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**GEOGRAPHICAL DETERMINANTS OF INSECT SPECIES
DIVERSITY IN THE HAWAIIAN AND GALÁPAGOS
ARCHIPELAGOS: A BIOGEOGRAPHICAL ANALYSIS**

by

PATRICK WIGFULL, B.Sc.

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of
the requirements for the degree of

Master of Science

Department of Biology

Carleton University
Ottawa, Ontario
January 17, 1997

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THE HAWAIIAN AND GALÁPAGOS ARCHIPELAGOS: A
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Chair

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Date 01-17-97

Abstract

A complete species inventory of the insect fauna of the Hawaiian Islands and a complete species inventory of the smaller orders of the insect fauna of the Galápagos orders were examined using maximum likelihood estimation procedures. Highly significant relationships were found between number of species and both island area and island elevation. These results probably reflect the higher heterogeneity of habitats on larger islands, which in turn may provide resistance to disruption and resulting extinction. Area was found to be a better predictor of species diversity than elevation, because it encompasses more factors that affect species numbers than does elevation. Elevation, on the other hand, proved to be a more exclusive measure of habitat diversity than area. Age was a poor predictor of species diversity, particularly in the Galápagos Islands where the relative youth of the archipelago and history of recent disturbance prohibit predictions of species diversity from island age.

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Introduction

For centuries, naturalists have been attracted to the biotas of insular environments, particularly those of oceanic islands. The most obvious attractions of these biotas are the often striking differences in species composition when compared to the more familiar biotas of continental areas, and the presence of organisms that display unusual physical or behavioral differences from their counterparts in the larger, more familiar environments. More importantly, oceanic islands are intriguing for the ecological trends they display. They offer a more simplified study of such trends, which lends insights into patterns of community structure, the processes involved in the colonization of new habitats, and the dynamics of speciation. Oceanic islands possess unique characteristics that are an invaluable aid for the understanding of many such evolutionary and ecological topics.

When presented with any community of species, usually one is also presented with the products of millions of years of evolution and community interactions. In a continental area, it is difficult to deduce the past patterns of evolution and community interactions that have shaped the presently observed species because the time involved is vast, as is the area of the community under investigation. Sampling small sub-areas of land within a continent can neglect the influence of surrounding environments, and their inhabitants, on the sample area being studied. Obviously, when dealing with samples in continental areas, it is usually impossible for an investigator to control characteristics of the sample area in question. Oceanic islands, however, allow for some degree of “control” over variables such as area and time. Oceanic islands --

particularly those of volcanic origin -- are relatively short-lived on a geological timescale (Wagner, 1991), and are inhabited by recent products of evolution and colonization. Thus, such patterns as species composition and community structure observed on an oceanic island are the products of much more recent colonization and evolution than patterns seen on continental areas. The processes and trends which shaped the present biota is therefore much easier to evaluate when past history is not such a dominant factor.

Partitioning sample sites into smaller areas is not as important an issue when dealing with oceanic islands. Compared to continental landmasses, islands are often easier to sample as a whole; rather than having to take subsamples within a particular island, it is often possible to sample an entire island thoroughly. This reduces the effects of environments outside the sample area. Although biotas of neighbouring islands within an island group may still have an effect on the island in question, there still remains a physical barrier (in this case, the open sea between islands) which reduces this influence. This isolation makes each island a far more homogeneous universe than a rich continental biota (Mayr, 1967), and its biota is less affected by factors outside the sample area (the island) than is observed in a mainland sample.

The relatively short history of an oceanic island, coupled with its more independently-evolved biota, make each oceanic island an experiment in its own right (Mayr, 1967) -- every island has unique biological and geological characteristics (including area, elevation, rainfall, latitude, etc.) the effects of which on its biota are more clearly observed. More isolated island groups can be a particularly fruitful subject of study. The animals and plants of such oceanic islands have had to travel

considerable distances over open sea, to have survived the journey, and to have been able to establish themselves in their new habitat. In cases of extremely isolated islands, this is a rare event. However, such islands are not lacking in fauna and flora. Thus, the study of such islands becomes a study of the origin and evolution of new forms from a limited ancestral stock.

Both the popular and scholarly literature is full of studies of the faunas and floras of many islands and island chains. Many of these have attempted to find characteristics or trends common to insular environments, and some have produced predictive or quantitative theories to explain island species diversity. The most representative, and probably the most influential and ambitious of such works, was MacArthur and Wilson's 1967 book The Theory of Island Biogeography. The most often cited component of their theory is the highly prevalent relationship between an island's area and its species diversity (measured as number of different species within the taxon under consideration) seen in a great many studies of different islands. Although superficially this relationship does not appear to be especially remarkable, a closer examination of the factors which shape this relationship produces substantial information about the processes of immigration, extinction, and speciation. Many subsequent authors have produced similar analyses, many of them basing their conclusions on MacArthur and Wilson's theory of island biogeography, and often extending the analyses to compare species diversity against other island characteristics such as elevation, age and climate. Gilbert (1980) has critically reviewed this approach. Studying the relationship between species diversity and various island attributes, leads to conclusions about the factors which dominate in shaping an island's

species composition, and this in turn leads to insights in the processes important in colonization and speciation. When examining the biotas of such islands, many different taxa have been investigated. Most studies have been on groups such as birds, angiosperm plants and reptiles. The study of the determinants of island insect diversity has been underrepresented (Abbot, 1974)., and is still underrepresented.

It is unfortunate that few studies have concentrated on the biogeographic determinants of insect diversity because, by their sheer numbers and dominant status in the natural world, they would seem the mostly likely subjects of such studies. Because of the large numbers of species, and high population sizes, insects provide very large sample sizes which allow statistical tests to carry more weight than those performed using the smaller diversities and population sizes of taxa such as birds. Also, because of their small body size, there is a greater number of insect species inhabiting an even modestly-sized island. On large oceanic islands, their small body sizes and large populations make the extrapolation of comparative results to continental areas less tenuous than for birds or reptiles.

This paper explores the species diversity of insect faunae of two of the most well-known oceanic archipelagos in the world: the Galápagos Islands and the Hawaiian Islands. Both are relatively isolated archipelagos and display some of the most striking biotas in the world. The Hawaiian Islands are noted for their isolation which, as stated above, provides clarity in biogeographical analyses. Similarly, the Galápagos archipelago, while not as isolated as the Hawaiian Islands, is the world's best preserved and protected tropical archipelago (Peck, 1991b) which allows for analyses relatively uncorrupted by the effects of human interference. Furthermore,

many taxonomic groups are relatively well known on the Galápagos, but a number of others, particularly among the invertebrates, have been little or not studied at all (MacFarlan & Cifuentes, 1995). Thus a biogeographical analysis of the insect fauna of the Galápagos is worth attempting in itself. Here, the insect fauna of both the Hawaiian and Galápagos Islands are explored in relation to simple physical characteristics of the islands such as age, area and elevation and inferences about the processes of evolution and colonization are made when possible. As will be seen, much information about these processes is revealed through such analyses.

Characteristics of the Hawaiian Islands

Of all the high volcanic islands of the world, those of the Hawaiian chain are the most remote from any continent or from other islands of appreciable size (Carlquist, 1970). The archipelago consists of a great chain of 17 islands, several satellite islands and various islets, reefs and shoals extending some 2400 km across a northwest-southeast line (Zimmerman, 1948, Howarth & Mull, 1992, Stearns, 1985). The total land area of the chain is 16,710 km²; the highest elevation (4169 m) is found on the Big Island of Hawaii. The islands are the summits of giant submarine volcanoes coming from a hotspot beneath the Pacific Tectonic Plate (Howarth & Mull, 1992). Build-up of lava has created the individual islands while the action of plate tectonics has moved the islands steadily to the northwest and away from the hotspot. Thus, as one travels from the southeast to the northwest, the islands are progressively older. Physical geographical characteristics of the islands are given in table 1.

Because of their extreme isolation, the Hawaiian Islands provide an excellent opportunity for investigations of the physical properties of islands in determining the diversity of their insect faunas. Besides being the most remote islands in the world, they are mountainous, volcanic and tropical (Moulton & Pimm, 1986). Geological evidence indicates that the Hawaiian chain has never been connected to a land mass (Carlquist, 1970). In such an extremely isolated environment, the complicating effects of frequent and repeated colonization from continental source areas is virtually negligible. The Hawaii Archipelago offers a unique opportunity to study the effects of the physical characters of the islands in structuring the diversity of its insect fauna.

The islands may be conveniently divided into two main groups:

- 1) the eight main "high" islands (those above 300m in maximum elevation) (Hawaii, Kahoolawe, Maui, Lanai, Molokai, Oahu, Niihau and Kauai); and
- 2) the small and low Leeward Islands (those less than 300m in maximum elevation).

The Leeward Islands range in age from about 7 to 28 million years, while the eastern main islands are younger, ranging from only 700,000 years (the island of Hawaii) to 4.9 and 5.1 million years (Niihau and Kauai). The atolls of the Leeward Islands of the

Table 1. Present areas, elevations, maximum ages, number of naturally occurring insect species, genera, and single-island endemics and species:genus ratios of the islands of the Hawaiian archipelago.

	Area (km ²)	Elevation (m)	Age (ma)	Total Genera	Total Species	Single-Island Endemics	Species:Genus Ratio
Leeward Islands							
Nihoa	0.8	277	7	38	48	19	1.26
Kure	1	3		11	13	0	1.18
Pearl & Hermes	1	3	21	14	18	2	1.29
Lisiansky	1	13		10	12	2	1.20
French Frigate Shoals	1	37	11.7	10	13	2	1.30
Gardner Pinnacles	1	58		2	3	0	1.50
Necker	1	84	10	19	28	7	1.47
Midway	3	13	28	39	69	0	1.77
Laysan	4	15	20	44	61	7	1.39
Main Islands							
Kahoolawe	113	450	1.3	4	5	0	1.25
Niihau	182	390	4.9	10	13	1	1.30
Lanai	358	1027	1.3	163	441	112	2.71
Molokai	677	1515	1.8	237	926	321	3.91
Kauai	1434	1598	5.1	286	1161	655	4.06
Oahu	1583	1247	3.2	397	1912	1099	4.82
Maui	1903	3055	1.3	303	1393	663	4.60
Hawaii	10437	4205	0.7	335	1633	833	4.87

western Hawaiian Chain are the remnants of once high volcanic islands (Carlquist, 1970), but over time they have been eroded and their area has been significantly reduced.

The Hawaiian climate is oceanic -- temperatures are moderate. The highest temperature recorded was 38°C at Pahala in the island of Hawaii (elev. 259 m) while the lowest was -10°C at the summit of Mauna Kea (4197 m) also on Hawaii. Thus, there is a temperature gradient of 48°C over an elevation gradient of 4000 m. Additionally, there is a dramatic rainfall gradient from the leeward to the windward side of islands ranging from 170 mm/year (Hawaii) to 12,350 mm/year (Kauai) (Moulton & Pimm, 1986). Throughout evolutionary time the Hawaiian Islands have always been in the same general location and have had the same general climate (Carlquist, 1970).

Characteristics of the Galápagos Islands

The Galápagos Islands are a large and complex archipelago, lying 800 to 1100 km west of Ecuador, straddling the equator and extending over 3 degrees east-west (MacFarlan & Cifuentes, 1995). The archipelago consists of 13 large islands varying in size from about 17 km² to 4700 km², some 32 smaller named islands, and over 80 smaller islands, islets and rocks, the vast majority of which are vegetated (Peck, 1991a, MacFarlan & Cifuentes, 1995). The islands comprise a total land area of almost 8000 km² which is spread over 45,600 km² of ocean (MacFarlan & Cifuentes, 1995). The highest elevation (1707 m) is found on the large island of Isabela. Similar

to Hawaii, the islands are strictly volcanic in origin (Peck, 1991a) arising from a deep mantle “hot spot”. Concentration of recent volcanism in the western islands defines the hot-spot, and plate movement to the east-south-east explains the older islands and submarine ridge in that direction as former products of the hot-spot (Simkin, 1984). Because of the action of plate tectonics, an age gradient exists: the older islands are to the south-southeast, and they are progressively younger to the west-northwest (MacFarlan & Cifuentes, 1995). Physical geographical characteristics of the islands are given in table 2.

The Galápagos Islands are the best preserved and protected tropical oceanic archipelago in the world (Peck, 1991b). Eighty-seven percent of the land area is protected as the Galápagos National Park, and it is still one of the least altered natural areas remaining on the earth (MacFarlan & Cifuentes, 1995). This fact makes the Galápagos Islands an excellent archipelago for the study of biogeography. Human interference has been less than on any other tropical archipelago anywhere else in the world. Also, the islands are quite well isolated (over 800 km from the nearest continental source area) (Peck, 1991b), and there is no evidence that they have ever been connected to any continental land masses (MacFarlan & Cifuentes, 1995). As in Hawaii, the study of the composition of the insect fauna is relatively free of the complicated effects of repeated colonization from continental source areas.

The Galápagos Islands are also a good subject for study because of their youth. The oldest islands date from approximately 3 to 4.6 million years of age while the

Table 2. Present areas, elevation, maximum and minimum ages, number of naturally occurring insect species, genera, and single-island endemics and species:genus ratios for the islands of the Galápagos archipelago.

	Area (km ²)	Elevation (m)	Maximum age (ma)	Total Genera	Total Species	Single-Island Endemics	Species : Genus Ratio
Mosquera	0.05			4	4	0	1.0
Coamano	0.05	10		1	1	0	1.0
Beagle	0.08			2	2	0	1.0
Campeon	0.1	46		3	3	0	1.0
Las Plazas	0.2	10		8	8	0	1.0
Eden	0.23	10		4	4	0	1.0
Daphne Major	0.33	10		5	5	0	1.0
Gardner	0.81	49		8	9	0	1.13
Darwin	1.06	168	0.7	7	7	2	1.0
Bartolome	1.25	109		9	9	0	1.0
Tortuga	1.29	186		4	4	0	1.0
Wolf	1.34	253	0.3	14	14	7	1.0
Seymour	1.84	100		21	21	1	1.0
Rabida	5.0	367	2.5	27	32	2	1.19
Genovesa	14.11	76		22	25	2	1.14
Pinzon	18.15	458	2.7	44	51	6	1.16
Santa Fe	24.13	259	4.6	15	15	1	1.0
Baltra	26.2	150		17	17	1	1.0
Pinta	59.4	777		50	52	2	1.04
Espanola	60.5	198	5.6	31	32	3	1.03
Marchena	130.0	343		33	34	1	1.03
Floreana	172.5	640	3.3	79	98	13	1.24
San Cristobal	558.0	715	6.3	77	94	8	1.22
Santiago	584.7	905	2.4	84	96	6	1.14
Fernandina	642.5	1494	0.3	59	67	6	1.14
Santa Cruz	985.6	864	3.6	171	229	42	1.34
Isabela	4588.1	1707		109	127	13	1.17

youngest, Fernandina Island, is estimated to be approximately 700,000 years of age (MacFarlan & Cifuentes, 1995). These islands as a whole have only been available for terrestrial colonization for 3-4 million years (Peck, 1991a) which is quite young by geological standards. Thus, biogeographical analyses are simplified by the recentness of the fauna under consideration.

The Galápagos is notable for its diversity in vegetational and climatic conditions. The island possess a highly variable climate with distinct hot and cool seasons, and major variations in rainfall over the years (MacFarlan & Cifuentes, 1995). June to December is known as the cold/dry or “garua” season. During this period, the daily temperature at sea level ranges from 19 to 23 °C. The remainder of the year (January to May) is the warm/wet season, with temperature ranging from 24 to 29 °C (Peck, 1996). The islands lie at the edge of the Central Pacific dry zone and are arid to semi-arid at their lower elevations (Colinvaux, 1972). The higher elevation islands, however, have increasingly more rain at progressively higher elevations which allows for the existence of a humid forest zone at about 300-600 m. Above this lies a climatic inversion zone and progressively drier conditions from 1000 to 1700 m (Peck, 1996). This variation in climatic conditions along altitudinal gradients creates some of the strongest or most compressed floristic zonation to be found anywhere in the world (Peck, 1991a). Thus, the islands provide a substantial diversity of habitats for both insects and the investigator.

Methods

Analysis of the Hawaiian Data Set

The data used in the analysis of the Hawaiian insect fauna were obtained from a catalogue of all known Hawaiian terrestrial arthropods compiled by Nishida (1994). This catalogue includes the names of all islands in the Hawaiian archipelago where each insect species is known to exist, and the categorization of each species as a native (naturally occurring in the archipelago and elsewhere), endemic (found only in the archipelago) or introduced by humans. This catalogue is the most complete data set available for island insects anywhere in the world; and the data set has never been analyzed from the viewpoint of relating species diversity to island characteristics.

These data were obtained in spreadsheet form and manipulated to extract counts using Microsoft Excel 5.0. Only Insecta and Parainsecta were included in the analysis, and introduced species were excluded from the data set. Numbers of single-island endemic species (those species found on only one island in the archipelago) were determined for each island. The species:genus ratio was also calculated for each island, to be used as an index of speciation in the present analyses. These ratios were also computed for each insect order as a whole.

To determine significant relationships between insect species diversity and geographical characteristics of the islands, a maximum likelihood estimation procedure was employed to fit the data to a power equation. The Genstat 5 computer program was used to perform these maximum likelihood procedures. The random component of the equation was specified as having a (compound) Poisson distribution, except in

the case of species:genus ratios where a gamma distribution was more valid.

Geographical and geological data are from Stearns (1985), except for measures of island area which are from Carson and Clague (1995). The data were also fitted to linear models, but the exponential models provided results of best fit in all cases.

All the islands of the Hawaiian Chain were incorporated into the analyses, except for the islands of Kahoolawe, Niihau, and the Gardner Pinnacles. Kahoolawe may be safely excluded because it has been used as a testing ground for military explosives in the past, has harboured a high population of ungulates resulting in an extremely disturbed and non-representative ecosystem, and further has not been adequately sampled for its insect fauna (Carlquist, 1970). Niihau may be excluded due to lack of sufficient sampling effort. This island is owned by a family who have been extremely protective about outside influence on the island and its inhabitants. The number of entomologists who have seriously collected on the island are probably limited to only a handful, and those opportunities were not for any substantial length of time. Gardner is essentially a rock outcropping and is extremely difficult to land on and manoeuvre on, thus this island also has not been adequately sampled.

Maximum likelihood estimation procedures were attempted for the total number of insect species against island area, total number of insect genera against island area, total number of insect species against island elevation, total number of insect species against island elevation, total number of insect species against maximum island age, number of single-island endemic species against island area, and the number of single-island endemic insect species against island elevation.

Maximum likelihood estimation procedures were also employed to determine any relationship between island area and total number of insect species, total number of insect genera, number of single-island endemic insect species and the species:genus ratio for each island. Maximum likelihood estimation procedures were employed to find any relationship between island elevation and total number of insect species, number of single-island endemic insect species, and the species:genus ratio for each island. Relationships between island age and total number of insect species as well as the species:genus ratio for each island were also explored with maximum likelihood procedures.

Analysis of the Galápagos Data Set

The data used in the analysis of the Galápagos insect fauna came from an unpublished inventory compiled by S.B. Peck containing all published records of insect species in the Galápagos, as well as unpublished data on an additional 17,052 individual insects identified to species, collected during various expeditions to the islands. At the time of these analyses, this catalogue included only the “smaller” insect orders (excluding Phthiraptera, Coleoptera, Lepidoptera, Diptera, and Hymenoptera), for a total of 457 species. The data set included species names and other taxonomic information, the island(s) each species is known to exist on, whether the insect is classified as native, archipelago endemic, single-island endemic or introduced, and also which lifezone(s) the species inhabits. For the present analyses, vegetational lifezones were classified as one of seven types -- littoral zone, arid zone, transition zone, humid

forest zone, evergreen shrub (*Miconia*) zone, pampa zone, and upper arid inversion zone. Introduced species were eliminated from the data set, so a total of 345 species were used in the analysis.

As with the Hawaiian data set, the Galápagos data were manipulated and analyzed in spreadsheet form using Microsoft Excel 5.0. Using this computer program, counts were extracted for total number of insect species, number of insect genera, and number of single-island endemic insect species for each island and each lifezone. Species:genus ratios were also calculated for each island and lifezone as an index of speciation. Species:genus ratios were also calculated for each insect order in the data set. Percentages of single-island endemics were computed for each lifezone.

Using the Genstat 5 computer program, maximum likelihood estimation procedures were performed to determine any significant relationships between insect species diversity and various island attributes. Island elevations and areas are from Wiggins and Porter (1971) and Snell *et. al.* (1995) respectively. Data on island ages are from Geist (1996).

In all analyses, maximum likelihood estimation procedures were used to fit the data to a power equation, as linear models proved to fit the data relatively poorly. The random component of the equation was specified as having a (compound) Poisson distribution, except in the case of species:genus ratios where a gamma distribution was more valid.

Maximum likelihood estimates were attempted for island area against total number of insect species, total number of insect genera, number of single-island endemic insect species, and the species:genus ratio for each island. Similar analyses

were performed for island elevation against total number of insect species, single-island endemic insect species and species:genus ratio. A maximum likelihood estimate of island elevation against species:genus ratio was also performed for islands with maximum altitudes lower than 300 m. Estimates were performed to determine significant relationships between maximum island age against total number of insect species, and the species:genus ratio for each island. A further estimate was performed on minimum island age against number of insect species.

Results

Analysis of the Hawaiian Data Set

The present data set shows a highly significant relationship between island area and total number of insect species (figure 1) ($df=12$, $se=0.006$, $P<<0.001$). In an attempt to factor out the effects of explosive speciation and adaptive radiation, a maximum likelihood estimation procedure (MLEP) was performed of the number of insect genera against island area (figure 3). As with number of species, the relationship was highly significant ($df=12$, $se=0.0092$, $P<<0.001$).

The MLEP performed to determine any significant relationship between island elevation and total number of insect species on each island showed significant results. The results are plotted on figure 2. As with area, the relationship was highly significant ($df=12$, $se=0.011$, $P<<0.001$).

Plotting the composite island of Maui Nui (which existed during low sea levels) instead of Lanai, Molokai and Maui does not give a species-elevation

relationship that differs significantly from that when the islands are plotted separately. The relationship between the number of insect species and maximum island age proved to be significant (figure 4) ($df=10$, $se=0.013$, $P<<0.001$). MLEs of the number of single-island endemic insect species against island area (figure 5) and elevation (figure 6) were found to be significant ($df=12$, $se=0.010$, $P<<0.001$ and $df=12$, $se=0.021$, $P<<0.001$ respectively).

The MLE of island area against the species:genus ratio for each island yielded a highly significant result (figure 7) ($df=12$, $se=0.0087$, $P<<0.001$). The MLE of island elevation against species:genus ratio (figure 8) was also found to be significant ($df=12$, $se=0.028$, $P<0.001$). A negative, but significant relationship was obtained in a maximum likelihood estimation of the relationship between species:genus ratio and island age (figure 9) ($df=10$, $se=0.088$, $P<0.002$).

Analysis of the Galápagos Data Set

Maximum likelihood estimation procedures of island area against total number of insect species returned highly significant results (figure 10) ($df=25$, $se=0.012$, $P<<0.001$). MLEs of the total number of insect genera against island area (figure 11) gave results of similar significance ($df=25$, $se=0.013$, $P<<0.001$).

MLEs of island area against number of single-island endemic species (figure 14) and against species:genus ratio (figure 16) for each island also gave statistically

significant results, but of somewhat less significance ($df=25$, $se=0.041$, $P<0.001$, and $df=25$, $se=0.0037$, $P<0.001$ respectively).

Similar analyses performed using island elevation as the dependent variable yielded significant results using total number of insect species (figure 12) and number of single-island endemic insect species (figure 15) as independent variables ($df=23$, $se=0.033$, $P<0.001$ and $df=23$, $se=0.12$, $P<0.001$ respectively). Relatively marginal significant results were obtained when a MLE was performed on island elevation against species:genus ratio (figure 17) ($df=23$, $se=0.0092$, $P=0.002$).

The MLE of maximum island age against number of insect species (figure 13) yielded significant results ($df=9$, $se=0.032$, $P<0.001$).

A MLE of maximum island age (figure 18) against the species:genus ratio for each island yielded non-significant ($df=9$, $se=0.019$, $P=0.10$).

In all of the analyses performed on the Galápagos data set, plotting the data as a power function gave the “best fit”.

Table 3 gives insect species counts for the smaller orders broken down into categories of origin (native, archipelago endemics, single-island endemics, or introduced by humans), as well as trophic category. Relatively few of the species in the inventory are introduced (about 25%). Herbivores dominate the smaller insect orders of the Galápagos Islands.

Table 4 breaks down the species counts by lifezone. Table 5 gives the number of species collected for each month of the year (where that information is available). It is evident that more species have been collected during the wet season, which is expected to reflect the fact that most species are active during this season.

Discussion: Hawaiian Analysis

Effect of Island Area

The frequent significance of the species-area relationship has been documented in a great many studies, and is seen both in flora and fauna. Various theories have been proposed to explain the phenomenon. MacArthur and Wilson (1967) believed that the use of area as a variable was a proxy for another related variable which could not be directly quantified. They proposed that area could be viewed as an indirect measure of habitat diversity. As islands grow larger, their topography becomes more complex and the result is a growing diversity of different habitats, allowing for the support of a more diverse array of species assemblages (MacArthur & Wilson, 1967). In other words, a larger area allows for more habitats which in turn allow for more species. This explanation does appear to be in concert with the situation in the

Table 3. Categories of insect species and numbers of the Galápagos Islands, and trophic categories and numbers.

Category	Total	Predators	Scavengers	Herbivores	Endoparasites	Ectoparasites
Single-Island Endemics	104	11	25	68	0	0
Archipelago Endemics	99	15	24	59	0	1
Native	124	31	38	54	1	0
Introduced	112	7	32	69	0	4
Total	439	64	119	250	1	5

Table 4. Categories of insect species and numbers known to occur in different elevational vegetation zones of the Galápagos (most species probably can occur in more than one zone).

Category	Littoral	Arid	Transition	Humid forest	Miconia	Pampa	Inversion
Single-Island Endemics	10	40	10	25	2	13	0
Archipelago Endemics	16	66	46	51	29	32	1
Native	32	69	56	59	34	37	2
Introduced	22	59	40	39	17	19	0
Totals	80	234	152	174	82	101	3
Predators	21	48	32	26	21	20	0
Scavengers	20	42	40	57	28	40	1
Herbivores	43	151	89	95	35	43	2
Totals	84	241	161	178	84	103	3

Table 5. Total insect species numbers and trophic category species numbers of insects collected during each month of the year in the Galápagos Islands.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Predators	24	22	38	28	29	19	7	2	3	2	0	4
Scavengers	11	12	10	9	14	8	4	2	3	4	4	2
Herbivores	48	88	64	70	76	56	24	6	9	5	5	27
Totals	83	122	112	107	119	83	35	10	15	11	9	33

Hawaiian Islands. The smaller leeward islands tend to have only a limited range of habitats. The larger main islands, on the other hand, tend to be higher, and thus tend to be wetter, so a greater variety of habitats is present and these can support a greater number of species (Carlquist, 1965). The larger, high islands such as Oahu, Maui and Hawaii support a much greater diversity of ecological zones; including lowland rain forest, montane rain forest, savannah and alpine scrub, which do not exist on the lower islands (Howarth & Mull, 1992). Thus, the higher islands offer more environments to many species which cannot be supported on the smaller, ecologically more uniform islands.

Another factor to be considered when exploring the biology behind the species-area relationship is the effect of extinction on the biota. The very process of formation of the Hawaiian islands by repeated volcanic eruptions has been a continued history of habitat disturbances and local extinction. But the larger islands, with a greater number of habitats, tend to be more resistant to ecological disturbances. Having a larger number of ecological conditions with large areas may provide a "buffer" against disruption, whereas the limited range of ecological conditions found in smaller areas can be upset more easily and completely (Carlquist, 1965). The result of this is that extinction must be more prevalent and complete on smaller islands with more homogenous environments (Levins & Heatwole, 1963). Therefore, extinction is a much more significant process on smaller islands and tends to limit the number of species which can be supported. Following MacArthur and Wilson's (1967) "equilibrium theory," equilibrium turnover rates on larger islands would be lowered and the equilibrium number of species would be raised (Simberloff, 1978).

Another possibility for the species-area relationship also suggests itself; the species-area effect may be largely due to larger samples collected on larger islands. This may be true in some cases, but could not account for all of the studies that have produced a significant species-area effect. The present analysis employs a very large insect data set which is judged to be 90-95% complete (Peck, 1996).

MacArthur and Wilson's (1967) general equation relating species number to island area, is:

$$S = cA^z$$

where S is the number of species, c is a constant determined by various factors inherent to the island(s) in question, A is the area of the island and the exponent z is a value which usually falls within a predicted range depending on the island type, the present data set gives an equation of the form:

$$S = 414.8 A^{0.421}$$

According to MacArthur and Wilson (1967), most z -values will lie in the range 0.20 to 0.35 for islands or similarly isolated sample areas. If one is analyzing non-isolated sample areas within islands or continents, the z -value shifts to 0.12 to 0.17. The z -value obtained in this analysis (0.421) is higher than the predicted norm. Basically, this tells us that in the Hawaiian Islands, area exerts a more significant effect on species number than in most other insular environments. The elevated z -value is most probably a reflection of Hawaii's isolation, demonstrating the lower dependence on colonization for collecting species from outside the archipelago. The lower values seen in sampling areas within continents may actually reflect "transient" species which cannot support themselves as a breeding population within the area sampled, but

originate in an area outside the sampling area (Simberloff, 1978). Similarly, the Hawaiian Islands cannot have such transient species because of their isolation from the continents and each other, and therefore the relationship of species number to area becomes much stronger.

An examination of figure 1 shows that Oahu, in particular, appears to have disproportionately more species than predicted by the species-area equation. Although it is not the largest island in area, it has the largest number of species. The explanation for this may be partly related to the historic origin of Oahu. The two mountain ranges of Oahu were at one time two islands separated by a narrow water barrier. The faunas of the two areas are distinct, although they are now connected by dry land (Zimmerman, 1948). Such geology must promote speciation by isolation, effectively making Oahu the amalgamation of two separate islands, each with a distinct array of species and habitats. Therefore, Oahu has a higher degree of habitat heterogeneity, lending support for the theory that area largely reflects the diversity of habitats. A second reason is that the island is the central location for entomological activities by institutions such as the Bishop Museum, Hawaiian Sugar Planter's Association, University of Hawaii, and the State Department of Agriculture. Thus, more insect related field work has been done by entomologists on Oahu than on the other islands.

Figure 1. The total number of indigenous insect species plotted against island area for the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

A similar disproportionate diversity result is obtained when the islands of Maui, Molokai and Lanai are combined into a single data point. In times of Pleistocene low sea levels, these islands were connected to each other, forming a single large island called "Maui Nui". When Maui Nui is plotted on the species-area curve, its data point sits alongside Oahu, denoting a disproportionately larger number of species than that predicted by the estimated species-area equation. However, when plotted separately, Molokai, Lanai and Maui do not show significant deviation from the species-area equation. Here, the species-richness of Maui Nui may be attributed to isolation of the four separate volcanoes that make up the island. Although it has been a continuous landmass, populations of species have become separated by physical barriers (lowlands or water between the separate four volcanic mountains of the islands), thus allowing the populations of the separate islands (volcanoes) to evolve separately.

These results do show a definite relationship between island area and total number of insect species. The most probable explanation for this relationship appears to be that area is an indirect measure of the diversity of habitats, as the larger islands show a larger variety of habitats than the smaller islands, largely due to their elevations.

Effect of Island Elevation

Area alone cannot be responsible for habitat heterogeneity. Another linked factor is the elevation of the island. Larger volcanic islands also tend to be higher, which is in keeping with their volcanic origins. These younger, larger islands haven't

had the time to erode and sink into the ocean (as has occurred in the Leeward Islands), and their greater altitudes allow for more habitats than in the smaller, low Leeward Islands. Moist forest can only exist above a certain elevation (about 600-750 meters) in the Hawaiian Islands (Carlquist, 1965). The high islands intercept moisture from storms and prevailing trade winds, creating extreme differences in annual rainfall, which can vary between averages of 25 cm on leeward coasts to over 1000 cm at mid-elevation windward areas only a few miles away (Howarth & Mull, 1992). Obviously, increased elevation allows for a more diverse array of habitats, simply because many of these are not available on a low island that cannot intercept moisture.

Figure 2 shows that elevation is indeed a physical variable which significantly reflects the total number of insect species. Because certain habitats can only exist on islands with sufficient elevation, it is clear that elevation must have an important effect on species number. In the case of the Hawaiian Islands, elevation is effectively interchangeable with area because the two are intimately related. Elevation, however, has a more demonstrable relationship to habitat diversity whereas with area the relationship is not as apparent. The fact that the relationship between species and area is more significant than that between species and elevation may show that the use of area as a dependent variable encompasses other factors such as habitat stability which is not as fully incorporated into measures of elevation. These results suggest that habitat heterogeneity is not the only factor which determines species diversity in the Hawaiian Islands, thus making measures of area preferable over elevation in predictions of species diversity.

Figure 2. The total number of indigenous insect species plotted against maximum elevation of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

The above theories offer good ecological explanations for species diversity. However, the impact of the process of speciation itself is often overlooked. It is possible that ecological explanations may be confounded or complicated by the results of insular explosive speciation and adaptive radiation. To explore this possibility in the Hawaiian archipelago, we suggest one should look at the diversity of insect genera rather than species. Although the Hawaiian Chain has a great many endemic insect species, there are relatively few endemic genera. The present data show that the number of insect genera on an island is significantly related to island area (figure 3). Since there are fewer endemic genera, this relationship factors out the influence of speciation, supporting the above theories of habitat diversity.

Effect of Island Age

One curious feature of the Hawaiian entomofauna is that the island of Hawaii appears to have fewer species than would be expected for its large size and elevation. The island of Hawaii does not have as many species as would be expected from the estimated species-area equation (figure 1). Although the number of insect species on Hawaii is second only to Oahu, this number is by no means commensurate with the much greater area of that island. The island of Hawaii does not lack habitat diversity, and its ecological diversity is related to its size (Carlquist, 1974). A possible factor for this apparent lack of species is its youth (Carlquist, 1965). Although the island of

Figure 3. The total number of indigenous insect genera plotted against island area of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

Hawaii is the largest (10, 437 km²) and highest (3052 m), it is also the youngest (probably less than 700,000 years old) (Howarth & Mull, 1992). Perhaps Hawaii's youth has not permitted it to collect a complete complement of species. In the terminology of MacArthur and Wilson (1967), the island of Hawaii has not yet reached equilibrium, and is therefore unsaturated -- there are still plenty of niches available for new colonists and opportunities for the evolution of new endemic species. As colonization is only a weak force in the Hawaiian Islands, 700,000 years may not be sufficient time for speciation to "fill" the island, especially since its relatively non-eroded surfaces do not yet offer as many isolating mechanisms as would ridges and valleys on older islands such as Oahu (Carlquist, 1974). Furthermore, the island of Hawaii is still volcanically active, and the surface available for colonization remains in an elevated state of turnover (Wagner, 1991).

Given that time is a prerequisite for the accumulation of species, one would expect species diversity to have a positive relationship with island age. In the Hawaiian Islands, however, the opposite is true (see figure 4), though the significance is much less than for the analyses using area and elevation as independent variables. This result is not a contradiction, however. The effect of time is confounded by the fact that habitat heterogeneity also changes as islands change -- in some cases increasing (e.g. through the erosional formation of valleys and ridges) and in other cases decreasing (e.g. through the loss of lava islands (kipukas) on the surface and the network of caves and underground rock crevices) (Otte, 1994). Like all hotspot islands, the Hawaiian Islands have subsided and shrunk with age (Paulay, 1994) and

Figure 4. The total number of indigenous insect species plotted against the maximum ages of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

will continue to do so. This is how the older Leeward Islands become smaller and lower. These islands may well have been as large as the big islands in the past and may have contained comparable species numbers, but over geological time their species numbers have been reduced drastically. Thus, age cannot be used as a good predictor of species diversity on an archipelago such as the Hawaiian Islands.

Insect Speciation and Adaptive Radiation

Owing to the extreme isolation of the Hawaiian Islands, immigration of new colonists alone cannot account for its diverse insect fauna. In fact, it has been estimated that only 350-400 ancestral colonizations have led to the over 5000 different insect species that are known on the islands today. This means that even if 400 colonists are responsible for Hawaii's entomofauna, and we consider the maximum age of the present chain (28 million years), the maximum average time span between successful colonizations is 70,000 years (Howarth & Mull, 1992). The resulting large number of present species over ancestral colonists may be attributed to speciation and adaptive radiation.

Adaptive radiation connotes the entry of a group into one or a variety of new habitats and dietary modes (Carlquist, 1974). Successful immigrants reaching Hawaii were confronted with much more ecological opportunity for diversification than in their source areas (Carlquist, 1970). Many "empty" niches must have existed, giving a new immigrant species much potential for entering new adaptive zones. The endemic fauna we see today has evolved to exploit the full range of available habitats. Using

Figure 5. The total number of single-island endemic insect species plotted against the areas of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

the above figures for ancestral colonizations, each colonizing species on average has given rise to 13 new species. However, using the figures presented in this thesis, it is impossible to separate speciation accompanied by adaptive radiation from simple speciation without niche shifts (radiation) because a simple species count does not convey any information about the occupation of new niches. Thus, although it is absolutely evident that adaptive radiation has occurred, its extent is impossible to analyze with the figures available.

The figures can however lend insights into the factors which affect speciation processes. In an isolated environment such as that of the Hawaiian Islands, we are presented with a situation in which colonization plays an almost negligible role in the accumulation of species, and analysis of the attributes of different islands in the chain can yield illuminating results. That speciation is furthered by physical extrinsic isolation has long been considered plausible, and as a complex topography provides just such isolation opportunity, speciation should be somehow related to island area. The significant relationship between island area and the number of single-island endemic species (figure 5) suggests that, as with total number of insect species, area probably reflects, at least in part, habitat diversity and hence opportunity for speciation to exploit these habitats. Complex topography may also be associated with area, as the larger, higher islands do have a more complex, mountainous topography. Appropriately, the relationship between island elevation and number of single-island endemic insect species (figure 6) was highly significant.

Figure 6. The total number of single-island endemic insect species plotted against the maximum elevations of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

As with total number of insect species, the number of insect species endemic to Oahu is the highest (1099). Again, this may be related to its complex topography. The island of Hawaii, on the other hand, has fewer endemic species (833) despite its larger size and complex topography. It appears that age is the limiting factor here.

Another measure which gives a more pronounced estimate of the amount of speciation that has occurred on an island is the species:genus ratio (Carlquist, 1974; Otte, 1994). The average number of species per genus for the entire Hawaiian native insect fauna is 9.59 (this is different from 13 species per colonization because genus level evolution has occurred). This number may change in time, as some genera with only a single representative may be found to be introduced, and some genera may eventually be synonymized by taxonomists (Zimmerman, 1948), but on the whole this figure is relatively high compared to continental areas. When comparing species:genus ratios of the individual islands of the Hawaiian chain, we find that the main islands have the highest rates of speciation. Obviously, there are attributes of these islands that must promote speciation.

The highly significant relationship between the species:genus ratio and island area (figure 7) implies that two factors are important for promoting speciation: habitat diversity and physical isolation. As discussed previously, the diversity of habitats is related to island area. With a variety of habitats available for exploitation comes greater opportunity for colonizing species to diversify and enter these new adaptive zones. The more complex topography associated with the larger islands provides

Figure 7. Species:genus ratios plotted against the areas of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

physical barriers, keeping populations isolated from each other and allowing them to evolve independently, or semi-independently (MacArthur & Wilson, 1967). Both these factors should be reflected in the elevation of an island, and the relationship between island elevation and the species:genus ratio for each island was also found to be significant (figure 8). These results help support the theory that speciation is fostered by ecological opportunity and by isolating mechanisms.

Some studies of islands suggest that speciation and adaptive radiation in insular environments can be extremely rapid (Paulay, 1994). Colonists arriving in an environment free of competitors, with plenty of empty niches to be filled will diversify and exploit these opportunities at a remarkable rate. It is difficult to arrive at sound conclusions about speciation rates in the Hawaiian Islands, as the older islands have eroded considerably and are a small fraction of their original area. If the Leeward islands had retained their original areas, rates of evolution could have been more easily studied. However, examining the relationship between time and evidence of speciation does lead to some insights.

The significant negative relationship between species:genus ratio and island age (figure 9) seems to imply that the younger islands indeed are experiencing a rate of speciation much higher than that of the older islands; however, such an explanation ignores the effects erosion and extinction may have on the older islands.

The atolls of the Leeward Islands were once high volcanoes themselves. How high and large is unknown, but the sizes of the present-day high islands probably simulate the former masses of the Leeward Islands (Carlquist, 1970). If speciation

Figure 8. Species:genus ratios plotted against the maximum elevations of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

Figure 9. Species:genus ratios plotted against the maximum ages of the Hawaiian Islands, with a line fitted by maximum likelihood estimation.

rates were comparable to those found in the present-day high islands, then there is no reason to suppose that the species:genus ratio would fall so uniformly across all insect orders if the main factor influencing this decline was a drop in the rate of speciation. This uniformity is apparent in figure 9 -- the Leeward islands have relatively uniform species:genus ratios tightly clustered around an average of 1.4. Rather, this uniform decline would more likely be attributable to loss of habitat and the resulting extinction. The Leeward Islands lack the elevation to maintain wet forest habitats. These habitats in the high islands are often much richer in species than lower, drier regions (Carlquist, 1965). The most common pattern of adaptive radiation seen on oceanic islands shows that initial colonists become established in the drier, more coastal areas and that radiation occurs from the drier habitats into the wetter areas at higher altitudes (Carlquist, 1970). Thus, a very high proportion of species inhabiting wet forest areas must be the products of adaptive radiation. No figures are currently available for the proportion of endemic species in each vegetative zone, but it is quite possible that wet forest areas will show a relatively higher amount of endemism. When the wet forest areas of the Leeward Islands were eroded away and lost, so too were the species within them, the majority of which must have had ancestors in the lower drier areas. Many of these ancestors, or similar descendants, may have survived in their less ephemeral environments. With the elimination of the habitats conducive to speciation came the elimination of the products of this speciation themselves, hence the uniform drop in the species:genus ratio.

The above hypothesis does not necessarily imply that speciation rates are faster on younger islands. Rather, they imply that extinction due to competition and

destruction of habitat is a much stronger force on older, more "saturated" islands. On the younger islands, with more ecological opportunity and less competition, novel species have a greater chance of survival, whereas on the more saturated, less opportune islands, their chance of extinction is much greater.

Looking at the individual figures for each island's species:genus ratio, we see that the island of Hawaii has the highest value (4.87). This would imply that competition on Hawaii is relaxed and that many ecological opportunities exist for the diversification of species in order to exploit open niches and new habitats. It is quite possible that the island of Hawaii has not reached its "peak" of speciation, or more accurately, it has not reached its capacity for support of newly evolved species. If it were left undisturbed into the future, the island of Hawaii may reach a much higher species:genus ratio as it eventually becomes saturated. The species:genus ratio could then remain at a relatively constant level for a time, and then the island would experience a loss of species as its wetter habitats were eliminated as the island eroded and sank into the ocean. In other words, long term survival of the products of speciation in an isolated, insular environment such as the Hawaiian archipelago is a cyclic, ephemeral phenomenon.

Naturally, not all insect taxa are equally represented in the endemic fauna; species:genus ratios are not uniform across the different orders found in the Hawaiian Islands (table 6). Only some taxa have experienced "explosive" evolution, allowing for

Table 6. Species:genus ratios of the insect orders found in the Hawaiian Islands. Figures in brackets indicate total number of indigenous species for each order.

Order	Species:Genus Ratio	
Lepidoptera	15.7	(955)
Psocoptera	15.3	(92)
Neuroptera	12.5	(50)
Diptera	12.0	(1058)
Hymenoptera	10.5	(653)
Coleoptera	10.5	(1379)
Homoptera	9.2	(385)
Odonata	8.3	(33)
Orthoptera	6.4	(64)
Heteroptera	5.6	(217)
Archeognatha	5.0	(5)
Thysanoptera	3.2	(29)
Collembola	2.9	(95)
Mallophaga	2.2	(56)
Siphonaptera	1.0	(1)
Dermaptera	1.0	(10)

the development of spectacular "swarms" of endemic species from one or few ancestral stocks (Peck & Kukalova-Peck, 1990).

An examination of table 6 reveals that Lepidoptera, Diptera, Hymenoptera, and Coleoptera have undergone a relatively large amount of speciation. For example there are over 600 species within the genus *Drosophila* (Diptera) and between 350 to 500 species of moths in the genus *Hypsmocoma* (Lepidoptera) (see Howarth & Mull, 1992 for other examples). Overall, these four orders comprise 79.2% of the indigenous insect fauna of the Hawaiian Islands, but more interestingly comprise a higher percentage of the species in the main islands (72% compared to only 57% in the Leeward Islands). This trend may reflect the elimination of endemic species on the Leeward Islands as postulated above. These four orders dominate the endemic totals, but in the Leeward Islands, where less ecological opportunity exists, and where regions which formerly fostered speciation have been destroyed, these dominant orders are reduced in proportion.

Thus it appears that the younger, main islands display higher species:genus ratios not as a result of increased rates of speciation (or "explosive" radiation), but rather because their varied habitats and relaxed competition allows for continued speciation as well as the retention of the products of such speciation.

Discussion: Galápagos Analysis

Effect of Island Area

The most commonly computed statistic when performing biogeographical analyses of a particular island or island group is the relationship between island area and the number of different species on each island. Superficially, this relationship can seem almost trivial. However, as one investigates the relationship more thoroughly, patterns of community structure and evolution are often elucidated.

There has been much debate over the form of the species-area plot. Some researchers have found that plotting both species and area on a linear scale yields the “best fit” to the data (Abbott, 1974). Still others have found that applying a logarithmic transformation to at least one of the variables yields more descriptive results. The power function, or Arrhenius plot, is accomplished through a logarithmic transformation of both the X and Y variables. This approach has become the most generally accepted “best model” (Connor & McCoy, 1979).

The present data set was analyzed using a linear model, a model in which only one of the variables was logarithmically transformed, and finally as a power function. Deviance from the estimated species-area equation was minimized through use of the power function (see figure 10), as were the other estimates employed in this study.

The consistent “goodness of fit” of the power function does not imply its universal appropriateness, however. Although the power function is the most

Figure 10. The total number of indigenous smaller order insect species plotted against the areas of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

common model to provide the “best fit”, there are plenty of data sets which are not made linear by it (Williamson, 1988). Some data sets have been found to fit non-transformed plots, or plots where only one variable has been transformed logarithmically. Connor and McCoy (1979) analyzed 100 previously published data sets, applying several models to each, but found no discernible pattern as to which model fit the data best.

Biological systems are complex, with many different factors affecting the makeup of a community. In every terrestrial community, there are variations in such attributes as elevation, slope, temperature and moisture, and a host of chemical gradients in the soil (Reice, 1994). Obviously, these factors differ between ecosystems across the globe, and may sufficiently differ between islands within the same archipelago. To assume that the power function is the best model to use for all terrestrial ecosystems and across all taxa is tantamount to ignoring these divergent factors. Therefore, it seems statistically sound to use whichever model gives the best prediction of the variance of the dependent variable with the independent variable (Hamilton et al, 1963). Expecting a biological system to rigidly adhere to the laws of mathematics seems rather unrealistic. Therefore, from this data set I ascribe no inherent appropriateness to the power function as a predictor of number of insect species from island area, but rather find it to be the best model for prediction of this relationship.

Any discussion of the species-area relationship must take into account the possibility that it is not area *per se* that exerts an effect on species number, but rather some other variable which is inaccessible for measurement and for which area acts as a

proxy. In this regard, area is only an indirect measurement of some other factor or factors which determine species diversity. An ultimate theory of species diversity may not mention area at all (MacArthur & Wilson, 1967), as other factors may be found to be more predictive and quantifiable. The prevalence of species-area plots in the literature also reflects research history, as few early workers considered anything but the relatively easily-obtained measures of area, elevation and isolation in their analyses (Abbott, 1974). In this light, discussion of the species-area effect is generally a discussion of those factors of which area is an indirect measure. Most commonly, three explanations are used to explain the relationship. These explanations explain the relationship as a result of (1) habitat heterogeneity, (2) sampling effect, and (3) “equilibrium theory” (Simberloff, 1978).

As a possible explanation for the species-area relationship, MacArthur and Wilson (1967) proposed that area could be viewed as an indirect measure of habitat diversity. As islands grow larger, their topography becomes more complex and the result is a growing diversity of different habitats, each of which supports its own assemblages of species which are ecologically semi-independent of each other (MacArthur & Wilson, 1967). The smaller the island, the more homogeneous its environment at any given time (Levins & Heatwole, 1963). In other words, a larger area tends to support a larger number of different habitats, thus allowing a larger variety of species, many of which would not be able to maintain viable populations in smaller areas simply due to unavailability of suitable habitats.

This effect is made obvious when examining the different types of life zones on oceanic islands. The Galápagos Islands possess some of the strongest or most

compressed floristic zonation to be found anywhere in the world (Peck, 1991a), and much of this zonation is dependent on the size of the island. In keeping with their volcanic origins, larger volcanic islands also tend to be higher (Carlquist, 1965). Higher islands are able to intercept more moisture than lower islands, and in the Galápagos the “high islands” have increasingly more rain at progressively higher elevations (Peck, 1996). Thus, sufficiently large (and correspondingly high) islands can support habitats that cannot exist on the lower islands. The lower, smaller islets and islands of the Galápagos are dry and have only 1-3 vegetation zones (littoral, arid and transitional) (MacFarlan & Cifuentes, 1995), their areas and corresponding altitudes not being high enough to intercept sufficient moisture for more humid life zones. The higher, larger islands and volcanoes, however, have a humid forest zone at 300-600 m (Peck, 1991a), and because of the existence of this more humid habitat, such islands may have up to as many as 2-4 additional zones (e.g. closed evergreen forests, mossy open evergreen forests, mossy evergreen scrub, non-wooded evergreen or summit pampas, etc.) (MacFarlan & Cifuentes, 1995). Intuitively, it is evident that the presence of a greater number of climatic zones allows for a greater number of insect species adapted to these zones which could not survive on a smaller, drier island.

The second of the most common explanations for the species-area relationship is less encouraging -- that the relationship reflects sampling effort, and larger samples are collected by researchers on larger islands. The present data sets for both Hawaii and the Galápagos, however, are compiled not only from recent collecting efforts, but

also from all records in a literature generated over 150 years of insect research in both archipelagos. Therefore, the data used are far from incomplete and should (hopefully) minimize the impact of sampling effort on these analyses.

The third common explanation for the species-area effect is not totally exclusive of the habitat heterogeneity hypothesis. This is the equilibrium theory of biogeography as outlined by MacArthur and Wilson (1967). The MacArthur and Wilson theory hinges on the idea that the composition of any island fauna or flora is dictated at any time by a balanced equilibrium between immigration of new species and extinction of others. In sufficient time, an island's flora or fauna will strike a balance between immigration of new species and extinction of old ones, and upon reaching this stage, the system is at equilibrium -- in a steady state, with overall species composition and relative abundances stable through time (Reice, 1994). Once this steady state has been achieved, the number of species on that island is termed the **equilibrium number** (Carlquist, 1965). Upon reaching this equilibrium number, the number of species inhabiting that island will not change, and the island is said to be "saturated" with a maximum number of species. The equilibrium number of species for any island is determined by a multitude of different factors which affect species viability on that island. MacArthur and Wilson (1967) cite island area and isolation from the source area for new colonists as the primary factors which shape the equilibrium number of species for any island (MacArthur & Wilson, 1967).

The equilibrium theory is often used as an explanation for the species-area relationship because an island's area affects both processes of immigration and extinction, upon which the theory is based. In an oceanic archipelago, such as the

Hawaiian and Galápagos archipelagos, immigration of new species is a process of colonization by individuals from a source area. Despite the very large distances involved in dispersal of a new species from a mainland source area across open sea to an isolated archipelago, the great difficulty in the dispersal of such animals appears to depend not so much on their being cast adrift and transported, but rather in their landing in another locality and becoming established in a foreign environment (Zimmerman, 1948). Establishment of a new colonist species would be impossible if there were no suitable habitats which would allow survival and reproduction of the colonist species. Obviously, a wide variety of habitats increases the likelihood of the establishment of new colonists, and following the habitat heterogeneity hypothesis, an island with a larger area provides a greater variety of habitats, and thus more opportunity for the establishment of new colonists.

Similarly, an island's area will have an effect on the processes which cause the extinction of species. Various factors influence the probability of extinction of any species. One of these factors is population size -- the likelihood of extinction increases inversely with the size of a population (Futuyma, 1986). A larger island permits larger populations of a species and therefore they have lower extinction rates because their larger populations are less vulnerable to stochastic events (Nilsson et al, 1988). Also, a population of an animal or plant species must consist of a certain minimum number of individuals otherwise inbreeding causes fatal defects to become common and deletes the population (Carlquist, 1970). Thus, a smaller island which supports smaller populations will have higher extinction rates, causing the equilibrium number on these islands to be lowered. Disturbance of a habitat is a prime cause of species extinction

(Reice, 1994). Severity and completeness of disturbance is related to an island's area. The very process of formation of volcanic, oceanic islands such as the Galápagos and Hawaiian Islands by repeated volcanic eruptions has been a continued history of habitat disturbances and local extinction. But larger islands, with a greater number of habitats, tend to be more resistant to ecological disturbances. Having a larger number of ecological conditions with large areas may very well provide a "buffer" against disruption, whereas only a limited range of ecological conditions of limited areas can be upset more easily and completely (Carlquist, 1965). The result of this is that extinction must be more prevalent and complete on smaller islands with more homogeneous environments (Levins & Heatwole, 1963). Following the equilibrium theory, this equates to smaller islands having higher extinction rates, and results in the lowering of the equilibrium number of species (Simberloff, 1978).

Of course, the equilibrium theory of biogeography only takes into account the processes of immigration and extinction. Another significant contribution to the diversity of any island's biota is through evolution of new species (Futuyma, 1986). Without reference to this fact, the equilibrium theory is primarily an ecological explanation for species diversity, but as long as evolution of new species is assumed to be a component of immigration then the theory is still valid for even the most remote archipelagos where immigration is overshadowed by speciation as a source of new

Figure 11. The total number of indigenous smaller order insect genera plotted against the areas of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

species. The maximum likelihood estimate of the relationship between total number of insect genera against island area (figure 11) was performed as a way to reduce the effect of evolution on the species-area plot, and its only slightly lower standard error value and correspondingly equivalent significance do not reduce the validity of the species-area plot.

Some authors have suggested that area *per se* has a direct effect on species number, independent of any linked factors such as habitat heterogeneity or sampling effort. To some degree, the equilibrium theory of biogeography assumes this contention (Nilsson et al, 1988). Larger areas allow for larger population sizes which are more resistant to extinction than smaller population sizes. In this regard, it is not unreasonable to attribute island area *per se* as a factor in the species-area relationship. D.S. Simberloff (1978) performed an ambitious experiment in which the insect faunas of several mangrove islands were carefully censused. The islands were reduced in area, time was allowed for re-equilibrium, and then a new census was taken of their entomofaunas. These islands were virtual monocultures of *Rhizophora mangle* trees and were structurally homogeneous, thus eliminating habitat diversity as a factor in the species-area effect. The result was a highly significant species-area relationship, independent of habitat diversity. Excluding the effect of population size on the species-area relationship, these results are difficult to explain in the absence of habitat diversity. However, taking the *Rhizophora mangle* flora as a homogeneous environment may have been an erroneous assumption. Even on a flat, seemingly structurally homogeneous island, there still exist variations in moisture, temperature, soil chemicals, etc. (Reice, 1994) Also, owing to their small body size, insects inhabit

many microhabitats which may not be readily apparent to the collector. Therefore, it seems likely that habitat diversity was not, in fact, factored out, and that Simberloff was falsely assuming a homogeneous environment. One of the greatest dangers in biogeography is the false assumption of a homogeneous environment (Reice, 1994).

MacArthur and Wilson (1967) attempted to devise a general equation from which the number of species on any island could be predicted from its area. This power function equation takes the form:

$$S=cA^z$$

where S is the number of species, c is a constant determined by various factors inherent to the island(s) in question, A is the area of the island, and the exponent z is a value which usually falls within a predicted range depending on the island type (MacArthur & Wilson, 1967).

Using the insect species data from the Galápagos Islands, we obtain the following equation for predicting the number of “smaller order” insect species from island area:

$$S=60.5 A^{0.346}$$

Additionally, if numbers of insect genera are used instead of species numbers (which may counter-effect the influence of speciation to some degree, and provide a more “ecologically-based” relationship) a similar equation is obtained:

$$S=52.0 A^{0.326}$$

MacArthur and Wilson (1967) predicted that the exponent of the equation, known as the z -value, should fall within the range 0.20 to 0.35 for islands, and between 0.12 to 0.17 for non-isolated sample areas within islands or continents. The

z-value obtained for the Galápagos data (0.346) appears to conform to their prediction.

Effect of Island Elevation

Because most biotic systems are extremely complex, it is highly unlikely that one geographic variable (e.g. area) is responsible for those factors (such as habitat heterogeneity, etc.) which determine the number of species on a particular island. Another, linked factor is the elevation of the island. Within an archipelago, larger islands also tend to be higher and generally younger, which is in keeping with their volcanic origins. On the Galápagos Islands, the high-elevation islands receive much more rainfall than the low-elevation islands (Johnson & Raven, 1973). Therefore, certain habitats cannot exist on an island which does not have a sufficient elevation. This is certainly the case in the Galápagos archipelago as the lower islands have only 1-3 vegetational zones, while the elevation of the higher islands allows for the presence of several other, more humid zones (MacFarlan & Cifuentes, 1995).

The present data show a significant relationship between island elevation and number of insect species ($df=23$, $se=0.033$, $P<<0.001$) when analyzed with maximum likelihood estimation procedures (see figure 12). The significance, however, is not as high as that obtained from the analysis of species number against island area, showing

Figure 12. The total number of indigenous smaller order insect species plotted against the maximum elevations of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

perhaps that island elevation does not encompass as many factors that affect species composition and number.

It is likely that number of available habitats (habitat heterogeneity) is reflected by the species-elevation relationship, and this relationship must be a substantial factor which creates the species-area relationship, as area and elevation generally go hand in hand. Elevation, however, appears to reflect habitat heterogeneity more exclusively than measures of area do, which explains the lower significance of the species-elevation relationship when compared to that of species and area. In fact, island elevation may well be a factor encompassed by the species-area relationship.

Elevation has a more obvious relationship to habitat diversity whereas this relationship is not so apparent with island area. A large flat island would seem to have little advantage over a small flat island, other than being a larger target for a colonizing desseminalule, but in the oceanic, volcanic islands of the Galápagos, area and elevation are intimately related. The fact that area shows a more significant relationship to species number than elevation does implies that use of area as a dependent variable encompasses other factors such as population/habitat stability or an area *per se* effect which are not as fully incorporated into measures of elevation. Thus, measures of island elevation may prove to be a more direct measure of habitat diversity than measures of island area. Since the higher islands in the Galápagos archipelago receive much more rainfall than the lower-elevation islands, elevation may indicate environmental richness in addition to ecological heterogeneity (Johnson & Raven, 1973).

As with island area, a further possible explanation for the species-elevation effect is that of collecting effort. High altitude areas of the Galápagos are more difficult to access, so collecting effort may be disproportionately less on the higher-elevation islands, depressing true species numbers on the higher islands (Cowie, 1995).

Overall, it would appear from the data gathered from the Galápagos archipelago, that island area is a better predictor of insect species number than is island elevation. That is not to say, however, that island elevation is not a useful variable for analysis, as it probably reflects habitat heterogeneity and environmental richness more directly than does island area.

Effect of Island Age

An island's age is expected to have an effect on its complement of species, because time is a prerequisite for the accumulation of species. Owing to their volcanic origin and relative isolation, the ultimate source of new species on the Galápagos Islands is through colonization from source areas (i.e. continental landmasses). The islands are distant enough from continental sources areas that the arrival of new colonists is a fairly infrequent event (Peck, 1991a), and consequently this low immigration rate makes evolution of new species an important factor in the accumulation of species. Thus, it is expected that the older an island is, the more time it has had to accumulate species, and therefore older islands should demonstrate a higher species diversity than younger islands within the archipelago.

The species-island age estimate performed on the present Galápagos data (figure 13) showed relatively low significance when compared to the relationships between number of species and island area and elevation.

However, these relatively non-significant results do not necessarily contradict the idea that species accumulate with time. The effect of age is confounded by the fact that habitat heterogeneity also changes as volcanic islands age -- in some cases increasing (e.g. through the erosional formation of valleys and ridges) and in other cases decreasing (e.g. through the loss of lava islands on the surface and the creation of networks of caves and underground rock crevices) (Otte, 1994). Thus, the unpredictable nature of erosional forces can conceal any inherent trends between island age and species diversity.

The species-age relationship is further confounded by the species-area effect. South Pacific islands such as the Galápagos are formed by eruption, over a relatively short period of time, of volcanoes from the depths of the ocean. Once formed, the islands slowly erode until they disappear under the sea. Consequently, the older the island the smaller it is (Williamson, 1988). As discussed previously, area exerts a strong effect on the number of species to be found on a particular island. As an island's area is reduced over time, its species diversity will also be reduced due to factors encompassed by the species-area effect. If an island's area was not reduced with its age, then a positive relationship between island age and species number would result. However, this trend will be opposed by the effects of its reduced area with age.

Figure 13. The total number of indigenous smaller order insect species plotted against the maximum estimated island ages of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

In the present data set, it would appear that the two opposing forces have balanced each other somewhat.

Independent of the effect of island area, the relative lack of a significant relationship between island age and species diversity may be partially explained through MacArthur and Wilson's (1967) equilibrium theory of biogeography. If an island is young enough, it is possible that it may have a depressed species diversity if it has not yet had time to reach equilibrium (Carlquist, 1965) and is therefore unsaturated -- there are still plenty of niches available for new colonists and opportunities for the evolution of new endemic species. There are two apparent factors which may provide evidence of non-equilibrium conditions on some islands: youth and past climatic changes.

The Galápagos Islands are remarkably young when compared to other still-active ocean archipelagos like the Azores, Canary, and Samoa Islands (Simkin, 1984), and became available for terrestrial colonization no more than 3-4 million years ago (Peck, 1991a). The youth of the archipelago may very well add to the lack of a discernible trend between island age and species number.

Climatic fluctuations during more recent periods in the history of the Galápagos have probably contributed to depression of species numbers. The severe bouts of aridity during times of Pleistocene glacial maxima in the northern hemisphere (Peck, 1991b) must have reduced the areas of humid habitats in the higher-altitude regions of the islands, reducing the number of humid zone insect species found on the larger islands. The destruction or reduction of the moist-humid forest zones may have occurred as recently as 10,000 years ago (Peck, 1991b) which is a very recent event in

terms of evolutionary time, and may have disrupted equilibrium conditions, particularly on the higher islands. Ten thousand years may not have been sufficient time for these regions to resaturate, especially as the inhabitants of these depopulated areas are most probably post-Pleistocene immigrants.

Overall, it is apparent that age is not a good predictor of species numbers, certainly not as good a predictor as is island area or even island elevation. The effect of island area distorts any clear relationship between the two variables, and the youth and past climatic instability also disrupt the relationship. Lack of reliable age data for many of the islands of the Galápagos reduces the effectiveness of age as a predictor.

Insect Speciation and Adaptive Radiation

The Galápagos Islands are a relatively isolated group of islands, with no evidence of ever being connected to any continental landmass (MacFarlan & Cifuentes, 1995). Consequently, all terrestrial life on the islands has had to cross an oceanic water gap to reach them and the islands are distant enough from continental source areas as to make arrival and establishment of colonists a fairly rare occurrence (Peck, 1991a). Thus, immigration is not as important a factor in the accumulation of species in the Galápagos as in less isolated, continental areas. The processes of speciation and adaptive radiation are of prime importance in the accumulation of the insect species that we observe today.

In any discussion of speciation and adaptive radiation, it is important to clarify the difference in meaning between the two terms. Speciation refers to the general

process of species formation (Ayala, 1982). Adaptive radiation refers to a more specific instance of speciation, which connotes the entry of a group into one or a variety of new habitats and dietary modes (Carlquist, 1974). In adaptive radiation, these evolutionary changes must be ones that allow a new way of making a living or promote living in a new habitat (Peck, 1996).

Adaptive radiation is a particularly prevalent phenomenon on isolated oceanic islands and ancient lakes. Such habitats are famous for having allowed the evolutionary development of spectacular “swarms” of endemic species from one or a few ancestral stocks (Peck & Kukalova-Peck, 1990). The Hawaiian Islands, for example, offer some of the most striking examples of both prolific speciation and adaptive radiation, resulting in vast numbers of species within certain genera, living in new habitats and doing new things. The *Drosophila* are the best known and best studied. These large numbers of species are not due to immigration, but rather evolution of new species from one or a few ancestral colonist species.

Why adaptive radiation is seemingly so prevalent on isolated, oceanic islands stems from their formation and isolation. Individual volcanic islands are, on a geological time-scale, relatively short-lived, and accordingly are inhabited by recent products of evolution or colonization (Wagner, 1991). Because of their ephemeral nature, all life on island groups such as the Galápagos and the Hawaiian Islands has had to cross an oceanic water gap to reach them (Peck, 1991a). With successful colonization occurring so infrequently, in their earlier history these islands must have been depauperate and disharmonic in terrestrial animal life. Successful immigrants reaching the islands were confronted with much more ecological opportunity for

diversification than in their source areas (Carlquist, 1970). New land open to colonization encourages speciation (Zimmerman, 1948), and the relative poverty of the islands has stimulated the development of adaptive radiations in the relatively few organisms that have successfully established themselves, causing these high remote oceanic islands to become fairly species-rich through time (Paulay, 1994). Many “empty” niches must have existed, giving a new immigrant species much potential for entering new adaptive zones. The endemic fauna we see in the Galápagos Islands today has evolved to exploit the full range of available habitats.

Unfortunately, the data used in the analyses in this thesis are not of sufficient resolution to separate speciation accompanied by adaptive radiation from “simple” speciation without niche shifts because a simple species count does not convey any information about the occupation of new niches. Thus, although it is highly probable that adaptive radiation has occurred, its extent is impossible to analyze with the data available.

These figures, however, can lend insights into the factors that affect speciation processes. In an isolated environment such as that of the Galápagos Islands, we are presented with a situation in which colonization plays an almost negligible role in the accumulation of species, and analysis of the attributes of different islands in the archipelago can yield illuminating results. That speciation is furthered by physical

extrinsic isolation has long been considered plausible, and as a complex topography provides such isolation opportunity, speciation should somehow be related to island area. The significant relationship between number of single-island endemic insect species and area (figure 14) suggests that as with total number of insect species, area probably reflects, at least in part, habitat diversity and hence opportunity for speciation to exploit these habitats. The relationship, however, is not as strong as that obtained for the total number of insect species against area, suggesting that while area plays a significant part in the determination of the number of insect species on an island in the Galápagos, it plays a lesser role in the determination of the number of species endemic to any one island, and perhaps a lesser role in speciation processes. Similarly, the estimated relationship between island elevation and number of single-island endemic species (figure 15) is less significant than that of island elevation against total species numbers.

The relatively weak relationship between area and endemism may be attributable to lack of moist habitats. As discussed previously, during Pleistocene glacials, the arid zone was much larger and the higher-altitude moist zone very much smaller than at present, and as a consequence the present moist zone plant communities may have been partly assembled quite recently (within 10,000 years) (Peck, 1996). The most common pattern of adaptive radiation seen on oceanic islands shows that initial colonists become established in the drier, more coastal areas and that radiation occurs from the drier habitats into the wetter areas at higher altitudes (Carlquist, 1970). Thus, with a large reduction in area of the moist life zones within

Figure 15. The total number of smaller order single-island endemic insect species plotted against the maximum elevations of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

quite recent times, a large proportion of its endemic insect fauna may have been eliminated and has not yet had sufficient time to re-equilibrate itself to saturation levels. Consequently, it can be predicted that moist zone habitats should have a lower number of endemic species, and a higher number of native species per unit area of habitat (Peck, 1996).

Table 7 gives counts of number of species, single-island endemics and genera for Galápagos islands which are at least 300m in height (and hence possess humid forest zones), as well as calculated percent endemism and species:genus ratios. Overall, the highest endemism is found in the transition zone, with the arid zone having the second-highest percentage. Although the humid forest zone does not possess the lowest endemism score, it is lower than both the transition and arid zones, and is at about the same level as the littoral zone. The apparent poverty of endemics in the humid forest zone is unusual, as most island groups show the highest proportion of endemics in the moist uplands (Johnson & Raven, 1973), which supports the prediction that recent drought conditions have eliminated much of the biota of these regions, and re-equilibrium (through speciation) has not had sufficient time to occur.

Table 4 breaks species counts into trophic category (predators, herbivores and scavengers). It would be expected that in the more humid regions, opportunity for specialization (and hence endemism) would be greater. Table 4, however, shows that the percentages of scavengers are highest in the humid forest, evergreen shrub and pampa zones, indicating generalist feeding habits are highest in these zones. Native insect species make up a higher percentage of the fauna in these zones when compared to the more stable arid zone. Generalist feeders and native species would be expected

Table 7. The number of naturally occurring insect species, single-island endemic insect species and naturally occurring insect genera for each lifezone of the Galápagos Islands. Also given are the species:genus ratio and percent endemicity of the insects inhabiting each lifezone. Only islands over 300 m in maximum elevation are included.

Lifezone	Species	Single-Island Endemics	Genera	Endemicity (%)	Species : Genus Ratio
Littoral	60	10	55	16.7	1.09
Arid	171	32	129	18.6	1.33
Transition	122	46	98	37.7	1.25
Humid Forest	138	23	105	16.7	1.31
Miconia	72	2	60	2.78	1.20
Pampa	87	13	68	14.9	1.28
Inversion	3	0	3	0	1.00

Table 8. The number of naturally occurring insect species, single-island endemic insect species, and naturally occurring insect genera for each lifezone of all the Galápagos Islands. Also given are the species:genus ratio, percent endemicity, and average zonal range of the insects within each life zone.

Lifezone	Species	Archipelago Endemics	Single-Island Endemics	Genera	Species : Genus Ratio	Zonal Range	Endemicity (%)
Littoral	62	16	10	58	1.07	3.06	16.13
Arid	182	66	40	130	1.4	2.7	21.98
Transition	122	46	10	98	1.24	3.59	8.20
Humid Forest	140	51	25	105	1.33	3.23	17.86
Miconia	68	29	2	60	1.13	4.46	2.94
Pampa	84	32	13	68	1.24	3.91	15.48
Inversion	3	1	0	3	1	6.33	0

to make up a smaller component of the more humid regions, but their prevalence in these data supports the hypothesis that recent climatic disturbance may have eliminated much of the endemic fauna that may once have existed in these areas.

As a result of the instability of the moist upland areas in recent times, the more stable arid and transition zones have given the most opportunity for speciation and resulting endemism. The arid lowlands (which include the arid and transition zones) are also the largest ecological zone of the Galápagos Islands (Peck, 1996), making up the major portion of the land area of the archipelago, and are also found on all islands (Johnson & Raven, 1973). This stability, large area and ubiquity lead to the relative high diversity and endemism in the arid lowlands. Also, during Pleistocene glacials, the arid-zone was much larger and the moist-zone very much smaller than at present (Peck, 1996), and it is possible that the reduction in area of the arid lowlands over the past 10,000 years may have lead to over-saturation of this zone.

The littoral zone is a narrow belt, extending from the high tide line inland 10 meters or more as a zone of salt-tolerant vegetation of halophilic mangroves and succulents (Peck, unpublished). The zone has a low area and low vegetational diversity (Johnson & Raven, 1973), and is frequently subject to storm disturbance. Immigration in this zone is naturally the highest compared to the other, more inland lifezones, and storm disturbance and its small area create a high extinction rate. High immigration and extinction rates reduce the opportunities for endemism (Johnson & Raven, 1973), hence the smaller endemicity value (see table 7) when compared to the arid and transition zones. The percentage of native insect species (which are most likely to be oversea colonists) is also highest in the littoral zone.

The evergreen shrub zone receives more rainfall than the humid forest zone, yet table 8 shows a very low degree of endemism (2.78%). Again, the relative youth and small area of this zone due to Pleistocene glacials contributes to this lack of endemism. The evergreen shrub zone (where it exists) is dominated on most islands by the endemic melastome *Miconia robinsoniana* over much of its range, which may form almost pure stands of virtually impenetrable 3–4 m tall mesophyllous evergreen shrubs with an almost closed canopy (Peck, unpublished). Thus lack of vegetational diversity may contribute to the reduced degree of endemism, but perhaps more importantly, the impenetrability of much of this zone may have reduced sampling effort, leaving much of its insect fauna uninvestigated. The sharp drop in endemism in the evergreen shrub zone when compared to the surrounding humid forest and pampa zones appears to reflect lack of sampling effort more than any other factor. Small area, low plant diversity, and small numbers of insect on *Miconia* itself may be other contributing factors.

Above the evergreen shrub zone, the pampa zone shows a much higher degree of endemism (14.9%). The difference between the two zones may again be due to differing areas and lack of sampling effort and vegetational diversity in the evergreen shrub zone. The endemism of the pampa zone certainly does not seem to be out of concert with that of the humid forest zone. The pampa zone is a much more accessible habitat for collectors than is the evergreen shrub zone, and thus is probably more completely sampled. The inversion arid zone shows absolutely no endemism from the data available. This is not surprising, as its upper elevations do not support the rich vegetation seen in the more humid zones, nor the arid lowlands. It is also a

difficult area to access for collectors, and sampling in these areas may be appreciably less than in other zones.

Another measure that can give a more effective estimate of the amount of speciation that has occurred on an island is the species:genus ratio (Carlquist, 1974; Otte, 1994). The results of the maximum likelihood estimate of island area against species:genus ratio (figure 16) are disappointing, because it was expected that the larger islands would have higher rates of speciation than the smaller islands. The significance of the relationship is lower than expected. This lack of significance may be attributable to the relative youth of the Galápagos as well as recent disturbances to the moist lifezones of the islands caused by both humans and Pleistocene glacials.

The present Galápagos Islands are no more than 4.6 million years of age (MacFarlan & Cifuentes, 1995), and as evolution of new species undoubtedly requires a certain amount of time, the youth of the Galápagos imposes a limit to the amount of speciation that has occurred thus far. Disturbance of the moist lifezones of some of the higher-elevation islands by Pleistocene glacials, and more recently by humans, may have removed a substantial number of endemic species. This is suggested by the fact that the higher islands of the Galápagos (those which support the moist lifezones) have disproportionately fewer endemic species than the lower elevation islands which contain only the more arid but more stable lifezones. The lower significance of the

Figure 16. Species:genus ratios of smaller order insects plotted against the areas of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

relationship between elevation and species:genus ratio (figure 17) may reflect this effect.

Comparison of Results from Hawaii and the Galápagos

Effect of Island Area

Comparison of two or more species-area equations employing the power function allows for some degree of evaluation of the power function itself, particularly the meaning of the variables used in the generalized equation of MacArthur and Wilson ($S=cA^z$).

There is extensive literature on the meaning of the z -value (see Abbot, 1983; Connor & McCoy, 1979; Williamson, 1981). The z -value of a species-area plot represents the slope of the regression line (Abbott, 1983) which gives an indication of the rate of increase in species number with area. Many biogeographical studies have been performed using many different islands and island groups, and overall most z -values of species-area curves do tend to fall within the narrow range of 0.20 to 0.40 (Connor & McCoy, 1979). Given this strikingly common observation, the contention in the literature centers around whether or not the z -value of a species-area plot holds some unique biological meaning.

MacArthur and Wilson's (1967) theory of island biogeography explains variations from the predicted range as a function of the degree of isolation of the island(s) under observation. Thus, they contend that the slope of the curve serves as an index of isolation. The argument is that in a non-isolated, small sample area, such

Figure 17. Species:genus ratios of indigenous smaller order insect species plotted against the maximum elevations of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

as that found on a continent, this sample area will contain more species than an island of the same size because it contains small numbers of individuals belonging to species that are not well-adapted to the sample area but persist in other places close at hand (MacArthur & Wilson, 1967). These individuals may not actually form viable populations within the sample area. However, on an island (especially an isolated island) such “transient” individuals have a lesser chance of “wandering” into the sample area (in this case, an entire island) as they would have to cross the open sea to reach the island. Since many transients are bound to be encountered in the non-isolated areas of continents, independent of area, species numbers in small areas of continents will be inflated, the result of which is a depression of the slope of the log-species/log-area curve (Connor & McCoy, 1979). Obviously, the more isolated an island is from other land masses, including neighbouring islands, the less the chance of a transient individual being collected in a sample, and the species collected on isolated islands are more representative of the indigenous fauna.

Comparison of the species-area curves for the Galápagos Islands and the Hawaiian Islands supports this hypothesis. Using the Hawaiian data set, plotting the log-transformed values for insect species number against the similarly transformed values for area yields the equation:

$$S=414.8 A^{0.420}$$

A similar analysis using the Galápagos data set yields the equation:

$$S=60.5 A^{0.346}$$

The z -value for the Hawaiian data (0.42) is substantially larger than that of the Galápagos (0.35), and well above the range of 0.20 to 0.35 predicted by the

equilibrium theory. This elevated z -value can be explained by the degree of isolation of the Hawaiian Islands. Of all the high volcanic islands of the world, those of the Hawaiian chain are the most remote from any continent or from other islands of appreciable size (Carlquist, 1970). The Hawaiian Islands lie some 3800 km west of continental North America and the same distance from the neighbouring high islands (Howarth & Mull, 1992) while the Galápagos Islands lie a relatively short distance (800 km) west of Ecuador (MacFarlan & Cifuentes, 1995). According to equilibrium theory, the high z -value of the Hawaiian Islands in comparison to the Galápagos, is accounted for by the extreme isolation of the former.

Since the equilibrium theory of biogeography hinges on the idea of a balance between immigration and extinction, isolation is reflected in the z -value because a high degree of isolation equates to a lowered rate of immigration (MacArthur & Wilson, 1967). This explanation seems to give the z -value a definite biological meaning as an index of isolation, but the equilibrium theory itself suggests another possibility -- that elevated z -values may also be due to high extinction rates, or a combination of high extinction rates and low immigration rates (Abbott, 1983). If it could be shown that the extinction rates of insects in the Hawaiian Islands is substantially greater than that in the Galápagos Islands, then the suggestion that the z -value is an index of isolation becomes less concrete. The Galápagos island chain is the world's best preserved and protected tropical oceanic archipelago (Peck, 1991b), while the Hawaiian Islands are much more heavily populated, and conditions there have changed drastically since the arrival of humans (Zimmerman, 1948). Thus, it is reasonable to believe that extinction rates in the Hawaiian archipelago are now substantially higher than in the Galápagos.

The present data sets, however, do not provide this information, and this idea remains a good subject for future study.

Despite the arguments presented above, there remains the possibility that the slope of the species-area plot holds no unique biological meaning. Connor and McCoy (1979) made the contention that the observed narrow range of z -values could be better explained to result from the characteristics of the regression system, and not from underlying log-normal relative-abundance distributions. Through examination of the statistical methods of regression analysis and regressions of relationships other than the species-area plot, they concluded that such a narrow range is not uncommon, even for measures of completely different biological parameters. Although there is plenty of evidence to suggest that the slope represents degree of isolation and/or extinction, researchers must not lose sight of the possibility that the slope of the species-area curve has no real meaning.

As most z -values tend to fall in a quite narrow range, the natural extension of studies of species-area relationships is whether or not a general power function could be devised which could predict the number of species on any island. By use of a generalized equation ($S=cA^z$), MacArthur and Wilson (1967) imply that this equation can be readily adapted for use universally, as long as the z -value and the constant, c , are known. However, there is no indication in the literature that the c - and z -values can be readily deduced before running a regression analysis. Also, these values change when different taxa are considered. Since there appears to be no clear way of obtaining these values beforehand, the predictive nature of the generalized power function seems very limited.

That is not to say, however, that the power function and the equilibrium theory are not useful models. Many inferences about such processes as colonization, species composition, and evolution may be drawn by examination of the species-area curve and through comparison to similar analyses of other islands and/or taxa. The importance of dispersal, evolution and environmental heterogeneity on the pattern of biogeographical distributions all come together in the species-area effect (Williamson, 1988). Providing a careful interpretation is employed, many patterns and trends which affect the structuring of an island community may be uncovered.

Effect of Island Elevation

Comparison of the species-elevation relationship of the Galápagos data (figure 12) to that estimated from the Hawaiian insect data shows a less significant relationship. This difference may reflect the history of the Galápagos Islands, as the climate has not been as constant in the higher elevations than it has been for Hawaii. The islands experienced severe bouts of aridity during times of Pleistocene glacial maxima in the northern hemisphere (Peck, 1991b). This means that the moist-humid forest zones on the islands were much reduced in size or eliminated as recently as 10,000 years ago. This suggests that the inhabitants of the more humid upper elevations of the higher islands are post-Pleistocene immigrants, and that these regions may not have had sufficient time to have reached saturation. The number of species in the higher regions of the Galápagos, therefore may be depressed, reducing the significance of the species-elevation relationship.

Effect of Island Age

In comparison with the Galápagos Islands, youth and past climatic instability are not such dominant forces in the Hawaiian Islands. The species-island age estimates performed on the Hawaiian data set show a higher significance than those performed on the Galápagos data set. In the case of the Hawaiian Islands, the relationship between island age and species number is a negative one -- as islands age, their species diversity decreases due to their reduced area. It is quite possible that this significant relationship has been made possible due to the greater age of the Hawaiian archipelago (which range up to 28 million years in age) allowing for equilibrium conditions, particularly on the older islands, and the relative stability of the climate on the Hawaiian Islands.

Also, the data on the ages of the Hawaiian Islands are far more complete than those of the Galápagos. Only fourteen of the islands in the Galápagos Islands are reliably dated, while the islands of Hawaii have been the subject of many more geological studies. Attempts to date the rocks of the Galápagos have met with several difficulties: the younger lava flows tend to cover the older ones, erosion in most parts of the islands is too slow to cut through to the older interior, potassium, the parent element whose radioactive decay to argon is most commonly measured in age determinations, is present in only very small quantities in most Galápagos lavas, and the dry, rubbly lava flows that make up so much of the islands have daunted much diligent searching for the islands' oldest rocks (Simkin, 1984). If these difficulties are

overcome in the future, and more research is conducted into dating the islands, then more conclusive species-island age analyses will be made possible.

Insect Speciation and Adaptive Radiation

Although analysis of the Galápagos data set produced a significant relationship between number of single-island endemic insect species and island area (see figure 14), in comparison, the data from the Hawaiian Islands shows a substantially more significant relationship between these two variables (see figure 5). Even more striking was the difference in significance of the species/genus:area relationships for the Galápagos (see figure 16) and Hawaii (see figure 7).

In comparison with the Hawaiian Island data, however, the weak relationships obtained through analysis of the Galápagos data may be explained. The relationship between island area and species:genus ratio for the Hawaiian Islands (figure 7) was found to be highly significant. This significance implies that two factors are important for promoting speciation: habitat diversity and physical isolation. As discussed previously, an island's habitat heterogeneity is related to its area. Thus, as the area of an island increases, so does its variety of habitats. With a variety of habitats available for exploitation comes greater opportunity for colonizing species to diversify and enter these new adaptive zones. Greater area also allows for larger population sizes, contributing to the survival of populations of new species.

Physical isolation is also reflected in the area of an island. The more complex topography associated with the larger islands provides physical barriers, keeping populations isolated from each other and allowing them to evolve independently, or

semi-independently (MacArthur & Wilson, 1967) as gene flow between populations is discontinued or limited. Both factors (habitat diversity and topographical isolation) should also be reflected in the elevation of an island, and appropriately a significant relationship was found between island elevation and the species:genus ratio (see figure 8) for the Hawaiian Islands.

With the highly significant results obtained from the Hawaiian data set, it is somewhat surprising that the Galápagos data did not show similar trends in its species:genus ratios. A potential factor which confounds the relationship may be the youth of the moist lifezones in the archipelago. The higher islands which support these lifezones have disproportionately fewer species, particularly endemic species, which depresses the relationship.

Overall, the Hawaiian insect fauna shows a much higher species:genus ratio than does that of the Galápagos (9.59 and 1.83 respectively). The most obvious cause for this large difference is that the Galápagos data set contains only the “smaller orders”, excluding holometabolous orders (see table 9 for species:genus ratios for various insect orders in the Galápagos). These orders, excluded in the Galápagos data, show the highest species per genus ratios in the Hawaiian data (see table 2) and

Table 9. Species:genus ratios of the smaller insect orders of the Galápagos Islands. Only those orders whose species:genus ratio exceeds 1.0 are given.

Order	Species:Genus Ratio
Blattaria	2.33
Homoptera	2.24
Hemiptera	1.95
Orthoptera	1.83
Collembola	1.52
Isoptera	1.33
Odonata	1.33

their absence from the Galápagos data must contribute to the depressed species:genus ratio. These “higher” orders contribute significantly to the endemism of the Hawaiian Islands, and must also contribute similarly to that of the Galápagos, as they represent more evolutionarily plastic and successful groups of insects.

Even with the exclusion of the higher orders from the Hawaiian data, however, the species:genus ratio remains relatively high (7.16), reflecting a much higher degree of diversification in the smaller orders. Much of the difference between the species:genus ratios between Hawaii and the Galápagos may be attributable to the greater isolation of the Hawaiian archipelago. In general, the overall diversity of Hawaii is not so remarkable as the fact that some of its genera are rich in species (Otte, 1994). In comparison, the Galápagos Islands are not nearly as species-rich and genus-poor. The overriding factor creating this difference may be the great distance of the Hawaiian Islands from source areas. As all the native terrestrial insect fauna originated from colonists that have had to travel across such a large stretch of open ocean, few lineages have contributed to the final composition of the insect fauna, thus creating much opportunity for these lineages to diversify to fill empty niches. The Galápagos, in contrast, is substantially closer to the mainland than Hawaii, and consequently has had a higher immigration rate of new colonists, making its fauna less disharmonic.

Differences in the insect orders analyzed and degree of isolation withstanding, the lower degree of speciation observed in the Galápagos when compared to Hawaii may also be attributed to the relative youth of the archipelago. The Galápagos Islands are no more than 5 million years old (MacFarlan & Cifuentes, 1995), while the

Hawaiian Islands range up to 28 million years in age, and the island chain has been in existence for over 70 million years (Howarth & Mull, 1992). With time being a prerequisite for speciation, there has obviously been more time for the evolution of new species in the Hawaiian archipelago than in the Galápagos Islands.

Many biogeographical studies of islands suggest that speciation and adaptive radiation in insular environments can be extremely rapid (Paulay, 1994), and evolution in such environments is often described as “explosive”. Colonists arriving in an environment with relaxed competition and predation, and which has plenty of empty niches, are thought to evolve to exploit these opportunities at a remarkable rate. Thus, the early history of an island fit for colonization is marked by accelerated rates of speciation. It is difficult to deduce rates of speciation in the Galápagos and Hawaiian archipelagos from the data presented here, but the youth of these islands (relative to continental areas) coupled with the “species swarms” present (particularly in the Hawaiian archipelago) suggest that the process of speciation occurs much more rapidly than in continental areas, with rates of speciation declining as a particular island ages. The relationship between island age and species:genus ratio in the Hawaiian Islands (figure 9) appears to support this assertion. However, such an explanation ignores the effects erosion and extinction may have on older islands.

The uniform drop in the species:genus ratio on the older islands of Hawaii is not easily explained by a decline in the rate of speciation. Rather, this uniform decline would more likely be attributable to loss of habitat and resulting extinction. The older Leeward Islands of Hawaii have eroded to the point that they no longer can maintain the higher elevations necessary to support wet forest habitats. As these habitats in the

higher islands are often richer in species than lower, drier regions (Carlquist, 1965) and the general pattern of adaptive radiation seen on oceanic islands is that of diversification from drier regions into wetter areas at higher altitudes (Carlquist, 1970), a high proportion of species inhabiting wet forest areas must be the products of adaptive radiation. Thus, when these areas were eventually eroded away, so were the species within them, eliminating a large proportion of the products of adaptive radiation causing the uniform drop in the species:genus ratio observed in the older islands. Thus, the higher species:genus ratio found on younger islands does not reflect higher rates of speciation, but rather persistence of the products of speciation. Extinction due to competition and destruction of habitat is a much stronger force on older, more saturated islands.

The lack of significance in the relationship between maximum island age and species:genus ratio observed in the Galápagos Islands (figure 18) supports this hypothesis. If much of their wetter habitats were eliminated in by climatic change in glacial periods, it would be expected that persistence of moist forest habitats on the higher, younger islands would not contribute as much to an increased species:genus ratio on these islands, and that the islands as a whole should show more uniformity in their species:genus ratios despite differences in age. The slope of the curve (see figure 18) does not, in fact, differ significantly from zero, suggesting that rates of speciation do not differ between the islands despite the differences in age. Assuming a more

Figure 18. Species:genus ratios of the smaller order insect species plotted against the maximum island ages of the Galapagos Islands, with a line fitted by maximum likelihood estimation.

stable climate in the future, the relationship between island age and species:genus ratio should become more pronounced as the depauperate wetter regions of the islands become approach saturation with species. However, there is no reason to think that glacial-interglacial climatic changes are unlikely to continue.

Summary/Conclusions

The above analyses are based on some of the largest data sets available for island faunas. They support various theories of island biogeography and hopefully have added some insight into this already voluminous field of study. The significance of the relationship between insect species number and island area reflect that habitat diversity is an important factor controlling the number of different species which can co-inhabit a particular island. Higher extinction rates on smaller islands may also contribute to the species-area effect. There appears to be no convincing evidence, however, that area *per se* has an effect on species numbers. The species-area effect is unlikely to be substantially due to amount of sampling effort in this case, due to the completeness of the data sets analyzed.

The power function was found to be the best for the data studied in this investigation. This is not to say, however, that the power function is necessarily the best model to use in all cases, but rather it is appropriate to use whichever model provides the best fit to the data.

Comparison of the z -values for the species-area power functions of Hawaii and the Galápagos supports the hypothesis that the z -value acts as an index of isolation (resulting in lowered immigration rates) but the possibility exists that it may also reflect increased extinction rates. Further investigation is required to isolate these factors.

Overall, the predictive power of the power function seems limited. Rather it has a *post facto* utility, as many trends of colonization, species composition and evolution may be elucidated through careful analysis of it.

Elevation proves to be a good predictor of insect diversity. Compared to measures of island area, elevation appears to be a more exclusive measure of habitat heterogeneity on oceanic islands as it encompasses less factors which affect species diversity than do measures of island area. Therefore, area proves to be a better predictor of species diversity because the measure of area incorporates more factors which affect species diversity.

Island age proves to be a poor predictor of species numbers, as it is confounded by the effects of decreasing island area as an island ages and subsides through erosion. Recent extinction on the Galápagos Islands further reduces its suitability as a predictive parameter.

Recent disturbance in the Galápagos Islands appears to have reduced species numbers, perhaps below saturation. This poverty reduces the strength of species-area, species-elevation and species-age relationships. These relationships are stronger in the Hawaiian Islands due to their greater age (and subsequent saturation) and relative climatic stability.

Analyses of number of single-island endemic insect species as well as species:genus ratios suggest that endemism, and hence speciation, appears to be affected by an island's area, as the number of habitats/niches available for exploitation fosters adaptive radiation and speciation, as well as isolating mechanisms provided by an island's topography. Speciation in the Galápagos appears to have been hindered by

climatic change in the higher elevation zones. An archipelago's isolation stimulates speciation, as less immigrants are available to fill adaptive zones, providing greater opportunity for existing species to diversify.

Speciation is not necessarily an "explosive" event marked by an increased rate of adaptive radiation when organisms are presented with opportunity for adaptation. Rather, speciation appears not to proceed at a rate fundamentally different from that of continental areas. Instead, species of relatively young, isolated environments are more likely to survive than in more saturated continental environments. This prosperity is ephemeral, however, and in the island groups studied, the more recent products of evolution will eventually disappear naturally as the moister regions which the majority inhabit are eliminated through erosion and subsidence.

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