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Diversity and species breadth of carrion insect communities along an altitudinal gradient

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Abstract

Detritivores play a crucial role in nutrient cycling within tropical forests by returning nutrients to the ecosystem. The purpose of this study was to inventory carrion feeding insect communities and show the change in insect diversity along an altitudinal gradient. Five sites were visited every 200m along the gradient from 800 m to 1600m using carrion as bait to attract insects. A total of 1507 individuals were collected, representing 21 species. Six of the ten diversity comparisons using a variation of the Shannon-Weiner Diversity Index and modified t-tests were significantly different ($p < 0.05$). The number of individuals was found to decrease as elevation increased (simple regression, $p = 0.0158$, $r^2 = 0.01$). It is believed that the lower elevations harbor a higher diversity and species richness due to unfavorable conditions at the higher elevations.

Resumen

Descomponedores tienen un lugar crucial en el ciclo de nutrientes en los bosques tropicales, devolviendo los nutrientes de nuevo al ecosistema. El propósito de este estudio fue hacer un inventario de las comunidades de insectos en animales descompuestos carrion y mostrar los cambios en la diversidad en un gradiente altitudinal. Cinco lugares fueron muestreados cada 200 metros en el gradiente de 800 metros a 1600 metros usando cebo del carrion para atraer insectos. Un total de 1507 individuales fueron recogidos para un total de 21 especies. Las se encontraron diferencia significante entre seis de los diez comparaciones de la diversidad a ($p < 0.05$) usando índice de diversidad de la Shannon-Weiner Diversity Index y una prueba de t para comparaba. El número de disminue al almientos elevación aumentó ($p = 0.0158$, $r^2 = 0.01$). Se cree que las elevaciones más bajas tienen una riqueza mayor de la diversidad debido a un clima más cálido y más frío en las elevaciones superiores.

Introduction

Carcasses and discarded animal parts are nutrient-rich resources that sporadically fall upon habitats all over the world (Janzen 1983). It is within tropical forests that the cycling of these nutrients is done most efficiently. Nutrient recycling in tropical forests is able to recover 60-80% of most nutrients (Terborgh 1992). It is critical that this recycling is done efficiently because the majority of minerals available to tropical ecosystems are tied up in dead and living organic systems (Went and Stark 1968). Trapped nutrients within dead animals are released in large part by the activities of necrophagous bacteria, fungi, and animals (Cornaby 1974). More specifically, carrion insects play a pivotal role in the decomposition of these nutrient-rich resources. Such insects assist in converting dead animal material into simpler substances that can be reintroduced into the trophic structure for use by other organisms (Borror et al. 1989).

The carrion insect’s purpose is much less altruistic than the idea of nutrient cycling and restoration of ecosystem productivity. Their food resources are highly ephemeral in time and space (Klein 1989) and carrion insects depend on these limited resources for food and support of larval development. Specifically, dipterans and certain carrion beetles use carcasses as a host for their eggs (Borror and Delong 1971). The insect’s dependency creates a high local abundance and diversity at these short-lived carcasses. Predation on dipteran larvae by non-dipteran scavengers (e.g. formicids, beetles) prevent dipterans from overwhelming the community and help to maintain a high diversity in this ephemeral community (Kneidal 1984). Houston (1987) reported ants taking away larvae and that this predation seemed to prevent the baits from being totally consumed by maggots. In general, dipterans, adult formicids, and adult scarabids are the most important detritivores associated with carrion (Cornaby 1974).

The diversity of carrion insects is not solely affected by inter- and intraspecific competition. Insects are intimately associated with their respective environments, being so specifically adjusted to them that any significant change in conditions exerts a substantial influence in their spatial and temporal distributions (Fleishman et al. 1998; Townsend 1924). Entomologists who have collected in the Central American tropics record substantial variances between insect species diversity, composition, and abundance when sampling at adjacent habitats (Schoener and Janzen 1967). Inhospitable temperature and moisture conditions or lack of required biotic conditions at higher altitudes may largely prevent the movement of carrion feeding insects to these elevations. Altitudinal gradients, in particular, strain the spatial and temporal distributions of myriad organisms, including insects (Meyers and Giller 1988).

The purpose of this study was to take an inventory of carrion insect communities along an altitudinal gradient and attempt to show the change in insect diversity along the gradient. An additional intent of this survey was to show certain patterns that follow an altitudinal gradient. These patterns include (1) a decline in the abundance and diversity of most insect taxa at higher elevations and (2) altitudinal peaks in specific family abundance according to their tolerance ranges and physical conditions.

Materials and Methods

Study site

Research began on April 10th, 2003 and continued until May 12th, 2003. The research was conducted on an altitudinal gradient from 800 m in San Luis to 1600m by la Estación Biológica de Monteverde, Puntarenas, Costa Rica. Five sites were chosen 200 m apart in elevation. They started at 800m and were recorded using an altimeter. Each site was in a well-forested area to control for habitat heterogeneity. The sites 800 m and 1000m were in premontane moist forest in lower San Luis. The site 1200m was located in premontane moist forest in upper San Luis at the base of La Trocha. The site 1400m was located in premontane wet forest on a hillside overlooking San Luis. The site 1600 m was located in lower montane wet forest (Haber 2000) just above la

Estación Biológica de Monteverde. At each site, three separate points were placed at least 50 m apart to prevent insects from moving between points.

Data Collection

A piece of raw chicken (breast and leg) was used to attract insects. Chicken was placed in a bucket for two days before it was placed in the site.

The first site recorded was at 800m. Three equally sized chicken pieces were placed on rocks 50m away from each other. The rocks serve to keep the chicken from direct contact with the ground where ants may prevent other insects from arriving. In Costa Rica formicids tend to arrive sooner than other invertebrates and remain with the carcass preventing other insects from establishing themselves (Payne 1963). Ants were not taken into account for this experiment.

Observation started at 0800 hrs. and insects were collected and counted from each of the three sites every 15 minutes until 1200 hrs. Insects were caught and placed into containers according to which one of the three points they were captured. A net or tweezers were used to catch the insects, the tweezers being easier for the more sessile organisms. An insect was only placed into 70% alcohol and collected for the reference collection if it could be identified as a new morpho species. This process was repeated a total of three times at 800 m and repeated three times at every other elevation.

New species that were collected were taken back to la Estación Biológica de Monteverde for identification using guide books (Borror and Delong 1971, Solis 1999, Zumbado 1999).

Data analysis

Each elevation's insect individuals were totaled and identified to respective families and morpho species. A Shannon-Weiner Diversity Index was executed for each site and modified t-tests for diversity indices (Zar 1984) were used to find differences between the diversity of each site. Number of individuals at separate sites were graphed against elevation and placed into a linear regression.

Results

Twenty-one different species of carrion insects were found along the altitudinal gradient (Table 1) for a total of 1508 individuals. The number of individuals found per species ranged anywhere from one to 200 at any given point. The number of morpho species found at a site ranged from seven to thirteen (Fig. 1).

The highest diversity of morpho species was found at site 800m and the lowest diversity at site 1600m. The sites 1200m and 1600m had diversity indices that were substantially lower than the sites 800 m, 1000 m, and 1400 m (Fig. 2). T-tests were performed between all five site diversity indices for a total of ten tests. A positive relationship was found between the sites 1200 m and 1600m paired with sites 800m, 1000m, and 1600m (Table 2).

The highest number of individuals was found at site 800m and the lowest at site 1000 m (Fig. 3). There was a negative relationship between number of individuals and elevation (Fig. 4, simple regression, p = 0158, r^2 = .01).

Order Choleoptera was represented by nine morpho species, Hymenoptera and Diptera by five morpho species, and Hemiptera and Lepidoptera by one morpho species (Table 1). The three most abundant morpho species were Calliphoridae (Blow Flies), Sarcophagidae (Flesh Flies), and *Agelaia panamaensis* (Vespidae) (Fig. 5 and Fig. 6).

Calliphoridae was most abundant at site 800 m and least abundant at site 1200m. There was a negative relationship between number of individuals and an increase in elevation (simple regression, $y = 81.2 - 0.039x$, $n = 15$, $p = .002$, $r^2 = .877$). Sarcophagidae was most abundant at 1200m and least abundant at 800m. *Agelaia panamaensis* peaked in abundance at 1000 m and was lowest at 1400 m (Fig. 5 and Fig. 6).

Discussion

One intention of this research was to inventory carrion insects along an altitudinal gradient. 21 different morpho species were identified; however, they were represented by a disproportionate number of individuals. Seven of the 21 morpho species were represented by only one individual (Table 1). These single individuals had a large impact on the total number of morpho species found at a site and on the overall diversity.

The lowest diversity being found at the 1600 m corresponds with the hypothesis that an increase in elevation will result in a decrease in diversity. The substantial drop in diversity at site 1200 m does not correspond with this hypothesis (Fig. 2). Site 1200 m had 11 morpho species, which is the second lowest overall (Fig. 1). Contrary to this, site 1200 m had 322 total individuals, which is the second highest (Fig. 3). However, 200 of these individuals were of the same morpho species (Sarcophagidae, Table 2). A low number of total morpho species and a disproportionately large number of a single individual contribute to the low diversity of this site.

The two lower diversity indices at sites 1200 m and 1600 m paired with any one of the three higher diversity indices at sites 800 m, 1000 m, or 1400 m supported a positive relationship when compared in a t-test. The four other diversity index comparisons that can be made were not found to be significant because the diversity indices were too similar (Fig. 2).

The diversity indices of sites 800 m and 1000 m are nearly identical (Fig. 2), but the number of individuals at each site is notably different. Site 1000 m had the lowest number of individuals with only 265. The low individual count can be attributed to 1000 m having the least number of Calliphoridae and Sarcophagidae, the two most abundant species at every site (Fig. 6). Although site 1000 m had the lowest number of individuals it also had the highest number of total morpho species (Fig. 1). The high number of morpho species and increased evenness between the two most abundant species (Table 1, Fig. 6) account for the discrepancy between number of individuals and diversity.

Even though there was an incongruity at site 1000 m (Fig. 3), there was still a significant negative relationship between the number of individuals and elevation

(Fig. 4). This trend may be explained by "Rapoport's Rule". Rapoport proposed that in the tropics animals have restricted home ranges due to their inability to cope with variations in temperature. Rapoport applies this to a latitudinal gradient, but it can also be applied to an altitudinal gradient. As elevation increases the mean annual temperatures decrease (Coen 1983) and areas used by insect communities are restricted due to these colder temperatures. Restricted communities account for fewer individuals caught per point at sites of increased elevation (Fig. 1 and Fig. 3).

Although there were obvious restrictions on the insects at certain sites, Calliphoridae (Blow Flies), Sarcophagidae (Flesh Flies), and *Agelaia panamaensis* (Vespidae) remained abundant throughout (Fig. 5 and Fig. 6).

Agelaia panamaensis peaked at two different elevations (Fig. 5), however, this trend was not found to be significant. These peaks may be attributed to the fact that these two points were in continuous forest aiding in an individual insect's movement. Their ability to find carrion rapidly (Cornaby 1974) suggests they have an essential role in carrion decomposition. More research on *Agelaia panamaensis* would help establish a better understanding of its role in carrion insect communities and about the communities as a whole.

Calliphoridae and Sarcophagidae showed alternate trends in the elevations where they were most abundant (Fig. 5 and Fig. 6). One explanation for this is these two flies thrive within different abiotic conditions. For example, Calliphoridae may thrive in the lower elevation because of the drier conditions while Sarcophagidae prefers the wet conditions of the higher elevations. Another explanation could be Calliphoridae and Sarcophagidae are experiencing niche partitioning through competition of similar resources. Since these particular detritivores are so common, a decrease in their abundance may have a profound effect on nutrient cycling (Hogue 1993).

Nutrient cycling of dead organic material is of paramount importance in tropical forests. Detritivorous invertebrates aid in the nutrient cycling by increasing the rate of nutrient availability, which is then incorporated back into the trophic structure of the community. Any decrease in the carrion insect population through elevation increase, or otherwise, decreases the rate at which these nutrients are available. This lack of readily available nutrients negatively affects all organisms tied to the community food web.

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Table 1. Number of individuals found in any given taxa recorded at five elevations.

	800m	1000m	1200m	1400m	1600m
Sphecidae	43	5	-	-	-
Vespidae 1	9	1	8	2	-
Agelaia panamaensis (Vespidae 2)	21	36	16	12	30
Trigona 1 (Apidae)	3	1	-	7	-
Trigona 2 (Apidae)	6	21	11	31	1
Tephritidae	10	3	7	4	-
Syrphidae	-	-	-	3	15
Sarcophagidae	58	70	200	147	155
Calliphoridae	174	114	70	78	74
Bombylidae	-	2	-	-	-
Scarabaeidae 1	1	-	-	-	-
Scarabaeidae 2	-	4	2	-	-
Chrysomelidae	1	-	-	-	-
Staphylinidae	8	1	3	2	7
Nicrophorus quadrimaculatus (Silphidae)	-	-	-	2	-
Oxelyrum discicolle (Silphidae)	-	-	-	1	-
Histeridae	6	6	3	9	-
Erotylidae	-	1	-	-	-
Choleoptera unknown	-	-	1	-	-
Pyrrhocoridae	-	-	1	-	-
Pteronymia simplex simplex (Nymphalidae)	-	-	-	-	1

Table 2. P-values for modified t-tests comparing Shannon-Weiner diversity indices of insects that arrive to carrion at different elevations in Monteverde, Puntarenas, Costa Rica. *indicates comparisons of elevations that are significantly different

Elevation (m)	1000	1200	1400	1600
800	> 0.50	0.001*	0.5	0.001*
1000		0.001*	0.5	0.001*
1200			0.01*	>0.50
1400				0.001*

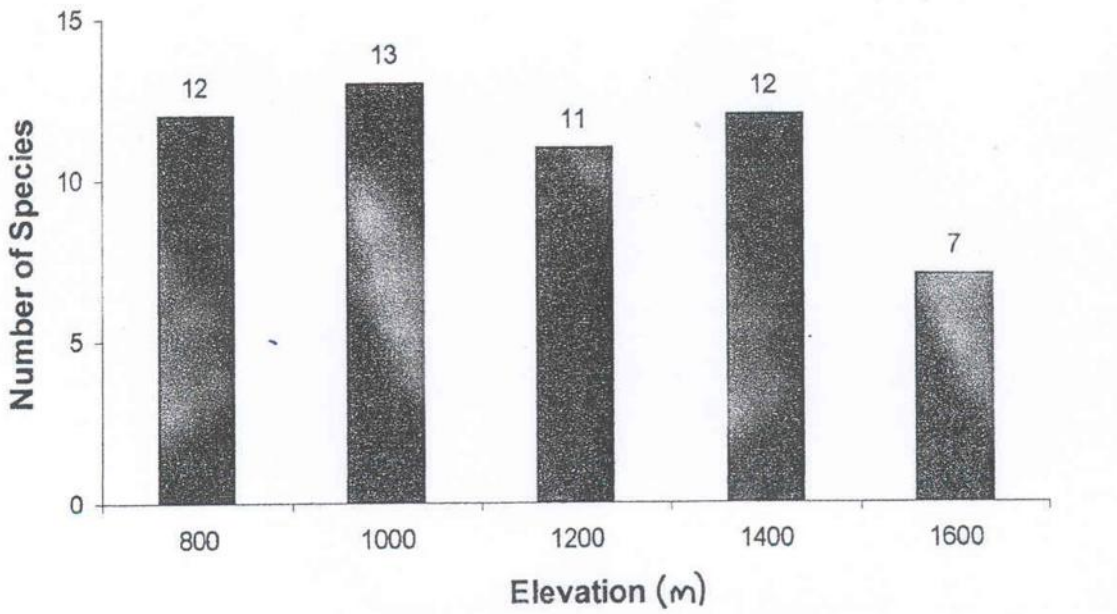

Figure 1. Relative species richness of carrion insects along an altitudinal gradient from 800m to 1600m in the Monteverde, Costa Rica area. The species richness peaks around mid-elevations.

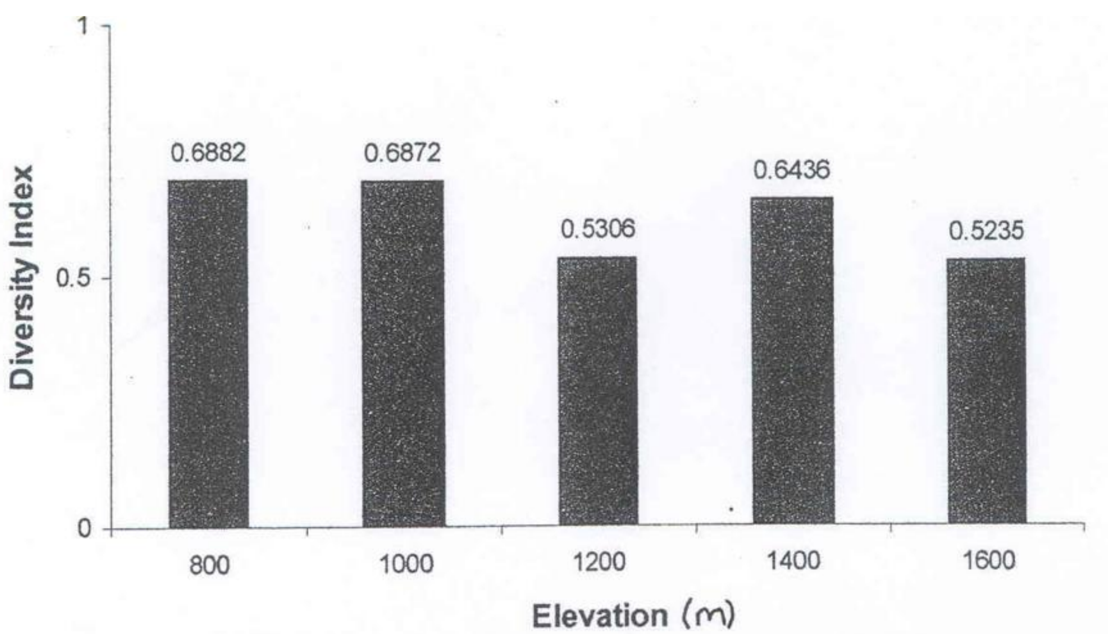

Figure 2. Shannon-Weiner Diversity Indices of carrion insects along an altitudinal gradient from 800m to 1600m in the Monteverde, Costa Rica area. The highest diversities were found in the two lowest elevations. Site 1200m is an outlier with an unexpected low diversity.

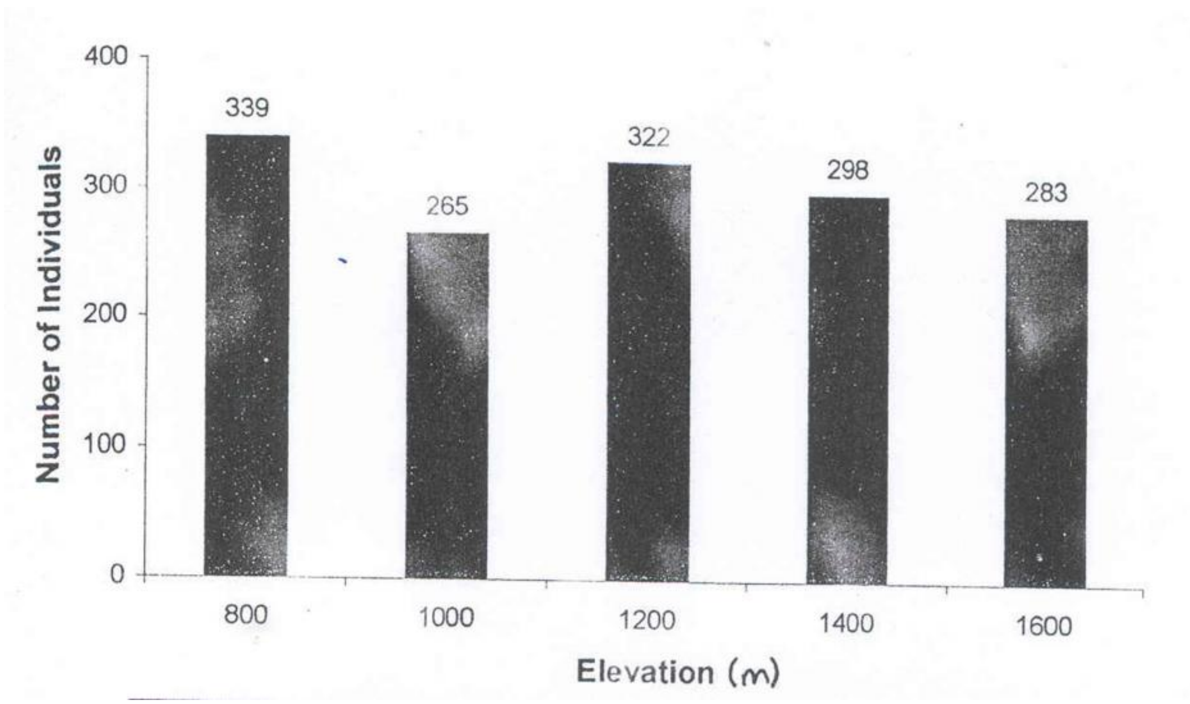

Figure 3. Relative number of individuals of carrion insects along an altitudinal gradient from 800 m to 1600m in the Monteverde, Costa Rica area. The highest number of individuals was found at the lowest elevation and the least number of individuals found at the highest elevation. There was a incongruity in individuals at 1000m altering the trend of decreasing individuals with increasing elevation.

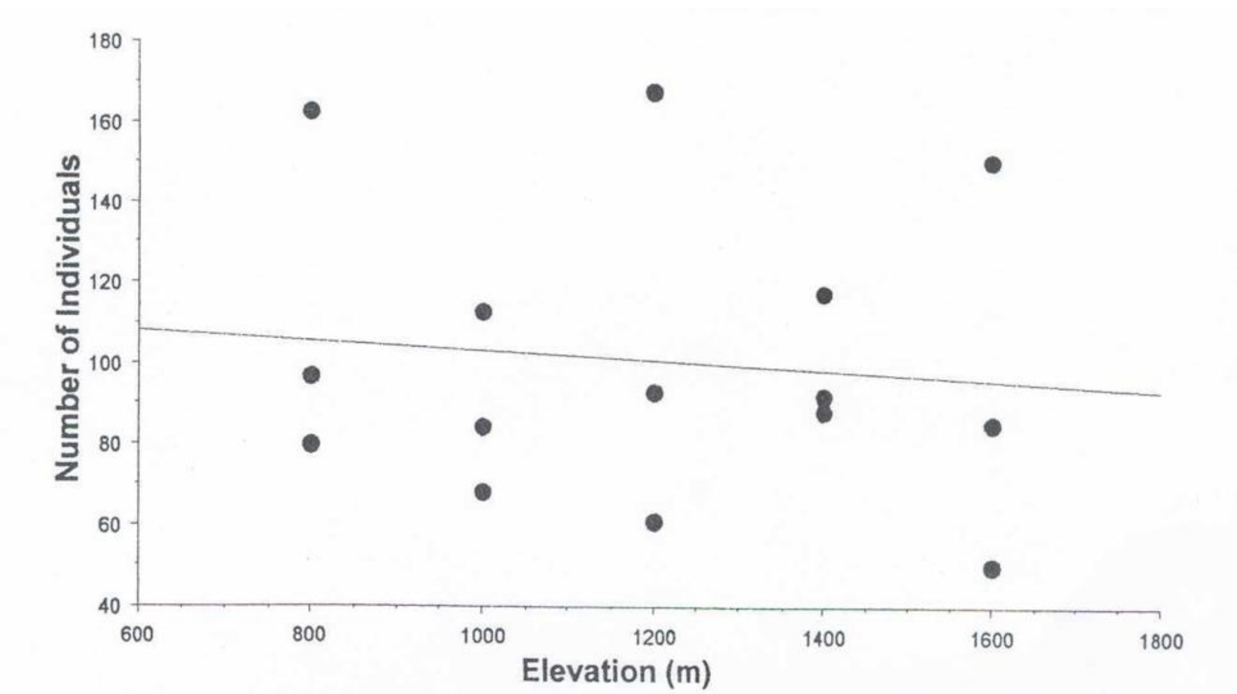

Figure 4. As elevation increases from 800 m to 1600m the total number of carrion insect individuals decreases (Simple-regression, p = 0.0158, r^2 = 0.01). At each site insect communities were recorded three times, each circle being a separate number of individuals for a community.

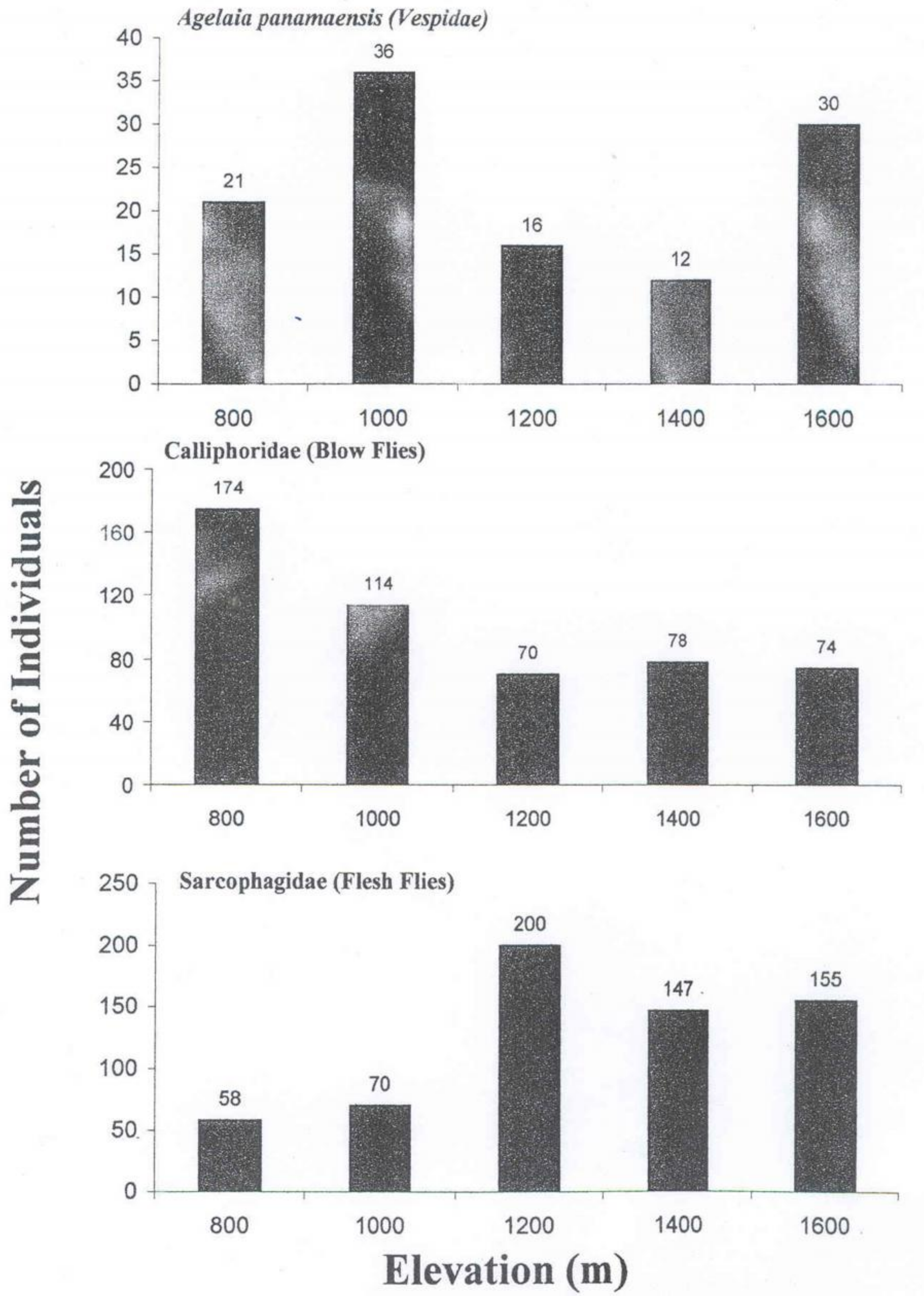

Figure 5. Relative species abundance of the three most abundant insects found along an altitudinal gradient. The first being a common necrophagous wasp (Vespidae) and the other two, flies (Diptera).

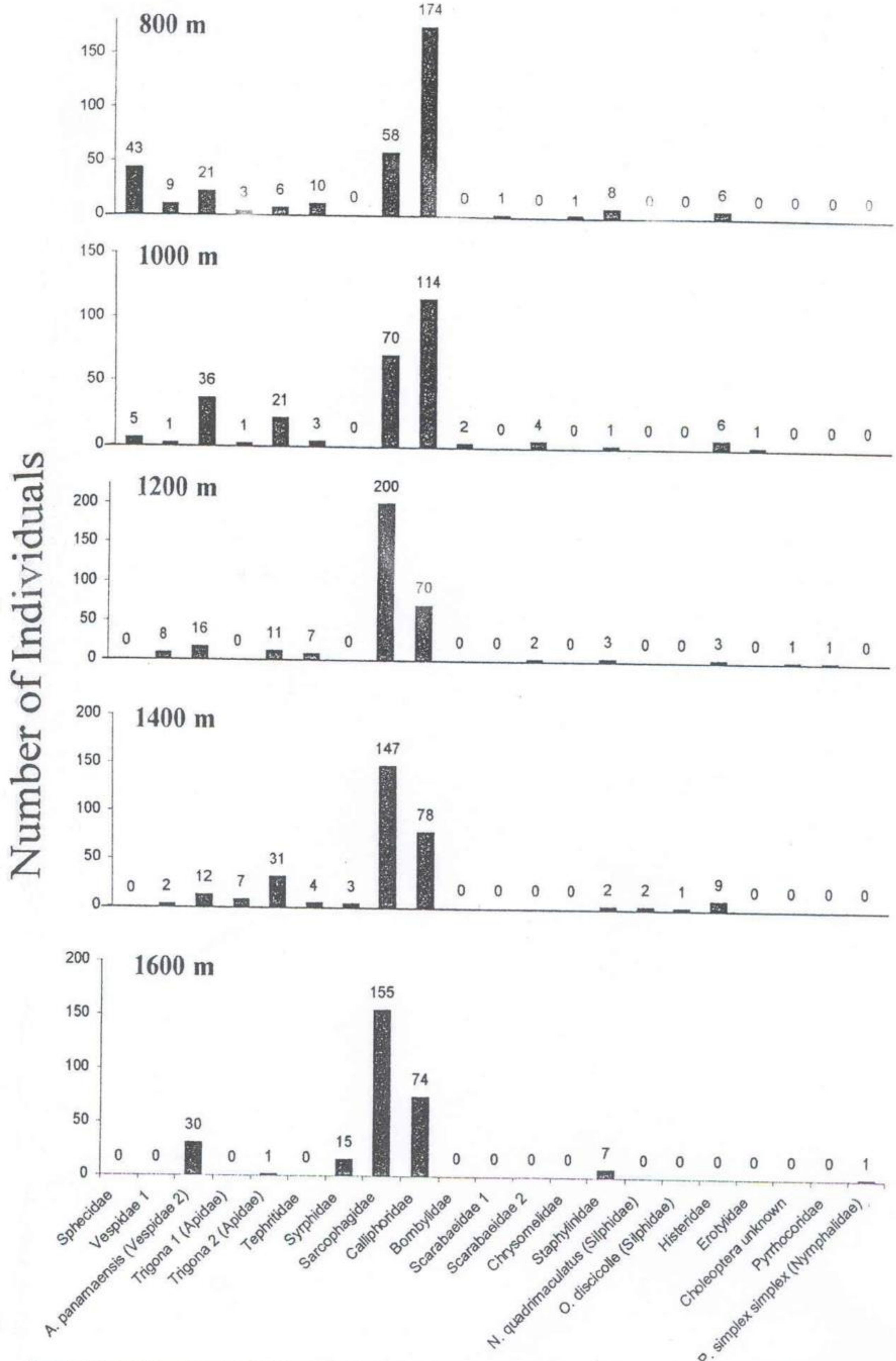

Figure 6. Relative species abundance of carrion insects collected along an altitudinal gradient from 800 m to 1600 m in the Monteverde, Costa Rica area.