist primary forest of the "Barranca site", and it is one only member of the genus found there, and this is probably true for other localities in lowland dry forest (Guanacaste). In the representative lowland dry forest, genera such as *Pacarina, Proarna* and *Diceroprocta* are the endemic cicadas, while pockets of wetter forest here support *Fidicina mannifera, F. amoena, F. pronoe, Quesada gigas* and *Zammara smaragdula;* the former genera are associated with secondary forests and pastures. However, the populations of *F. amoena, F. pronoe* and *Q. gigas* are very fragmented with these cicadas occurring as small isolates. At another locality further north in lowland Guanacaste, "Playas del Coco", huge populations of *Diceroprocta bicosta* are associated with leguminous trees along the ocean shore and nearby houses. Thus the indicative cicada genera of this region are presently associated with secondary habitats created by man.

In addition to variation in the regional or geographical distribution and habitat associations at different localities, adults of different species are active at different times of the year, especially where marked seasonality of rainfall prevails (Table 2). In the northeastern wet lowlands (e.g., "Tirimbina") several species are active during the short dry season (January-March). Although fewer species are active strictly during the long wet season here, there are more species active during both seasons (e.g., throughout most of the year) than for any other locality studied (Table 2). But in the northwestern dry lowlands, there are no species active over both seasons, so seasonality is very sharply delineated, presumably due to the clear separation of seasons, and the long dry season. In both the highlands and Meseta Central, most cicadas are dry season species, although several of these are also active during the brief, irregular transitional period between dry and wet seasons. Transition between dry and wet seasons is less distinctive here than in the Meseta Central, dry lowlands, and even wet lowlands In general, however, the wetter geographical regions of Costa Rica tend to have cicadas with either emergences throughout most of the year (e.g., "Tirimbina"), or emergences during the transition from dry to wet seasons.

DISCUSSION

The present-day geographical, habitat, and seasonal distributions of cicadas in Costa Rica must be the result of three different types of environmental effects, namely, (1) the original geographic distribution in undisturbed primary forest, (2) the impact of creation of secondary forest habitats through cultivation, human population expansion and movements, and (3) monthly patterns of rainfall. Clearly these three sets of environmental factors are not mutually exclusive. I would like to account for these present-day distributions of cicadas in terms of known differences of the regions and localities, with some emphasis on the impact of past and present cultivation practices.

For cicadas, a group of insects that needs trees and other plants for feeding and oviposition, the regional and local faunal complexity will be determined to a large degree by the availability of niches in primary and secondary forest habitats. When both sets of niches are available, complexity can be high. At "Tirimbina", the high faunal complexity of cicadas is the result of many niches available in primary and secondary rain forests, and relatively stable climatic conditions of the lowland tropical rain forest region that promote high species richness. The abundance of niches for cicadas in lowland tropical rain forest are not available in terms of high

tree species diversity, but rather in terms of the dependence of most cicada species on the unusually abundant leguminous tree, *Pentaclethra macroloba* (Gavilán). In secondary habitats of lowland tropical rain forest, some species of cicadas are associated with different plant families, apparently representing a shift in the niche from the viewpoint of the plant taxonomist, but perhaps not from the cicadas' viewpoint.

In other regions, such as the dry lowlands of northwestern Costa Rica, faunal complexity may be high if cicadas can occupy both small pieces of forest and pastures. Thus a locality such as "Puntarenas" supports several cicadas that thrive in very disturbed habitats such as yards, ocean-front scrub forest, and pastures. But here, as in other places, there are small pieces of original primary dry forest, and nymphal casts of three or more genera are often cumped around very large trees such as *Enterolobium* (Leguminosae). Only *Pacarina* has moved away from trees, being found in open pastures (**Young,** 1974). Even in the Meseta Central and coffee-growing regions of the Pacific slopes of the Cordillera Central, large trees *(Inga; Zygia* - Leguminosae) along streams support the greatest complexity of the cicada fauna, while a few of these species have moved onto the shade trees *(Inga* spp.) of the coffee. For example, at "San Rafael de Ojo de Agua", *Zammara smaradgula, Quesada gigas,* and *Fidicina amoena* are associated with large *Zygia* trees along stream-edge, while *Fidicina pronoe, Conibosa* sp., and to a lesser extent *Quesada gigas,* are associated with shade trees of coffee away from the stream. A similar situation occurs at "Rosario de Grecia" for *Zammara smaragdula, Fidicina amoena, Quesada gigas,* and *Conibosa* sp. Thus there is a general pattern: high faunal complexity of cicadas, regardless of the geographic region, is maintained primarily by the local availability of original forest, be it large areas or small, scattered pieces; local species richness is maintained to a lesser degree by secondary habitats, where one or two species might occur. This generalization must be qualified with the need for certain leguminous tree species to be present, whether primary forest or secondary. The cicada niche in Costa Rica has the Leguminosae playing a mejor role in determining the local spatial distribution of species. The precise reasons as to why virtually all neotropical cicadas in the Costa Rican fauna (and perhaps elsewhere in Central America) should be associated with the Leguminosae have yet to be determined. Even at the "Esparta" locality, the fragments of primary semi-deciduous forest in deep ravines among the hills of this region contain individuals of leguminous trees that have several genera *(Fidicina, Zammara, Quesada)* associated only with them, and not other trees. The pattern is indeed striking.

Within a geographical region, there can be differences in habitat associations for the same species of cicada. A good example of this is a comparison of "Alajuela" and "San Rafael de Ojo de Agua" in the Meseta Central. At the former locality, *Fidicina amoena* is associated with shade trees of coffee, while at the latter, it is found in forest remnants (Table 1). This difference might be attributable to the lack of forest remnants at "Alajuela" which resulted in this species surviving on shade trees in the coffee plantations. The intensity of cultivation in a region may be an important factor in determining the habitat associations of cicadas. At "Esparta", where there are strips of primary forest confined to ravines and slopes, most cicadas are associated with forest; but at other Pacific mountainous localities, such as "Naranjo" and "San Ramon", both heavily cultivated, some of these cicadas (e.g., *Zammara smaragdula, Fidicina amoena)* are also present but associated mostly with shade trees for coffee.

In montane wet forest ("Cariblanco"), high faunal complexity of cicadas is maintained by the large number of leguminous tree species in primary forest. Unlike primary lowland tropical rain forest where cicada species are clumped around *Pentaclethra,* the forest cicadas at "Cariblanco" are associated with several different genera and species of Leguminosae. The reduction in cicada species here is probably due to less stability of climatic factors and cooler temperatures. Higland regions in the tropics are similar in terms of climate and stability to temperate regions **(Janzen,** 1967). A very different situation occurs at another montane locality, "Bajo la Hondura", where there are only two species of cicadas. Unlike the other localities studied, where there exists pieces of remnant primary forest, here all of the forest is old secondary. When the original forest was cleared, there might have occurred large scale extinction of the cicada fauna, followed by survival or invasion of the few species present today. The region is likely unstable for environmental and biotic conditions that influence cicadas, since one of these species, *Procollina biolleyi,* has large annual fluctuations in adult emergences in old secondary forest **(Young,** 1975), while cicada numbers are far more stable at localities where primary forest is found and even more so in wet lowlands.

The small pieces of primary forest surviving along streams provide a precariously stable environment for some cicadas in the Meseta Central. When the original vegetation cover of the Meseta Central was removed for cultivation, the persistance of forest remnants provided a refuge for cicada species. Like the original vegetation cover, which probably was a mixture of tree species from both non-seasonal wet regions and seasonal dry regions of the surrounding mountains **(West,** 1964), the original cicada fauna was also likely a mixture of the faunas characteristic of the mountains. Mixing with the Caribbean slope and lowland wet fauna could have been *Fidicina mannifera, F. pronoe, F. amoena, F. sericans, Quesada gigas* and perhaps *F. spinocosta.* Only *F. amoena, F. pronoe,* and *Q. gigas* have survived to the present in the Meseta Central, with populations of the two former species, associated mostly with shade trees for coffee, being very small relative to those of *Q. gigas* and *Zammara smaragdula.* The latter cicada probably represents a contribution to the Meseta fauna from the Pacific highlands where it is associated with forest trees along streams, and to a lesser extent, shade trees for coffee. The ability of *Zammara* to survive in the Meseta Central at the present is largely the result of the affiliation of this genus to very wet places such as edges of forest streams and rivers **(Young,** 1972). The restriction of the three Costa Rican species of this genus to wet micro-habitats may be responsible for its relatively slow rate of speciation as contrasted with *Fidicina,* a genus found in a greater range of habitat and micro-habitat conditions. While it is difficult to explain radiative adaptation within genera, the noticeable association of *Zammara* with wet places and the association of *Fidicina* with many more different conditions, suggests differences in levels of adaptive flexibility between the two genera. But flexibility in habitat and micro-habitat utilization by cicadas can be manifested within a single species, rather than resulting in speciation. A good example of this is *Quesada gigas,* perhaps the most widely distributed cicada over Central America and northern South America. This species occupies both primary and secondary forests, cultivated lands, and even plots of introduced tree species.

The cicada fauna of the Meseta Central was perhaps originally derived primarily from the Caribbean slope and lowland faunas, but with infiltration of *Pacarina* and *Zammara* from the Pacific side. There was probably an original distribution of other wet region cicadas such as *Fidicina mannifera* into the Pacific

highlands and even into moist forests within the lowlands of Guanacaste. The cicadas that probably were present but went extinct in the Meseta Central included: *Fidicina mannifera, F. spinocosta, F. sericans, Proarna sallei,* and perhaps one or two species of *Carineta.* Endemic mountain species that probably never entered the Meseta Central included: *Procollina biolleyi* (which is even one of the rarest cicadas in mountain regions), *Fidicina "variegata",* and *Zammara tympanium.* Strictly tropical rain forest species are *Zammara smaragdina,* and *Carineta indecora.* Strictly lowland dry forest cicadas are *Pacarina* sp., *Proarna* sp., and *Diceroprocta bicosta.* These cicadas very likely never entered into the Meseta Central. Distributional limitations of cicadas in Costa Rica are likely the result of the interaction of several environmental factors that vary geographically, including rainfall and its seasonality, tree species, and perhaps soil-type and temperature.

It is interesting that many cicadas are active as adults during the dry season in regions where seasonality of rainfall is evident. The majority of cicadas are large-bodied insects and therefore, presumably have minimal dessication problems to cope with. In addition, many species show behavioral thermo-regulatory patterns such as moving to the shaded sides of branches at hottest hours of the day. The dry season offers optimal conditions for many cicadas, in terms of mating success. In regions where the distinction between season is less clear, cicadas have less seasonal emergence patterns. Thus in the tropics, the geographical variation in rainfall patterns on an annual basis greatly influence the temporal emergence of cicadas. Seasonality in cicada emergences is least distinctive on the Caribbean slopes (e.g., "Cariblanco") because rainfall occurs mostly throughout the year here, even more so in lower wet regions such as "Tirimbina". The dry season as a period of environmental stress does not affect cicadas as it presumably does many small-bodied insects (**Janzen** and **Shoener,** 1968), but for many species it is likely a time for optimal breeding and perhaps escape from competing species, assuming some form of resource limitation such as availability of chorusing and oviposistion sites. The geographical variation in rainfall and accompanying seasonality provides neotropical cicadas in Costa Rica with an opportunity to divide the local environment in time, for whatever adaptive reasons. Thus geographical distribution patterns cannot be separated from seasonal patterns.

There is noticeable regional differentiation in the Costa Rican cicada fauna especially between the Caribbean and Pacific slopes of the Cordillera Central and accompanying lowlands. The high present-day faunal complexity of cicadas in lowland tropical rain forest is presumably the result of more niches being available here, as reflected also in the great body-size range of these insects in the region. But as more and more of the original forest cover of this region is removed for cultivation, which is presently going on at a fast rate, cicadas will face a similar survival problem that these insects faced in the Meseta Central. If forest refugia are left in the lowlands, a high portion of the present-day fauna might hold on. If, however, all of the original forest cover is removed over large areas, the result will be similar to the present-day situation at "Bajo la Hondura", that is, the cicada fauna will become greatly impoverished, even if secondary forest is allowed to regenerate. But the resiliency for the lowland cicada fauna to spring back and adapt to extensive secondary and cultivated habitats might be considerably less than their counterparts at higher elevations where original environmental conditions were presumably less stable and thus selective for adaptive flexibility (**Pianka,** 1966). Certainly with the exclusion of isolated pieces of primary lowland dry forest in Guanacaste, the cicada fauna of this region is greatly impoverished, presumably as a result of the large-scale removal of the original vegetation cover.

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RESUMEN

Se estudió la distribución geográfica, estacional y de habitat de las cicadas neotropicales en doce localidades, de noreste a suroeste, en el norte de Costa Rica. Las regiones geográficas estudiadas fueron: bosque pluvial de bajura, bosque muy húmedo de montano y bosque estacional (de altura y de bajura). Las asociaciones de habitat (primaria, secundaria y bosquetes; y tierras de labanza) con aquellas en donde se encuentran los cascarones de la última muda. En este estudio se encontró 23 especies de cicadas y su mayor complejidad faunística, tanto de géneros como de especies, se encuentra en el bosque pluvial de bajura. Hay una gran diferencia entre las faunas de las vertientes del Caribe y del Pacífico en la Cordillera Central. La fauna actual de la Meseta Central es similar a la de las regiones húmedas, con infiltraciones ocasionales de algunas especies selváticas. En el bosque seco de bajura la fauna es muy escasa, probablemente a causa de la destrucción de la cubierta vegetal original, aunque existen refugios pequeños de bosque que albergan cicadas que no se encuentran en habitats perturbados (potreros). La fauna original de la Meseta Central probablemente contenía más de las especies que hoy se encuentran en las regiones húmedas y que se extinguieron al ser eliminada la vegetación. Aquí, la complejidad faunística se mantiene alta debido a que varias especies viven en refugios forestales pequeños alrededor de riachuelos, en asocio de aquellas que viven en áreas cultivadas. El empobrecimiento de las especies ocurre en una región de bosque tropical de montano. La complejidad faunística del bosque muy húmedo primario es apenas menor que la del bosque pluvial de bajura, posiblemente como resultado de la creciente inestabilidad climática y otros factores. En todo el territorio de Costa Rica muchas especies emergen durante la estación seca y el tiempo en que emergen en ambas estaciones se correlaciona bien con el ciclo pluvial. La complejidad geográfica de Costa Rica, las variaciones climáticas y de vegetación bien marcadas en una área pequeña y la existencia de muchos bosques secundarios y de tierras de labranza, son los mayores determinantes de la diversidad faunística entre las cicadas. Al ceder los bosques tropicales al paso de las explotaciones agrícolas y madereras, muchas especies de cicadas llegarán a extinguirse, especialmente si no quedan refugios forestales.

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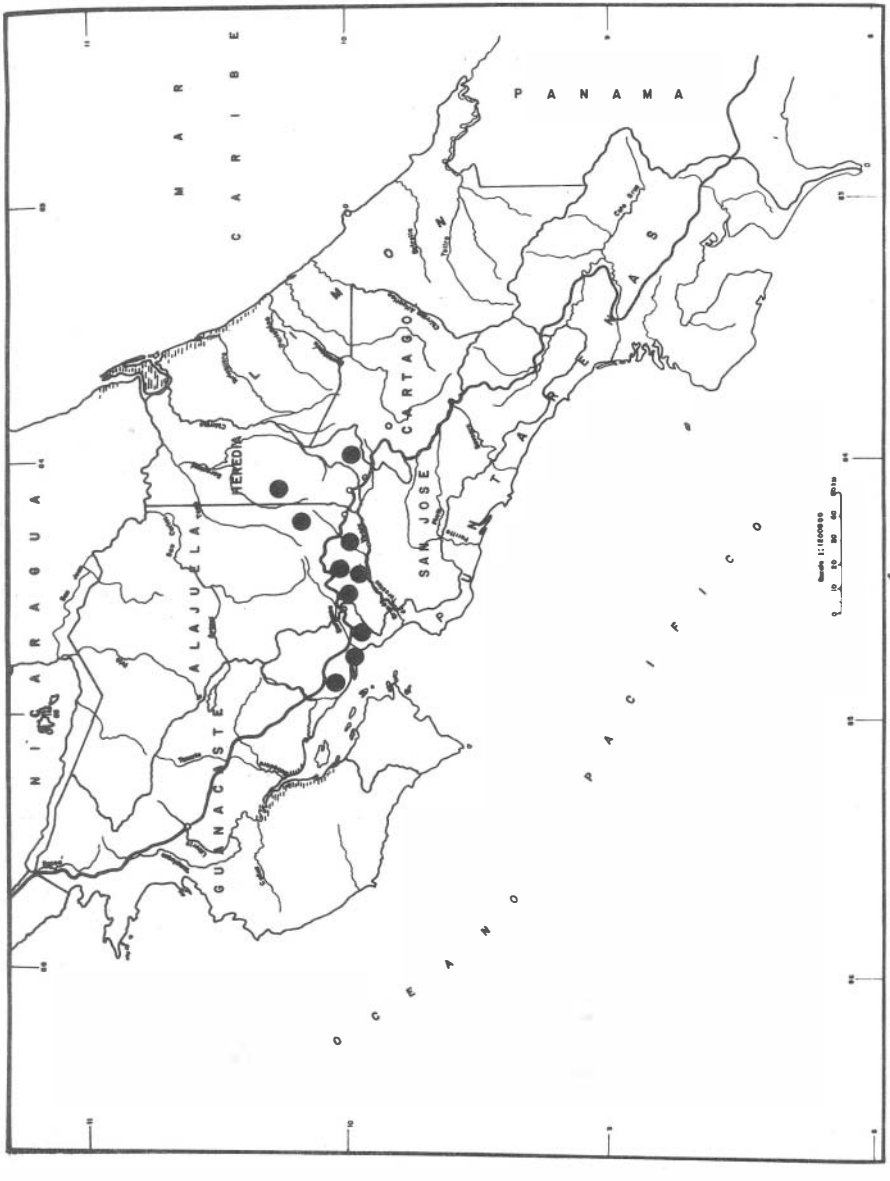
Fig. 1. The geographical distribution of cicada-study localities in a roughly northeast-to-southwest transect across Costa Rica. Ten of twelve localities studied are indicated by the black dots. Beginning in the uppermost right, the first dot shows "Tirimbina" (lowland tropical rain forest); below it and slightly to the right is "Bajo La Hondura" (montane wet forest). Following the sequence of dots that begins just left of "Tirimbina", there are these localities indicated: "Cariblanco" (montane wet forest), the clump of four localities within or near the Meseta Central ("San Rafael de Ojo de Agua", "Alajuela", "Rosario de Grecia", and "Naranjo"), "San Ramon" (Pacific highlands; semi-deciduous forest–same for "Naranjo"), "Esparta" (Pacific highlands), and "Puntarenas" (Pacific lowland dry forest). Not shown are five other localities in the Pacific dry lowlands which have been sampled primarily for adults instead of population censuses: "Barranca site", "Taboga", "below Monteverde", "Playas del Coco", and "Santa Rosa National Park".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