GAMMA DIVERSITY: DERIVED FROM AND A DETERMINANT OF ALPHA DIVERSITY AND BETA DIVERSITY. AN ANALYSIS OF THREE TROPICAL LANDSCAPES

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RESUMEN

Utilizando tres grupos taxonómicos en este trabajo examinamos como las diversidades alfa y beta influyen en la riqueza de especies de un paisaje (diversidad gamma), así como el fenómeno recíproco. Es decir, como la riqueza en especies de un paisaje (un fenómeno histórico-biogeográfico) contribuye a determinar los valores de la diversidad alfa por sitio, por comunidad, la riqueza acumulada de especies por comunidad y la intensidad del recambio entre comunidades. Los grupos utilizados son dos subfamilias de Scarabaeoidea: Scarabaeinae y Geotrupinae, y la familia Silphidae. En todos los análisis los tres grupos taxonómicos son manejados como un grupo indicador: los escarabajos copronecrófagos. De una manera lateral se incluye información sobre la subfamilia Aphodiinae (Scarabaeoidea), escarabajos coprófagos no incorporados al manejo del grupo indicador. Los paisajes estudiados son tres (tropical, de transición y de montaña), situados en un gradiente altitudinal en la parte central del estado de Veracruz. Partimos de las premisas siguientes. La diversidad alfa de un grupo indicador refleja el número de especies que utiliza un mismo ambiente o recurso en un lugar o comunidad. La diversidad beta espacial se relaciona con la respuesta de los organismos a la heterogeneidad del espacio. La diversidad gamma depende fundamentalmente de los procesos histórico-geográficos que actúan a nivel de mesoescala y está también condicionada por las diversidades alfa y beta. Es a nivel de paisaje o mesoescala donde las acciones humanas como cambio y fragmentación de comunidades, tienen sus efectos más importantes, efectos que en muchas ocasiones escapan al análisis ecológico puntual. En el conjunto de los tres paisajes se realizaron muestreos regulares en 67 sitios, más muestreos complementarios en 69 lugares más. Se estudiaron 26 tipos de comunidades vegetales. Se capturó un total de 16,152 ejemplares de 60 especies, 52 especies de Scarabaeinae, 4 de Geotrupinae y 4 de Silphidae. En el paisaje tropical la comunidad más rica en especies es la selva baja caducifolia; en el paisaje de transición es el bosque mesófilo. Ambas, son las comunidades naturales más importantes de sus pisos altitudinales. Por el contrario, en el paisaje de montaña la mayor riqueza se encuentra en praderas y potreros, un tipo de comunidad favorecido o incluso creado por la intervención humana. Esto se explica por la expansión a estos lugares de especies heliófilas del Altiplano mexicano. En el paisaje tropical los potreros presentan una riqueza en especies próxima a la de las selvas, pero una composición parcialmente diferente, caracterizada por la dominancia de especies heliófilas y coprófagas, a las que se suman las especies más ubicuistas compartidas con la selva. En el paisaje de transición se puso en relieve la importancia para la conservación de la fauna del bosque mesófilo, de los cafetales de sombra poliespecífica. Estos cafetales, el tipo de comunidad con cubierta arbórea que ocupa la mayor superficie en este paisaje, permiten a los grupos estudiados la intercomunicación entre los fragmentos remanentes de bosque mesófilo. Para los escarabajos que constituyen el grupo indicador, a nivel de paisaje (no puntualmente) la fragmentación de las comunidades naturales no parece haber ocasionado pérdidas en el número de especies. Aparentemente, la perturbación humana ha sido superada por razones distintas en cada paisaje. En el tropical porque existe una fauna heliófila característica de los potreros, fauna que incluso ha aumentado con dos especies invasoras recientes. En el paisaje de transición por el efecto de los cafetales de sombra poliespecífica que crean una matriz de intercomunicación. En el de montaña porque la expansión de las praderas ha ampliado las condiciones favorables para las especies heliófilas. Estos resultados no tienen forzosamente que repetirse con otros grupos de organismos.
Palabras Clave: diversidad alfa, beta y gamma; paisajes antropizados; Scarabaeinae; Geotrupinae; Silphidae; Veracruz.

ABSTRACT

Using three taxonomic groups of beetles we examine how alpha and beta diversity influence the species richness of a landscape (gamma diversity), and vice versa. That is, how the species richness of a landscape – which is a historical and biogeographical phenomenon – contributes to the values of alpha diversity (1) at a given site, (2) in a community, (3) in terms of cumulative species richness by community, and also contributes to (4) the intensity of species exchange between communities. To explore this question, we used two subfamilies of Scarabaeoidea: Scarabaeinae and Geotrupinae, and the family Silphidae. In all analyses these three taxonomic groups are considered as a single indicator group: the copronecrophagous beetles. Information is also included on the subfamily Aphodiinae (Scarabaeoidea), coprophagous beetles not included in the indicator group. Several types of vegetation located in three landscapes (tropical, transition and mountain) were studied, and these are located along an altitudinal gradient in the central part of the state of Veracruz, Mexico. We base this study on the following concepts. The alpha diversity of an indicator group reflects the number of species that use a given environment or resource in a given place or community. Spacial beta diversity is related to the response of organisms to spatial heterogeneity. Gamma diversity depends primarily on the historical and geographic processes that operate on the mesoscale level and is also affected by alpha and beta diversity. It is on this scale of landscape that human actions, such as the modification and fragmentation of vegetation, have their most important effects. These are, however, often beyond the scope of ecological analyses carried out on a local scale. In the three landscapes, sampling was carried out regularly at 67 sites, with complementary sampling at another 69 sites. Twenty-six types of vegetation communities were studied. A total of 16,152 specimens representing 60 species were captured (52 species of Scarabaeinae, 4 Geotrupinae and 4 Silphidae). In the tropical landscape the community richest in species was low deciduous forest. In the transition landscape, cloud forest was the richest. Each of these communities is the most representative of their respective altitudinal bands. In contrast, the greatest species richness in the mountain landscape occurred in the mountain grasslands and pastures; types of community favoured by or even created by human intervention. This is explained by the expansion of heliophilous species from the Mexican High Plateau into these areas. In the tropical landscape the species richness of the pastures is similar to that of its forests, but with a partially different composition which is characterized by the dominance of heliophilous and coprophagous species; the latter, in addition to the more ubiquitous species that are shared with the tropical forest. In the transition landscape the cloud forest and the coffee plantations with polyspecific shade are important in the context of conserving the fauna. This type of community offers arboreal cover and occupies the majority of this landscape, allowing the groups of insects studied to move between remnant fragments of cloud forest. On the landscape scale but not locally, the fragmentation of natural communities does not appear to have reduced the number of species for the beetles of the indicator group. In each landscape disturbance by human activity appears to have been overcome for distinct reasons. In the tropical landscape we find the heliophilous beetle fauna characteristic of pastures, and this has increased by two species of recent invaders. In the transition landscape, the coffee plantations with polyspecific shade create a communication matrix, while in the mountain landscape the expansion of the mountain pastures has made conditions more favourable for heliophilous species. These results are not necessarily expected for other groups of organisms.
Key Words: alpha, beta and gamma diversity; anthropogenic landscape; Scarabaeinae; Geotrupinae; Silphidae; Veracruz.

INTRODUCTION

The most widely used level of biological organization in the study of biodiversity is the species or organismal level (the last name sensu Harper & Hawksworth 1994). The most compelling reason is that species, in spite of the different criteria applied by different schools of systematics, are easily detectable and quantifiable in nature. The number of species of an indicator group that can be found in a particular site, community or region is a variable that can be measured without any notable technical or conceptual challenges.

Spatial scale is very important in the evaluation of species diversity since the processes that influence biodiversity vary with scale. So, at the local or community level, ecological processes exert the greatest influence: niche structure, biological interactions, environmental variables, etc. At the regional level, evolutionary and biogeographical aspects (dispersal, extinction, speciation, etc.) are the most important. On the mesoscale or landscape scale both sets of processes affect the number and quality of species (Ricklefs & Schluter 1993).

To study the dynamic relationships among the different types of diversity we studied three different landscapes along an altitudinal gradient in the central zone of the state of Veracruz, Mexico (Fig. 1). We worked with three groups of insects to form a reliable indicator group[1]. The usefulness of these taxa has been demonstrated in previous studies (Halffter & Favila 1993, Favila & Halffter 1997, Halffter 1998 a, b, Halffter & Arellano 2002). They include two subfamilies of Coleoptera Scarabaeoidea: Scarabaeinae (family Scarabaeidae) and Geotrupinae (family Geotrupidae), plus a third group of necrophagous beetles, family Silphidae. The subfamily Aphodiinae (Scarabaeoidea: Scarabaeidae) forms an important part of the guild of coprophagous beetles and, in the mountain landscape, replaces part of the Scarabaeinae group. This group was only sampled occasionally for several reasons, but most importantly owing to the fact that when this study began, the identification of the Aphodiinae of Mexico was very difficult. Currently there is more information available, but further study of this group is still required (M. Dellacasa, com. pers.). In addition, we did not expect the Aphodiinae to be as numerically important as they turned out to be. In order to correct this error as far as possible, the species of Aphodiinae captured during complementary sampling of the landscapes and reports gleaned from the literature are included in Appendix 1. In the Discussion we use the information summarized in this Appendix, however it was not included in tables or in the data presented in the Results section.

The use of landscape units for the evaluation, monitoring and conservation of the diversity of species has been considered by a growing number of specialists (Noss 1983, Franklin 1993, McNaughton 1994, Forman & Collinge 1996, Harris *et al.* 1996, Miller 1996, Noss 1996, Halffter 1998a,b) as having notable theoretical and practical value since it allows for the integral analysis of a complex problem. In a landscape, the composition and number of species changes from one community to another. This means that the species diversity of a landscape (gamma diversity) includes the richness of species in the individual communities that make up the landscape (alpha diversity) and the degree of difference between those communities (beta diversity). The alpha diversity of an indicator group reflects the number of species that use a given environment or resource. Beta diversity represents the response of the

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1) The term "indicator group is used in different contexts in ecology: to designate groups that reveal the occurrence of disturbance (such as the stage) or for groups that allow us to estimate the species richness of a site or landscape. As Favila and Halffter (1997) remark, "... the function of the indicator group is to make possible the approximation of an answer to a complex and labourious problem, that of measuring and monitoring total biodiversity". It is in this sense that the term indicator group is used in the present study.

organisms to spatial heterogeneity. Gamma diversity depends primarily on historical and evolutionary processes that operate on the mesoscale level and is also affected by alpha and beta diversity (Whittaker 1972, 1977). It is on the landscape or mesoscale level that human activity (contamination, degradation, change and fragmentation of ecosystems) has effects that often elude ecological analysis carried out on a local scale (Halffter 1998a, b). Modifications caused by human activities have resulted in the creation of landscapes that are complex mosaics of primary vegetation, secondary communities, pastures, annual and perennial crops. These landscapes represent a challenge for the study of biodiversity.

Veracruz is one of the three states in Mexico with the greatest biological diversity, but it is also one of the areas in the country with the highest degree of anthropogenic disturbance. In Veracruz, the main consequence of human activity has been the fragmentation of natural communities such that what remains are patches of the original vegetation with differing degrees of modification and that retain some of the components of the original forests (for Scarabaeinae see Halffter *et al.* 1992, Halffter & Arellano 2002). The central part of Veracruz is a region where the disturbance occurred a long time ago and so it is difficult to find anywhere that has not been disturbed. Before the Spanish Conquest this area was densely populated by indigenous peoples who, among other activities, practiced slash and burn agriculture. From the 16th century onwards, sheep ranching (practically abandoned today) and cattle ranching (Barrera-Bassols & Rodríguez 1993) were added to this form of agriculture and then came the cultivation of sugar cane (Prieto 1968, Rodríguez 1970, Ponce & Núñez 1992).

In the anthropogenic landscapes of central Veracruz our research team is carrying out various projects on biodiversity related to the present study. With dung beetles (Scarabaeinae and Geotrupinae) and Silphidae we have studied the biogeographical elements of regional biodiversity (Halffter *et al.* 1995). Using only Scarabaeinae we have compared the biodiversity of different tropical rainforests with that of an induced pasture (Halffter *et al.* 1992). In addition, we have examined the relative importance of arboreal cover with respect to food availability and its influence on species diversity and the structure of the Scarabaeinae guild (Halffter & Arellano 2002). Using bats as an indicator group, we have also analyzed the relationship between the different levels of diversity (Moreno & Halffter 2001).

Using Scarabaeinae, Geotrupinae and Silphidae to form an indicator group in this study we examine how alpha and beta diversity influence species richness (gamma diversity) in three landscapes of central Veracruz. We also explore the inverse phenomenon. That is, how the species richness of a landscape – a historical, biogeographical element affected by anthropogenic transformations, mainly community fragmentation – contributes to determining the values of alpha diversity of a given site, of a given community, and the cumulative species richness of a community, as well as the intensity of species exchange between communities.

MATERIALS AND METHODS

Some definitions

In the interest of clarity, we present the meaning of some of the terms used in this manuscript, including several terms generally used in ecology.

Alpha diversity is the number of species (belonging to the indicator group we have defined for our work) found at a site or in a community. Although not specified in the majority of studies on biodiversity, alpha diversity corresponds to the number of species that exist over a short period of time during which the number of species does not change. The rate of change in the number of species at a given site varies greatly over longer periods of time owing to emigration, the local extinction of some species and the arrival of others previously not present.

Alpha diversity can be expressed for a site or a community type, and in both cases the total number of species or mean values can be used. The mean value is the arithmetic mean of the values recorded for the sites of a given landscape or at the sampling sites of a certain type of community.

The cumulative species richness of a community is the sum of the number of species belonging to the indicator group collected in that community over a given period of time. Beta diversity is the difference in the number of species between two sites, two types of community or two landscapes. This difference could originate from available space and changes associated with space when the diversity of the places being compared is obtained simultaneously. It could also result from comparing alpha diversities that were obtained at different times.

Gamma diversity is the total number of species recorded for the group of sites or communities that make up a landscape.

Community refers mainly to different types of vegetation, but in some cases, also to areas which have been visually characterized for practical purposes.

Pasture refers to deforested areas where grass has been sown (or grown spontaneously) and used for livestock, almost exclusively cattle, in the region.

A site is the minimum area, in terms of space and time, that has a sample of a given functional assemblage or community (definition as given by G. Halffter and C.E. Moreno, pers. com.). For a study such as this, it is the same as "point" or "place".

High altitude vegetation includes all the community types found above 3,500 m asl. The use of this term is general since the beetles of the indicator group are scarce (both in species and individuals) in this type of vegetation and show no marked affinity towards any given community at these altitudes. The most extensive community types at these altitudes are: pine forest (*Pinus hartwegii*) with *Juniperus monticola* and *Berberis schiedeana* in the shrub layer and *Muhlenbergia macroura, Stipa ichu, Trisetum spicatum* and *Calamagrostis tolucensis* in the herbaceous understorey. This type of vegetation is found between 3,500 and 4,000 m asl. Mountain grassland, found between 4,000 and 4,200 m asl, is a predominantly herbaceous community that has the shrub species mentioned above, but with species different to those found in the pine forest (see Narave 1985).

Landscape units, sampling sites and capture methods

A landscape is a unit of space, with geographic limits and a specific area, characterized by its relief, climate, soil and vegetation (Noss 1990, Castillo-Campos 1995, Geissert & Castillo-Campos 1997). Each landscape has its own biogeographical history (Halffter 1998 a,b) which emerges as a result of two types of processes that are constantly interacting: ecological or current, and historical-evolutionary; the latter referring as much to the biota as to the physical components of the landscape. Of the current processes that determine the characteristics of each species assemblage, some are natural (occurring without direct human intervention) and some are the direct or indirect, desired or undesirable, result of human activity.

In agreement with generally accepted criteria for climatological and physiographical limits (INEGI, SEDUE), for this study we have classified the landscapes as three successive levels along an altitudinal gradient that ranges from sea level to 4,250 m asl in the central region of the State of Veracruz (19º 90'-19º 25' lat. N, 96º30'- 97º20' long. W) (Fig. 1). The delineation of the landscapes was compared with site classification by species composition using the program Statistica (Statsoft 1991, see Fig. 2), and refined using information from a study by Halffter *et al.* (1995), which included a biogeographical analysis of copronecrophagous beetles from the central region of Veracruz. The landscapes are:

a) Tropical. 0-1,000 m asl. Coastal plains. Soil: feozems, luvisols and rendzinas (Zolá 1987). Characterized by limestone, sandstone and rocks of volcanic origin (INEGI 1988). Climate: Aw'(i)g, warm, subhumid with rain during the summer (García 1981). Mean annual temperature ranges from 22.3°C to 24.5°C. Total annual precipitation: 1,500 - 2,000 mm. Vegetation communities: coastal sand dunes, mangrove, halophyte vegetation in the swales of fixed dunes and around mangroves, deciduous forest on the more elevated terrain, tropical oak forests, medium semi-deciduous forest in the most humid ravines (Castillo-Campos 1985, 1991, Acosta 1986, Robles 1986, Cházaro-Basáñez 1992). Land use: agriculture with irrigation, sugar cane and mango cultivation, extensive cattle ranching.

b) Transition. 1,000 - 2,000 m asl. Terrain with tablelands and hill and valley formations. Soils: andosols, lithosols and feozems (INEGI 1988), on volcanic ash, basalt, cinder, lapilli and andesites (Zolá 1987). Climate: on the border of two climate types, C(fm)w''b(i)g, humid temperate with rain year round, and (A)C(fm)w''a(i)g, semi-warm humid (Soto & Angulo 1990, Angulo 1991). Mean annual temperature ranges from 12.26°C to 22.3°C. Total annual precipitation: 1,200 - 2,500 mm. Vegetation communities: medium altitude oak forest, cloud forest, oak forest, pine-oak forest (Castillo-Campos 1991, Zamora 1992, Narave 1985). Land use: predominantly coffee plantations, but also corn cultivation and dairy cattle ranching.

c) Mountain. > 2,000 m asl. Soils: andosols (De Luna 1983). The most common rock types are volcanic ash, basalt and andesites. Climate: C(fm) humid temperate with rain year round, C(m) humid temperate with rain during the

summer, CW_2 subhumid temperate with rain during the summer, CW_1" dry and cool subhumid temperate (Soto & Angulo 1990). Mean annual temperature ranges from 11.04°C to 12.85°C. Total annual precipitation: 800 - 1,500 mm. Vegetation communities: pine forest, fir forest and mountain pastures (Narave 1985). Land use: mainly dairy cattle ranching, but also seasonal agriculture (corn, wheat, potato, oats, etc.) with apple, pear and plum orchards (Narave 1985).

Part of these landscapes is covered by an extensive zone of rocky lava flows (type Aa) formed by numerous basalt extrusions originating from a string of small volcanos (such as El Volcancillo, Xocotepec and La Joya) located along the lava flow (Geissert 1994). We sampled at sites located on: a) the La Joya-Acajete flow which is estimated to have occurred no more than 36,000 years ago and is covered by a layer of ash that is continuous and of varying thickness; b) an extrusion covered by a discontinuous layer of ash of varying thickness that is 5,000 to 10,000 years old, begins near La Joya and extends towards Rafael Lucio, El Duraznal, Teapan and Jilotepec; c) the chaotic rocky lava flows which begin at the Volcancillo and end near Actopan, more than 50 km from their origin (Fig. 3). The latter are recent; less than 5,000 years old according to C_{14} dating (Geissert 1994). At most this formation is 2,400 years old (Ortega 1981; for more information see Negendank *et al.* 1985).

Based on site classification, for the analysis of the alpha and beta diversity we decided to separate the communities located on the rocky lava flows from those found on soils that are not rocky since, in most cases, these communities formed separate groups (Fig. 2).

In the tropical landscape, samples were taken at 18 sites and complementary samples at 20 additional sites. Five community types were studied. In the transition landscape samples were taken regularly at 29 sites and additional sampling carried out at 30 other sites. Thirteen community types were studied. The heterogeneity in vegetation of this landscape required a greater sampling effort. In the mountain landscape samples were taken at 20 sites and complementary sampling was carried out at 19 additional sites. Eight community types were studied. Figure 1 shows the locations of the sampling sites.

For regular sampling, we baited traps with human excrement, carrion (decomposing squid) or fruit (mango, guava, mamey), and specimens were also collected from small cadavers, fruit, wild animal scat and livestock dung (cattle, horse and sheep). During regular sampling we placed baited traps at each site each month for a 24 hour period. The bait was placed on the surface of four traps (two with cow dung and two with decomposing squid), and at the bottom of six traps (three with human excrement and three with rotting squid). The designs of the pitfall traps are described in Halffter and Arellano (2002). Regular sampling covered a total of 723 capture days with the participation of two people per day: 190 days in the tropical landscape, 375 days in the transition landscape and 158 days in the mountain landscape. Sampling was carried out mainly during the rainy season (May to October) of 1990, and from 1994 through 1996.
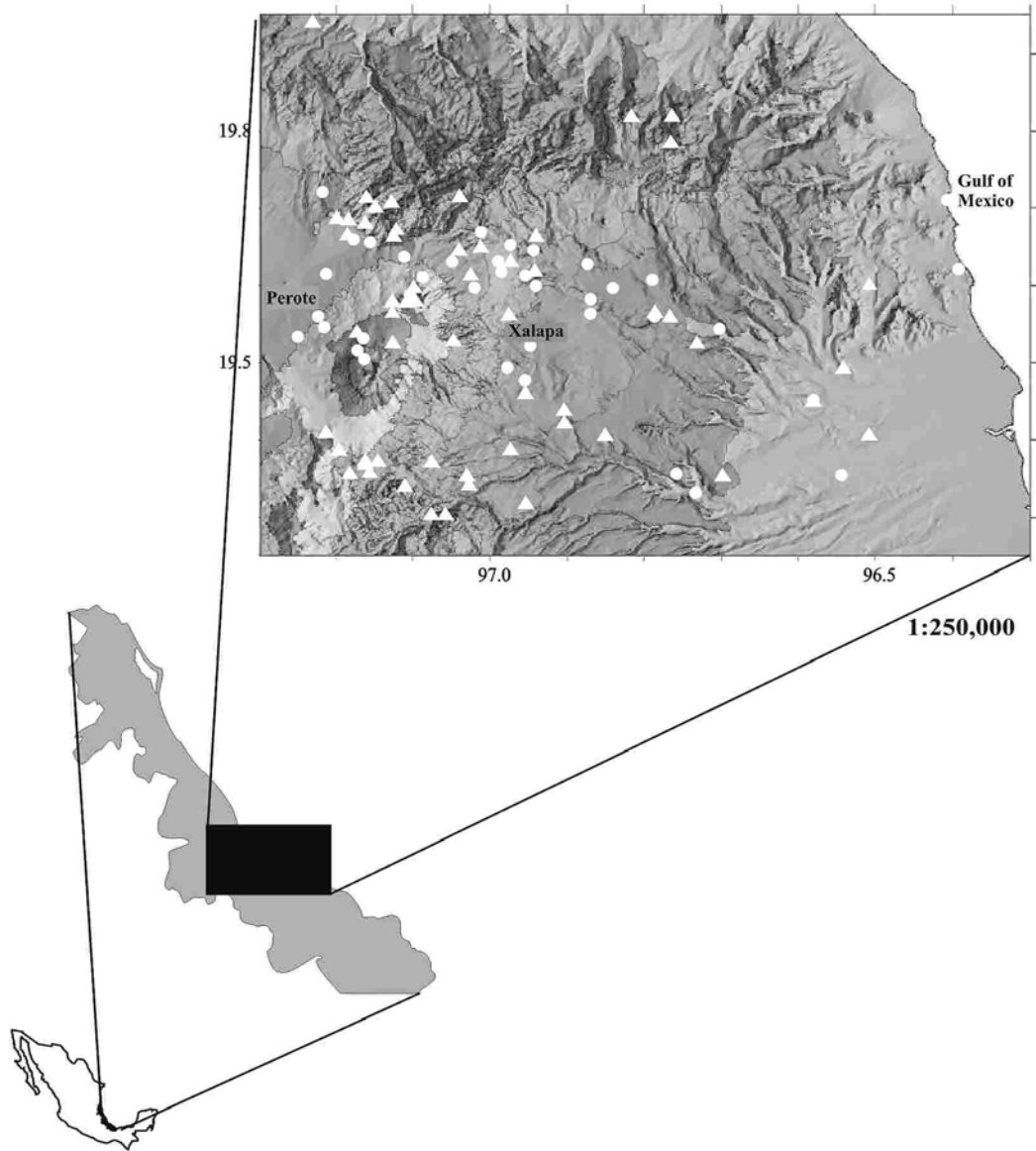
Figure 1
Location of the region studied in Veracruz State, Mexico. The circles represent the regular sampling sites and the triangles represent complementary or occasional sampling sites.
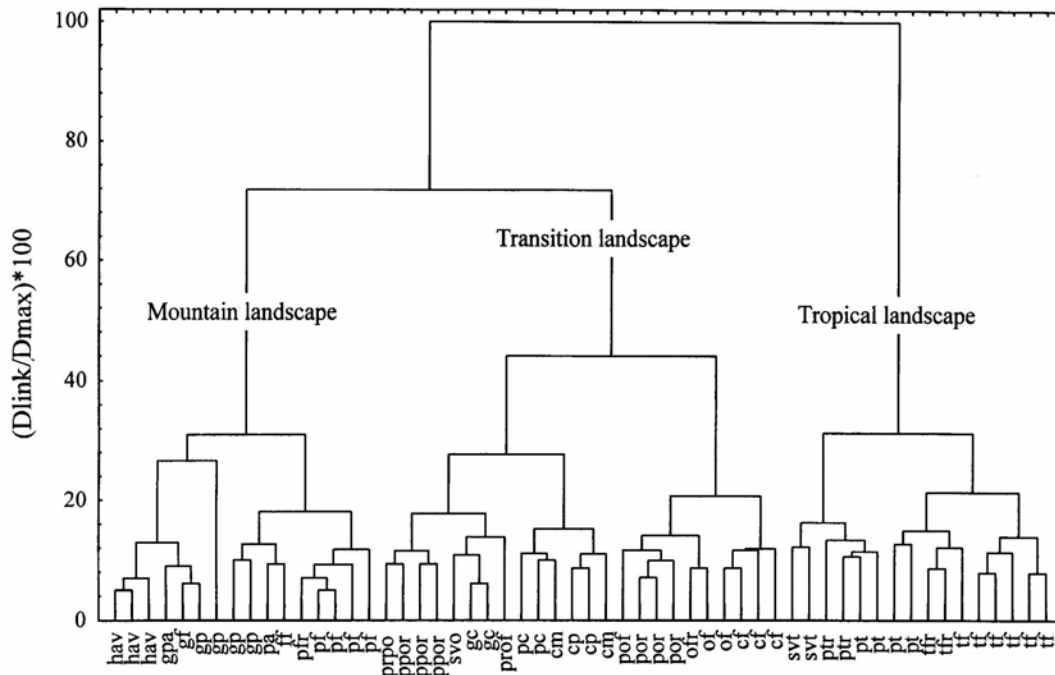
Figure 2
Dendrogram of the cluster analysis done of the data from the regularly sampled sites. Similarity was generated using the Euclidian distance (converted to percentage) and the unweighted pair group method with arithmetic average linkage rule (UPGMA) was used. The three landscapes separate into three large groups of sites. The names of the vegetation communities are indicated by their abbreviations in letters. See the reference list. Dlink/Dmax is a standarization of the Euclidean Distance to 0-100 scale.

For the complementary sampling, beetles were only collected from excrement. This occasional sampling allowed us to complete the list of species for a given landscape. As complementary methods in forests and coffee plantations, we used a NTP 80 trap (Morón & Terrón 1984) that was checked every 30 days. In pastures, specimens were collected from ten dung piles (mainly cow and horse). During the occasional sampling (1989-1997) specimens were only collected from excrement that was encountered, and these were used to complete species lists for each landscape.

Data analysis
To evaluate sampling efficiency for each site, species accumulation models and Abundance-base Coverage Estimator (ACE), non-parametric estimators of species richness, were used (Colwell 1997). The unit of effort used was a day of sampling, including all methods of capture, excluding the data from occasional or complementary sampling.

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Abbreviations used for plant communities in figures, tables & appendices:

Plant Community	abbreviations
Tropical Landscape	
Tropical deciduous forest	tf
Pasture adjacent to tropical deciduous forest	pt
Secondary vegetation adjacent to tropical deciduous forest	svt
Pasture adjacent to tropical deciduous forest on rocky lava flow	ptr
Tropical deciduous forest on rocky lava flows	tfr
Transition Landscape	
Cloud forest	cf
Coffee plantation with polyspecific shade	cp
Pasture adjacent to pine-oak forest on rocky lava flows	ppor
Pasture adjacent to cloud forest	pc
Oak forest	of
Pasture on rocky lava flows, adjacent to pine-oak forest	prpo
Coffee plantation with monospecific shade	cm
Oak forest on rocky lava flows	ofr
Pine-oak forest on rocky lava flows	por
Pine-oak forest	pof
Gap in cloud forest	gc
Secondary vegetation adjacent to oak forest	svo
Pasture on rocky lava flow, adjacent to oak forest	prof
Mountain Landscape	
Grassland adjacent to pine forest	gp
Pine forest	pf
Pine-alder forest	pa
Grassland adjacent to fir forest	gf
Fir forest	ff
Grassland adjacent to pine-alder forest	gpa
Pine forest on rocky lava flows	pfr
High altitude vegetation	hav

Randomized data (100 times, using EstimateS Colwell 1997) were adjusted to two asymptotic models: the linear dependence model and Clench's model (see Soberón & Llorente 1993, León-Cortés 1994, León-Cortés *et al.* 1998) using SIGMASTAT (Jandel 1995). We did not use the results obtained from the Linear Dependence Model because it underestimated richness values. Only the asymptote values obtained with Clench's model were used to to select those of the 67 regularly sampled sites where capture effort provided close to the maximum diversity expected. 85% of the total estimated fauna, though arbitrary,

is considered an acceptable degree of efficiency. When the data did not meet the criteria of the accumulation model, the ACE non-parametric estimators proposed by Colwell & Coddington (1995) was calculated applying the criterion of 85% for the selection of adequately sampled sites. In the end, 56 sites were selected for diversity analysis. These analyses were also carried out at the level of community type for each landscape.

The folloling were calculated: alpha diversity for each site, mean alpha diversity for each community type, mean alpha diversity for each landscape, and cumulative species richness for each community.
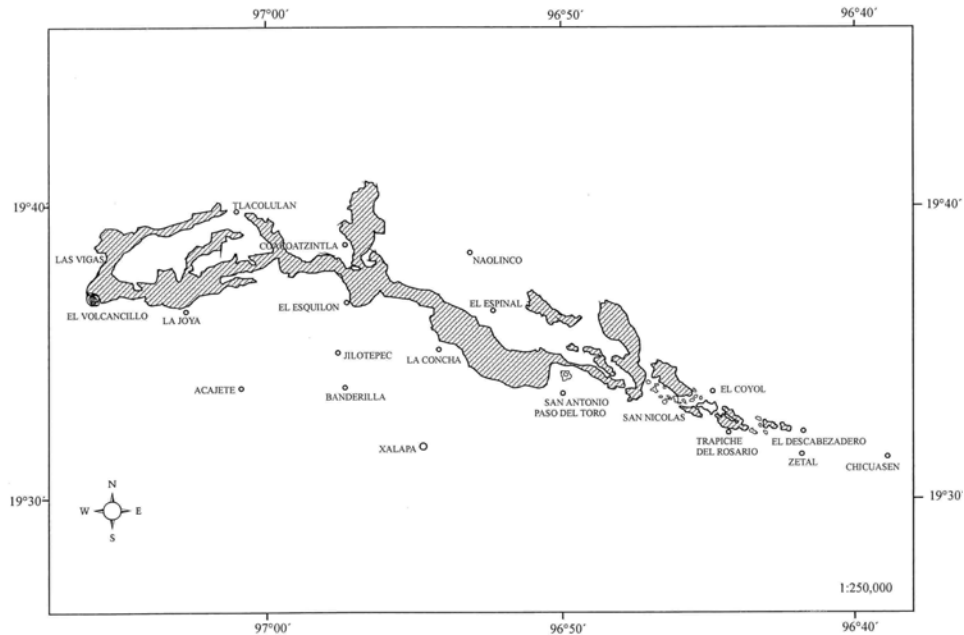
Figure 3
The relatively exposed (50-70%) rocky lava flow Volcancillo-Actopan, in the region of central Veracruz, Mexico. Modified from Ortega (1981).

Beta diversity was calculated for all pairs of sites from the same community, after which mean beta diversity per community was obtained. Beta diversity was also calculated for all pairs of sites from adjacent communities, these values indicating the highest exchange rates. Whittaker's modified index was used (Harrison *et al.* 1992):

$$\beta = \{[(S/a)-1]/(N-1)\} \times 100$$

where:

S = the number of species recorded for the landscape (gamma diversity)

a = the mean number of species in a given community type (mean alpha diversity)

N = the number of study sites

This index is similar to that of Whittaker (1972), except that it is expressed as a percentage. The closer the value is to zero, the more similar communities are. Higher values indicate greater differences (less similarity) between communities. Using the program Orden (Ezcurra 1990), an uncentred, unstandardized Principal Components Analysis (56x58) was conducted to graph the trends in beta diversity. Sites that have a similar number of species and species composition are closer together (Ter Braak 1983, Cody 1993). It is important to note that estimation of real variability of axes (with respect to means) was calculated by eliminating the first Eigen value, because in uncentered presence/absence analysis, Axis 1 is affected by the decision not to center data, and data variability increases artificially (Montaña & Ezcurra, 1991).

The gamma diversity for each of the three landscapes, measured as the cumulative number of species captured, was calculated using the following index proposed by Schluter & Ricklefs (1993):

$$\gamma = \alpha \times isd \times sd$$

where:

α = the mean number of species per site in a landscape unit,

isd = the inverse of the species dimension; that is, 1/the mean number of communities or locations occupied by a species,

sd = sample dimension or total number of sites sampled.

Gamma diversity can be obtained from the general species list for each landscape. However, the use of the formula above gives us an idea of which component of gamma diversity is the most important in each landscape, whether it is the mean alpha diversity, landscape heterogeneity or the number of communities occupied by species. This allows us to compare the different components of gamma between landscapes.

To estimate the degree of dissimilarity in the species composition of the landscapes, we calculated complementarity between pairs of landscapes (Colwell & Coddington 1995). The complementarity for landscapes A and B is expressed as:

$$C_{AB} = U_{AB}/S_{AB}$$

where U_{AB} is the sum of the species unique to each of the two landscapes, calculated as:

$$U_{AB} = a + b - 2c$$

with:

a is the number of species of landscape A,

b is the number of species of landscape B,

c is the number of species in common to landscapes A and B

and where S_{AB} is the total species richness of both landscapes combined, as follows:

$$S_{AB} = a + b - c$$

For the data on the cumulative richness and gamma diversity of tropical low deciduous forest and the pastures adjacent to them, we included species captured by G. Halffter at Laguna Verde, a site close to the Gulf of Mexico where our group has carried out studies over the past 20 years and where more than 95% of the existing species have been collected (see Appendix 2).

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RESULTS

A total of 16,152 specimens belonging to 60 species were captured from the 67 sites that were regularly sampled. Of these, 52 species belong to Scarabaeinae, 4 to Geotrupinae and 4 to Silphidae. Of the total 15,716 individuals belonging to 60 species were caught in the 56 sites selected for diversity analysis.

The different estimates of sampling quality by community type were satisfactory: more than 85% of the estimated species were caught (see tables 1 and 2).

Table 1

The number of copronecrophagous beetle species recorded, as well as the parameters and predictions of Clench's asymptotic accumulation model fitted for each plant community from three landscapes in central Veracruz. *a* is the slope at the beginning of sampling, *b* is a parameter related to the shape of the curve indicating the accumulation of new species during sampling, *a/b* is the asymptote, R^2 is the coefficient of determination, *n* is the number of samples for each community and % is the percentage of the asymptote recorded. See abbreviations list for the complete names of the plant communities.

Community	spp. obs.	*n*	R^2	*a*	*b*	*a/b*	%
Tropical landscape							
tfr	7	14	999	2105	258	8	8750
pt	14	51	1000	3788	253	15	9333
svt	17	19	999	3793	195	19	8947
Transition landscape							
cp	16	63	992	2476	145	17	9411
cm	10	23	814	2536	242	10	10000
gc	8	22	999	1552	169	9	8888
of	11	16	997	4030	385	10	10000
svo	7	8	997	1064	1356	8	8750
prpo	11	12	997	294	230	13	8462
pc	12	40	972	1338	95	14	8571
pof	8	13	846	3621	398	9	8888
ppor	13	34	990	2845	210	14	9286
prof	6	18	995	2733	392	7	8571
ofr	9	8	997	3222	318	10	9000
Mountain landscape							
pa	5	7	999	3421	687	5	10000
ff	3	7	1000	1272	371	3	10000
gpa	5	7	996	1428	259	6	8333
gf	2	7	967	1819	816	2	10000
pfr	2	7	995	2662	1202	2	10000
gp	16	54	989	1117	68	16	10000
hav	2	17	994	277	120	2	10000

Table 2

The number of copronecrophagous beetle species recorded and prediction of nine non-parametric estimators of species richness (Colwell & Coddington 1995) for some plant communities of central Veracruz, Mexico.

	Tropical Landscape	Transition Landscape		Mountain Landscape
Community	tf	cf	por	pf
No. of samples	91	71	29	53
No. of species observed	19	18	8	8
ACE	20	18	8	8

ALPHA DIVERSITY

Alpha diversity by site

   Species distribution in each site and community, as well as the values for alpha diversity are given in Appendix 3.

   In the tropical landscape, alpha diversity on sites 1, 2, 3, 4, 5 and 6 was significatively higher (Kruskal, H = 73.11, d.f. = 15, P < 0.001, Dunnet's Method, P < 0.05) than on sites 7 and 8, two tropical forests growing on the fairly exposed rocky lava flows. In the transition landscape there were significant differences among the alpha diversity of sites with 5-7 species - sites with pine-oak forest on rocky lava flows, monospecific coffee plantations, pastures and secondary vegetation- and the others with higher alpha diversity (Kruskal, H = 118.43, d.f. = 23, P < 0.001, Dunnet's Method, P < 0.05). In the mountain landscape differences were observed (Kruskal, H = 82.03, d.f. = 15, P < 0.001, Dunnet's Method, P < 0.05), as at 3,900 m asl and higher, none of the species belonging to the groups studied were found. (For biogeographical analysis explaining the presence of these beetles at these altitudes, see Halffter *et al.* 1995, Peck & Anderson 1985).

Mean alpha diversity by community

   There were significant differences in the mean alpha diversity of communities among landscapes (ANOVA, F = 17.21, d.f. = 2, P < 0.001). The values for the communities of the transition and tropical landscapes were similar (Tukey, q = 1.382, P > 0.05), while those of the mountain and tropical landscape (Tukey, q = 7.021, P < 0.05), and those of the transition and mountain landscape (Tukey, q = 7.289, P < 0.05) were not.

The effect of substrate type and the age of the rocky lava flow sites

   In the tropical landscape there were significant differences in number of species (t = 3.936, d.f. = 6, P = 0.008), and in number of individuals (t = 3.035, d.f. = 6 , P = 0.007) between the tropical forests growing on the fairly exposed

rocky lava flows (< 5,000 years old) and those growing on other types of soil. Significant differences in the number of species (Mann-Whitney, *Tx* = 658.0, *P* = 0.02) and in the number of individuals (Mann-Whitney, *Tx* = 682.0, *P* = 0.05) were also found between the forests on the rocky lava flows and the pastures adjacent to them. These differences were notable at La Concepción where only 5 species and 42 individuals were found in the forest, but 10 species (277 individuals) were caught in the adjacent pasture. There were no significant differences in number of species (*t* = 0.804, d.f. = 4, *P* = 0.466), and in number of individuals (*t* = 0.887, d.f. = 4, *P* = 0.425) between pastures adjacent to tropical forests growing on the fairly exposed rocky lava flows and the other sites.

For the transition landscape, there were no significant differences in the number of species caught in forests located on the relatively older (5,000 - 10,000 year old) soils of the rocky lava flows and those on other soils (Mann-Whitney, *Tx* = 13, *P* = 0.381), nor were there differences in the number of individuals (*t* = 0.752, d.f. = 4, *P* = 0.494). There were no significant differences in the number of species collected in the forests on the rocky lava flows and their adjacent pastures (Mann-Whitney, *Tx* = 2117.00, *P* =0.709), nor in the number of individuals (Mann-Whitney, *Tx* = 2474.5, *P* = 0.730). In spite of this, we did record marked differences between a pine-oak forest growing on the predominantly rocky soil of a lava flow (Teapan) and its adjacent pasture, both in the number of individuals (forest = 139, pasture = 224) and in the number of species (forest = 6, pasture = 11). In the transition landscape, for sites that occur on an ancient lava flow (36,000 years old) where the soil is not very rocky, there were no significant differences between the forest and the adjacent pasture in the number of species (Mann-Whitney, *Tx* = 210.0, P = 0.359), or in the number of individuals captured (Mann-Whitney, *Tx* = 135.5, P = 0.781).

For the mountain landscape there were no significant differences in the number of species (*t* = 2.079, d.f. = 6, *P* = 0.083) or in the number of individuals captured (*t* = 0.609, d.f. = 6, *P* = 0.565) between forests located on the predominantly rocky lava flows (5,000+ years old, Geissert 1994) or on other soils.

In the mountain landscape, there were no significant differences in the number of species (Mann-Whitney, *Tx* = 240, *P* = 0.372), or in the number of individuals (Mann -Whitney, *Tx* = 244, *P* = 0.378) between the forest and the pastures that grow on the rocky lava flows.

Cumulative species richness (cumulative alpha diversity) of the vegetation communities

Table 3 shows the cumulative richness of the different community types. Low deciduous tropical forest had the greatest number of species (22), followed by pastures adjacent to these forests and the lowest values (< 3 species) were recorded for high altitude vegetation and pine forest on the rocky lava flows.

For the three landscapes there were significant differences among communities in mean alpha diversity and cumulative species richness (t = -2.883, P = 0.007). In various communities cumulative species richness was approximately double the mean alpha diversity (Table 3).

Table 3
Mean alpha diversity and cumulative community species richness (CSR) of copronecrophagous beetles in three landscapes of central Veracruz, Mexico.

Community	Mean Alpha Diversity/ community ± S.E.	min no. spp.	max no. spp.	CSR
Tropical Landscape				
low deciduous forest	11.33 ± 0.97	8	15	22
pasture next to low deciduous forest	11.25 ± 0.84	9	14	21
secondary vegetation next to low deciduous forest	11.50 ± 2.00	9	13	17
pasture next to low deciduous forest on rocky lava flows	9.5 ± 2.50	7	12	14
low deciduous forest on rocky lava flows	4.5 ± 0.50	4	5	7
Transition Landscape				
cloud forest	11.67 ± 0.88	10	13	18
coffee plantation with polyspecific shade	12.50 ± 0.50	12	13	16
pasture next to pine-oak forest on rocky lava flows	8.33 ± 1.76	5	11	13
pasture next to cloud forest	8.5 ± 1.50	7	10	12
oak forest	9.00 ± 1.00	8	10	11
pasture on rocky lava flows, next to pine-oak forest	11.00 ± 0.00	11	11	11
coffee plantation with monospecific shade	6.50 ± 1.50	5	8	10
oak forest on rocky lava flows	9.00 ± 0.00	9	9	9
pine-oak forest on rocky lava flows	5.67 ± 0.33	5	6	8
pine-oak forest	8.00 ± 0.00	8	8	8
gap in cloud forest	7.00 ± 1.00	6	8	8
secondary vegetation next to oak forest	7.00 ± 0.00	7	7	7
pasture on rocky lava flows, next to oak forest	6.00 ± 0.00	6	6	6
Mountain Landscape				
grassland next to pine forest	5.75 ± 0.96	3	7	13
pine forest	3.25 ± 0.63	2	5	7
pine-alder forest	5.00 ± 0.00	5	5	5
grassland next to fir forest	2.00 ± 0.00	2	2	2
fir forest	3.00 ± 0.00	3	3	3
grassland next to pine-alder forest	5.00 ± 0.00	5	5	5
pine forest on rocky lava flows	2.00 ± 0.00	2	2	2
high altitude vegetation	0.67 ± 0.33	1	1	2

BETA DIVERSITY

Shared and exclusive species

The number of species shared among the different community types for each landscape was high (Table 4). In the tropical landscape the forests had the highest percentage of exclusive species (27.27%), followed by pastures adjacent to forests (14.29%) and pastures next to forests on the rocky lava flows (7.14%). Neither the forests on the rocky lava flows, nor the sites with secondary vegetation next to forests had any exclusive species.

In the transition landscape the greatest percentage of exclusive species was found in coffee plantations with polyspecific shade (12.5%), followed by oak forests (9.09%), pastures next to cloud forest (8.33%) and cloud forests (5.55%).

None of the other communities had any exclusive species (Table 4).

The communities with the highest number of exclusive species were found in the mountain landscape. In this landscape, unlike the others, no community shared 100% of its species with another (Table 4).
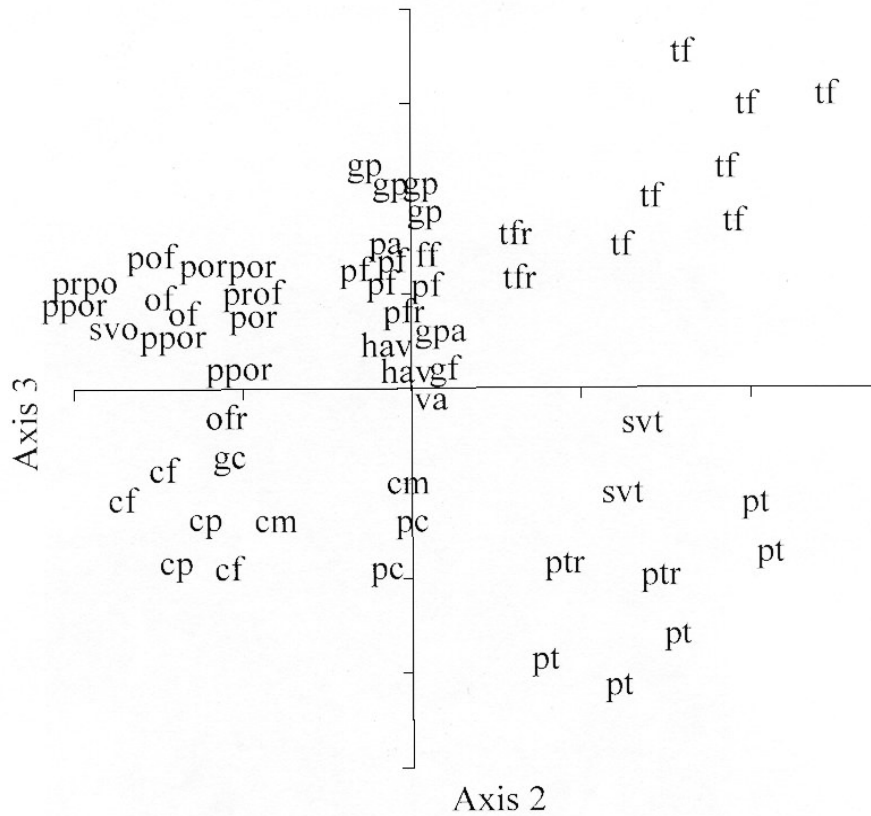
Table 4

Total number of species, number of exclusive species and shared species in each community type for the three landscapes studied. Community designation (first column) follows the text. In the last four columns on the right, all the community types have been grouped into four major community types. The dashes indicate the same community type in the column and the row (no comparison possible) or that no samples were collected from this community type in the corresponding landscape.

Community	total # of species	# of exclusive spp.	Number of species shared with			
			other forests	other pastures	secondary veg + gaps	coffee plantations.
Tropical Landscape						
low deciduous forest	22	6	6	13	13	-
pasture next to low deciduous forest	21	3	13	13	12	-
secondary vegetation next to low deciduous forest	17	0	13	12	-	-
pastures next to low deciduous forest on rocky lava flows	14	1	9	13	10	-
low deciduous forest on rocky lava flows	7	0	6	6	5	-
Transition Landscape						
cloud forest	18	1	13	10	8	16
oak forest	11	1	8	7	7	6
oak forest on rocky lava flows	9	0	9	6	-	9
pine-oak forest	8	0	8	8	-	3
pine-oak forest on rocky lava flows	8	0	9	8	-	5
coffee plantation with monospecific shade	10	0	10	8	-	8
coffee plantation with polyspecific shade	16	2	14	11	-	8
pastures next to cloud forest	12	1	10	4	-	10
pastures on rocky lava flows, next to oak forest	6	0	3	6	3	5
gap in cloud forest	8	0	8	4	-	8
secondary vegetation next to oak forest	7	0	7	2	4	5
pastures next to pine-oak forest on rocky lava flows	13	0	11	13	9	5
pastures on rocky lava flows, next to pine-oak forest	11	0	9	10	-	5
Mountain Landscape						
pine forest	7	2	-	4	-	-
pine-alder forest	5	2	-	3	-	-
pine forest on rocky lava flows	2	2	-	-	-	-
fir forest	3	1	-	2	-	-
pastures next to pine forest	13	9	-	4	-	-
pastures next to pine-alder forest	5	1	-	2	-	-
pastures nect to fir forest	2	2	-	-	-	-
high altitude vegetation	2	2	-	-	-	-

Mean beta diversity among vegetation communities

   The values of mean beta diversity among communities showed different tendencies depending on the landscape. In the tropical landscape, the greatest mean beta diversity was found between the tropical deciduous forests that grow on rocky lava flows (77.5%), followed by the species exchange between different types of tropical deciduous forests and their adjacent pastures (>68%). Beta diversity between deciduous tropical forests and their secondary vegetation was 53.25%. This is reflected in the Principal Components Analysis where axis 2 separates deciduous tropical forests from their adjacent secondary vegetation and from neighbouring pastures (Fig. 4). The lowest value for mean beta diversity was recorded between different sites with secondary vegetation, between deciduous tropical forests or between pastures (Table 5).

Figure 4
Uncentred, non-standardized Principle Components Analysis of sites with more than 85% of the estimated fauna. The names of the vegetation communities are indicated by their abbreviations in letters. See the reference list.

Table 5
Mean beta diversity by community for three landscapes in the Cofre de Perote region of central Veracruz, Mexico. β = Whittaker's index (modified), S.E. = standard error. A value of "indef" for S.E. is given when the beta value was obtained by comparing only one pair of sites. Mean beta diversity for patches with the same type of community are expressed to determine the heterogeneity of the most typical communities for each landscape. Mean beta diversity is also given where different community types are adjacent and the type of contiguity specified is the most common for that landscape (e.g. forests cf. pastures).

Community	Beta Diversity			
	β (%)	Std error	min	max
Tropical Landscape				
low deciduous forests	3733	343	1000	6470
pasture next to low deciduous forest	3902	302	2220	5455
secondary vegetation	3000	indef.	3000	3000
low deciduous forests on rocky lava flows	7750	250	7500	8001
pastures next to low deciduous forest on rocky lava flows	4440	indef	4440	4440
low deciduous forests cf. pastures	6861	1464	4290	10000
low deciduous forests on rocky lava flows cf. pastures	6957	1263	4444	10008
low deciduous forests cf. adjacent secondary vegetation	5326	1464	4290	6361
Transition Landscape				
cloud forests	3737	682	2380	4540
coffee plantation with monospecific shade	5385	indef.	5385	5385
coffee plantation with polyspecific shade	2727	indef.	2727	2727
oak forests	1579	indef.	1579	1579
cloud forests cf. oak forests on rocky lava flows	3547	730	2220	4740
cloud forests cf. oak forests	4764	416	3330	5790
pine-oak forests on rocky lava flows	3485	758	2727	5000
pine-oak forests on rocky lava flows cf. pine-oak forests	3161	1334	770	5380
pastures next to cloud forest	2860	indef.	2860	2860
gaps in cloud forest	1428	indef.	1428	1428
coffee plantation with monospecific shade cf. those with polyspecific shade	4641	494	3333	5550
pastures next to pine-oak forest	4737	135	4550	5000
pine-oak forests cf. pastures	3826	656	2730	5000
cloud forests cf. pastures	5555	1111	4444	6666
oak forests cf. adjacent secondary vegetation	1761	indef.	1760	1760
pine-oak forest on rocky lava flows cf. pastures	3240	510	2730	3750
cloud forests cf. coffee plantations with monospecific shade	5555	indef.	5555	5555
cloud forests cf. coffee plantations with polyspecific shade	1430	indef.	1430	1430
oak forests cf. adjacent pastures on rocky lava flows	6250	indef.	6250	6250
cloud forests cf. gaps	1580	indef.	1580	1580
Mountain Landscape				
pine forests	3059	631	1130	5000
pine forests cf. grasslands	5777	1309	4000	8333
pine forests cf. pine forests on rocky lava flows	3292	715	1500	5000
pine forests cf. pine-alder forests	3571	937	1111	5550
pine forests cf. fir forests	4718	428	4290	6000
grasslands next to pine forest	6392	799	4660	10000
grasslands next to pine forest cf. grasslands next to pine-alder forest	3713	625	2000	5000
grasslands next to pine forest cf. grasslands next to fir forest	7920	829	6000	10000
high altitude vegetation	10000	indef.	10000	1000

In the transition landscape the greatest mean beta diversity occurred between oak forests and neighbouring pastures on the rocky lava flows (62.50%), between cloud forests and coffee plantations with monospecific shade (55.55%), and between cloud forests and their adjacent pastures (55.55%). This is seen (Fig. 4) in the PCA where, on axis 3, cloud forests are separated from their pastures and from a coffee plantation with monospecific shade. The latter was the poorest in species (5) and had been subjected to treatment with herbicides. This coffee plantation had 38% fewer species than the other plantation examined (also with monospecific shade) in this study. The PCA also shows that the beta diversity of oak forest on rocky lava flows is closer to that of cloud forests and their gaps than to that of other oak forests. This can be explained by the fact that the oak forest on the rocky lava flows shares two thirds of its species with cloud forests and their gaps, but only 44% of its species with other oak forests above 1,600 m asl. The communities with the greatest similarity in their composition were cloud forests and coffee plantations with polyspecific shade, cloud forests and their gaps, and oak forests and their adjacent secondary vegetation (Table 5, Fig. 4). Cloud forests and their gaps, and the coffee plantations with polyspecific shade form a small group on axis 3 of the PCA (Fig. 4). Axes 2 and 3 explain 29.86% of the total variance.

GAMMA DIVERSITY

In the tropical landscape gamma diversity was 31 species, 30 Scarabaeinae and one Silphidae. Gamma diversity in the transition landscape was 30 species, 26 Scarabaeinae and four Silphidae. In the mountain landscape, gamma diversity was 17 species, 11 Scarabaeinae, four Geotrupinae and two Silphidae (see Appendix 2, Appendix 3, and percentages of species exclusive to each landscape in Table 6).

Table 6

Gamma diversity of copronecrophagous beetles for three landscapes in central Veracruz, Mexico. Exclusive species, shared species and complementarity (excluding Aphodiinae).

Indicators of Gamma Diversity	Landscape		
	Tropical	Transition	Mountain
Total # of species	31	30	17
% species exclusive to the landscape	61.29	40	47.06
% species shared			
with the Tropical landscape	-	29.03	3.22
with the Transition landscape	29.03	-	26.67
with the Mountain landscape	3.22	26.67	-
% complementarity			
with the Tropical landscape	-	82.69	98.87
with the Transition landscape	82.69	-	79.49
with the Mountain landscape	98.87	79.49	-

There were significant differences in the number of sites where each species was found in each landscape (Kruskal, *H* = 7.606, *P* = 0.022). In the mountain landscape, species were distributed in many fewer sites than in the transition (Dunnet's Method, *q'* = 2.65, *P* < 0.05), or the tropical landscape (Dunnet's Methos, *q'* = 2.279, *P* < 0.05).

From the general list of species (Appendix 3), some of the ubiquitous species, such as *Dichotomius colonicus, Onthophagus hoepfneri, Onthophagus chevrolati retusus* and *Oxelytrum discicolle*, were collected from more than one landscape. *Euoniticellus intermedius*, an invader species that has only been in the region for a few years (first record in 1995, see Montes de Oca & Halffter 1998), was found in the pastures of the tropical and transition landscapes from sea level up to 1,400 m asl.

The species composition of the tropical landscape was very different to that of the other two. This is seen in the Principal Component Analysis (Fig. 4). The complementarity of the tropical and mountain landscapes was 98.87%, for the tropical and transition landscapes it was 82.69%, and for the transition and mountain landscapes it was 79.49%.

The tropical landscape shared 29.03% of its species with the transition landscape and only 3.22% with the mountain landscape. The tropical landscape had the highest proportion of exclusive species (61.29%). The transition landscape shared 26.67% of its species with the mountain landscape, a value very similar to the percentage of species shared with the tropical landscape. In spite of its transitional character, 40.00% of the species of the transition landscape were exclusive to it. 47.06% of the species of the mountain landscape were exclusive (Table 6).

DISCUSSION AND CONCLUSIONS

We present the discussion of our results in two parts. In the first we discuss the three levels of biodiversity – alpha, beta and gamma – for each of the three landscapes studied. In the second part we draw some general conclusions and make some closing remarks.

ALPHA DIVERSITY

Tropical landscape
The complete dominance of the Scarabaeinae subfamily (97% of the total species) within the group of copronecrophagous beetles of this landscape is a biogeographical phenomenon characteristic of Tropical America (see Halffter & Matthews 1966). In addition to the Scarabaeinae and one species of Silphidae there were some species of Aphodiinae, almost all of the genus *Ataenius* (see Appendix 1).

The origin of the greatest difference found in the number of species per site is ecological, and this difference depends on the type of soil, its depth, shallowness, or scarcity as occurs where there are rocky lava flows (see below); and above all the effect on substrate of arboreal cover.

In the low deciduous forests, the alpha diversity of Scarabaeinae ranges from 8 to 15 species (mean: 11.33). These data coincide with those published for other low deciduous tropical forests in Mexico where there has been disturbance by humans: 12 species in Jojutla, Morelos State (Deloya *et al.* 1987), 15 species in Tepexco, Puebla State (Deloya 1992), and 16 species in El Crucero, Veracruz State (Pensado-Cadena com. pers.). On the Pacific slope 13 and 19 species were caught at two sites of tropical deciduous forest in the Manantlán Reserve in the States of Jalisco and Colima (García-Real 1995). At all of these sites, the number of species per site is much lower (from a quarter to a half, if not less), than the number found in Tropical America in sites with rainforest (see Montes de Oca & Halffter 1998, Halffter & Arellano 2002). The latter is even true when, for the comparison, we do not consider the number obtained in a given site or the mean value, but rather the cumulative richness for a given type of community. In the deciduous tropical forests of central Veracruz, cumulative species richness is 22. Comparing this with published data that we are certain refer to cumulative alpha richness, we have very similar values for similar ecological and biogeographical conditions: 20 species in the Manantlán tropical deciduous forest (García-Real 1995) and 22 species in patches of tropical forest in Tolima, Colombia (Escobar 1997). On the other hand, for southern Veracruz (Los Tuxtlas), in fragments of tropical rainforest, the cumulative richness of copronecrophagous beetles is 30 species (Estrada *et al.* 1998). In this region (Los Tuxtlas), for the entire landscape including fragments of rainforest, cocoa, coffee and citrus plantations, as well as pastures, the gamma diversity is 36 species, which emphasizes the greater predominance of the rainforest species (Estrada *et al.* 1998) as compared to that found in the tropical landscape we studied.

In the pastures of the tropical landscape species exchange is notable (see beta diversity), but the number of species remains fairly constant: from 9 to 14 species per site (mean: 11) with a cumulative richness for the community of 21 species (see Appendix 3).

In secondary vegetation next to patches of deciduous tropical forest, there were 9 to 13 species per site (mean: 11), with a cumulative richness of 17 species. These areas have dense vegetation which allows some forest species to coexist with heliophilous species from the open areas (Appendix 3). These data indicate an interesting constancy in the number of species, both for sites and for communities. This, even though there are some very important qualitative differences between the species of the forest (and, in part, in the surrounding secondary vegetation) and those of the pastures; species of the latter being more heliophilous and predominantly coprophagous.

The tropical forests that grow on the rocky lava flows are quite different from the three community types mentioned above, in that they are much poorer in species (4 to 5 species, cumulative richness: 7). None of these species is exclusive to this type of community, but rather all are the most widely spread and most ecologically tolerant. The volcanic extrusion on which these forests grow is one of the youngest of the lava flows in the three landscapes studied (less than 5,000 years old). The soil, formed by the disintegration of the lava, accumulates in fissures and depressions but is only a few centimetres thick. This could

adversely affect nesting for many Scarabaeinae species. As such, the number of individuals of the few species collected is lower than that for the other communities of the tropical landscape.

The species composition of the communities in the tropical landscape depends on the degree of arboreal cover (see Halffter & Arellano 2002). The more continuous the canopy, the greater the number of species from the forest and the fewer the number of heliophilous species. In the most intact forests (Jalcomulco, for example) more than 70% of the species are exclusively forest dwelling, while in sites with greater degrees of disturbance, and consequently reduced arboreal cover, as much as 70% of the species are heliophilous. The same has been observed in Colombia (Escobar 1997).

In the most disturbed patches of tropical forest, some species become very abundant. This is the case with *Canthon (Canthon) cyanellus* and *Deltochilum lobipes*. Favila and Halffter (1997) documented how the rank of *C. cyanellus* varies in terms of abundance according the degree of disturbance in the landscape. This species went from being the 11th of 27 species in the rainforest of Chajul, Chiapas, to ranking 12th of 24 species in the Los Tuxtlas, Veracruz rainforest, and to being the first of 18 species in pastures with forests remnants in Laguna Verde, Veracruz. One possible explanation offered by the authors is that *C. cyanellus* prefers the environment at the forest's edge and fragmentation increases the extent of this environment or similar conditions.

Kramer (1997) has indicated that the existence of abundant populations of some species of plants and animals appears to be a general characteristic of fragmented systems. Some species respond to an increase in the borders of the original community (the forest) resulting from fragmentation. Debinski & Holt (2000) and literature cited therein provide a review of the studies on the effects of fragmentation.

Transition landscape

Biogeographically, the three suprageneric taxa (Scarabaeinae, Geotrupinae and Silphidae) of the indicator group found in this landscape show an overlap between the species that follow a Neotropical distribution typical of the tropical landscape, and those that follow the Nearctic and Paleoamerican mountain pattern characteristic of the mountain landscape. However, there is a notable number of exclusive species (see Table 4, Appendix 3 and biogeographical analysis in Halffter *et al.* 1995). The same happens with Aphodiinae (see Appendix 1).

With 10 to 13 species (mean: 11.67), the alpha diversity in the cloud forest was among the highest found in the three landscapes; only bettered by that of the deciduous forests and their neighbouring pastures in the tropical landscape. In similar a cloud forest near the Orizaba Volcano, Veracruz, Pensado-Cadena (pers. com.) captured 8 to 15 species (mean: 11.5) per site.

With respect to the species richness of cloud forest, it is important to consider that those we have studied, as well as most of the other surviving patches of this type of forest in the region, have been intensely disturbed and fragmented by human activity.

At sites located in the gaps of cloud forest, i.e. with no arboreal cover, we captured 8 species. This represents a poor subset of the cloud forest fauna. As expected, 100% of the species caught are shared with the cloud forest.

The alpha diversity for sites of coffee plantations with polyspecific shade (12 - 13 species) is similar to that of the neighbouring patches of cloud forest. These plantations have the greatest area with arboreal cover in this landscape and comprise an important element of the matrix by linking the patches of cloud forest. Their three layers of vegetation (Jiménez-Avila & Correa 1980, Aguilar-Ortíz 1982, Cházaro-Basáñez 1982, Nestel 1990, Nestel *et al.* 1993) make them similar to the disturbed cloud forests that still exist. In addition, at least temporarily, there is more excrement available, especially human. This explains the abundance of some exclusively coprophagous forest species such as *Dichotomius satanas* (see Appendix 3).

There is a contrast between the results for coffee plantations with polyspecific shade, and those with monospecific shade. In the latter, the number of species is lower (5 to 8 species per site) than the number found in neighbouring cloud forests. These data are similar to those found in similar coffee plantations (4 to 7 species per site; Morón & López-Méndez 1985, Morón 1987, Nestel *et al.* 1993).

In the pastures next to cloud forests, site alpha diversity (7-10 species, mean: 8.5) was lower than that of the forests. Species inhabiting the pastures belong only to the Scarabaeinae family. These pastures serve as corridors that allow the heliophilous and thermophilous species such as *Dichotomius colonicus* and *Euoniticellus intermedius* from the tropical landscape to move to higher altitudes. In contrast with the tropical landscape, here there is no group of species that is specific to deforested areas, although some (such as *Onthophagus chevrolati retusus* and *Dichotomius colonicus*) are more abundant in the pastures and a few, such as *Canthon humectus* and *Phanaeus amethystinus*, are only found in this type of community. The latter two species are more abundant (and biogeographically characteristic) of the mountain landscape and, as such, their presence in the pastures of the transition landscape represent an altitudinal expansion down to lower levels.

The alpha diversity recorded for the oak forest (8-10 species, mean: 9) was lower than that obtained by Pensado-Cadena (pers. com.) for the region near the slope of the Orizaba Volcano in Veracruz (15 species). These notable differences are explained by differences in the type of oak forest and their altitudes. The forest of Pensado-Cadena's study was located at 750 m asl and at 1,600 - 1,800 m asl in the present study. The comparison and the number of species of the indicator group in the oak forests studied by Pensado-Cadena are similar to the values we recorded for the forests of the tropical landscape.

Secondary vegetation next to oak forest had 7 species, all of which were also found in the oak forests, and therefore represents a species-poor subset of the oak forest fauna.

The mean alpha diversity in the pine-oak forests of the transition landscape (8 species) was less than that found in the cloud and oak forests. As altitude increases (towards more temperate conditions) the number of Scarabaeinae species decreases (pine-oak forests are at a higher altitude). Mean alpha

diversity in the pine-oak forests we studied was greater than that reported by García Real (1995) for the Manantlán mountain range or by Pensado-Cadena (pers. com.) in the region of the Orizaba Volcano, both of whom captured a mean of 6 species.

In pastures next to pine-oak forest alpha diversity varied from site to site (5 - 11 species), but the mean was similar to the value for pastures next to cloud forest (8.5), even though the composition was very different. In pastures next to pine-oak forest we found species from the mountain landscape, such as *Canthon humectus*.

We attribute the variation among pastures to differences in the time elapsed since deforestation. Where less time has passed since the forest was cut, there has been less opportunity for the process of assemblage of new beetle communities. Similarly, in communities growing on rocky lava flows (discussed below), as the assemblage process matures, more niches are occupied and the number of species increases.

At the transition landscape the rocky lava flows are 5,000 to 10,000 years old, on a site that is 36,000 years old (Geissert 1994). This means the soils are deeper than those of the tropical landscape. Consequently, the number of species of the indicator group is equivalent to that recorded on the other kinds of soils (Table 3).

The mean alpha diversity for sites in the transition landscape (8.54 species) was similar to that obtained for the tropical landscape (10.25 species), and suggests a regularity in the number of species at sites located in the tropical and subtropical areas of Mexico that share a similar biogeographical history.

As for the tropical landscape, the cumulative species richness in the transition landscape was almost double the mean alpha diversity and indicates high values of temporal species exchange. In the cloud forests, characterized by a high degree of heterogeneity in their vegetation, cumulative richness was 18 species; a little less than that found in the tropical forests. In pastures next to cloud forest cumulative richness was only 66.66% of that recorded for the adjacent forests.

We have already mentioned that there is no specific group of species in the treeless environments of the transition landscape. Also noteworthy is the lack of Scarabaeinae roller species in the pastures. This absence truly leaves an empty niche given the high availability of dung which is only partially used by burrower species. There is ample documentation confirming that the coprophagous beetle fauna of various tropical and subtropical areas is made up of roller and digger Scarabaeinae species, and that the differences in their behaviour allow them to exploit excrement in different ways. In our study region, the roller species are found in the pastures of the tropical and mountain landscapes. They are not however found in the pastures of the transition landscape. The presence of *Canthon humectus* in some of the higher altitude pastures of the transition landscape is clearly the result of downward expansion from the mountain landscape and there is only one necrophagous roller species in the forests. This phenomenon has also been observed for sites at similar altitudes and with similar ecological conditions in Colombia (Escobar 1997, Escobar & Chacón de Ulloa 2001).

Mountain landscape

This landscape has species with biogeographical affinities that are distinct to those of the species of the tropical landscape (see Halffter *et al.* 1995). In terms of the representation of the indicator group there is a decrease in the relative importance of the Scarabaeinae and an increase in that of Geotrupinae and Silphidae (all together 6 species; see Appendix 3). There is also a substitution in Aphodiinae: *Aphodius* and relatives are the dominant genera and there is only one species of *Ataenius* in a site at a relatively low altitude in the landscape (see Appendix 1 and Lobo & Halffter 2000). Furthermore, this is the only one of the three landscapes studied where the richness of the indicator group is higher in treeless sites (3 to 7 species) than in the forests (2 to 5 species; see Appendix 3 and Table 3). In biogeographical terms, this landscape has more affinities with the nearctic element of North America. Sites without arboreal cover share geographic and ecological continuity with the large expanses of the Mexican High Plateau that have similar conditions. For ecological reasons the Scarabaeinae have greater affinity for higher light conditions. In this landscape there is a convergence with what is found in southern Europe: much greater species richness in the grasslands (see, for example, Kadiri *et al.* 1997).

In the grasslands of the mountain landscape during the day, insolation levels result in more temperate conditions. This community type has its own Scarabaeoidea (Scarabaeinae plus Geotrupinae) fauna. In the conifer forests *(Pinus, Pinus-Alnus* and *Abies)* which are much less heterogeneous than the tropical and subtropical forests, and colder than the treeless areas, the number of Scarabaeoidea and Silphidae is low (2 to 5 species). García-Real (1995) found 6 species of beetles in similar forests in the Manantlán mountain range. In highland vegetation, a harsh environment with marked changes between day and night time, we only found two species of Silphidae. Close to the Orizaba Volcano, Pensado-Cadena (pers. com.) did not find a single species belonging to the indicator group above 3,000 m asl.

In the mountain grasslands *Onthophagus hippopotamus* was found, along with 4 species of *Aphodius,* inside pocket gopher burrows (Rodentia Geomyidae: *Cratogeomys merriami perotensis* Merriam). These species are found between 3,000 and 3,100 m asl (see Appendix 1; Lobo & Halffter 1994). We captured *O. hippopotamus* at 2,450 m asl, the lower limit of its altitudinal range.

Silphidae show a preference for forests, both in this and the transition landscape. Within the genus *Nicrophorus*, there is an ecological and altitudinal substitution. *N. olidus* is mainly found in the cloud and oak forests of the transition landscape, while *N. mexicanus* is found in pine forests of the transition and mountain landscapes. Other authors (Arellano 1992, Halffter *et al.* 1995, Navarrete-Heredia 1995, Martínez-Morales *et al.* 1997, Arellano 1998, Navarrete-Heredia & Quiroz-Rocha 2000) confirm this segregation. *Tanatophilus graniger*, which has a clear northern affinity, is abundant in the forests of the mountain landscape. The only elements of the indicator group found in forests growing on the rocky lava flows were two species of Silphidae (Appendix 3).

The cumulative richness of 13 species in the mountain grasslands is almost double that of the richest of the neighbouring forests (Table 3). Under the most

open conditions, *Phanaeus amethystinus* and *Ontherus mexicanus* are found and these species were also collected in the transition landscape. The rest of the species form a group characteristic of the mountain landscape, a few of which are also found on the Mexican High Plateau.

BETA DIVERSITY

Tropical landscape
   In previous studies (Halffter *et al.* 1992, Halffter & Arellano 2002) we have indicated that there are two different groups of fauna in the tropical landscape: one of forest Scarabaeinae species and one with heliophilous species, characteristic of pastures. In spite of this, the number of species shared by different community types is relatively high (Table 4). The most characteristic fauna is that of the tropical forests (22 species in total, 6 exclusive). This fauna shares more than half of its species with the pastures and with secondary vegetation. Our results coincide with those obtained by Escobar & Medina (1996) for a region of Colombia with forests and pastures where the primary vegetation is rainforest. In contrast, in a landscape with rainforest fragments, plantations and pastures in southern Veracruz (Los Tuxtlas), the proportion of forest species is markedly greater than that of the pasture species (Estrada *et al.* 1998).
   Analyzing the beta diversity among the sites of a given community (Table 5), the exchange was low compared to those sites with better conditions for the beetles, and high among those sites with harsh environments. The highest beta diversity was found for tropical forests on the rocky lava flows (77.5%). This clearly indicates the relatively greater number of non-resident individuals (metapopulations, tourist species) under harsher conditions. A good many of these individuals could arrive from nearby communities to take advantage of occasional food, but they do not nest because of the scarcity of soil. Among these individuals, large species dominate (>70%) as do those with a greater ecological tolerance.

Transition landscape
   Species exchange among cloud forests was 37.37% (Table 5). On comparing beta diversity among sites with forest or with pastures for a given location, the greatest exchange was recorded between a small but well preserved fragment of cloud forest and its neighbouring pasture. The latter had species very characteristic of treeless areas, such as *Dichotomius colonicus* and *Scatimus ovatus*, that do not enter the forest. Taken together (Table 5) the differences between cloud forests and pastures are great. In contrast, between cloud forests and coffee plantations with polyspecific shade, the exchange was limited (14.3%, see Table 5). This similarity (lower beta) is confirmed for the number of shared species between the most widely distributed natural community (i.e. the cloud forest) - even though it is currently fragmented and partially altered - and the anthropogenic community that is most densely treed and covers the greatest area of this landscape (i.e. the coffee plantation with polyspecific shade).

This is very important for the conservation of the species originally limited to cloud forest. In other groups of organisms, such as for birds in both Chiapas (Greenberg *et al.* 1997) and in central Veracruz (Aguilar-Ortiz 1982) a similar phenomenon occurs. According to Muñoz *et al.* (2000) for the amphibians and reptiles of the El Triunfo Reserve in Chiapas, coffee plantations with polyspecific shade function as a community that preserves the species of both cloud forest and pine-oak forest, as well as connecting the patches of forest that still exist.

The Scarabaeinae and Silphidae of the transition landscape move through this mosaic of cloud forest, gaps in the forest and coffee plantations with polyspecific shade. To a lesser degree they enter the pastures and coffee plantations with monospecific shade. Thus, the greatest values for mean beta diversity (>55%) are recorded between cloud forest and the pasture, or between the cloud forest and coffee plantations with monospecific shade (Table 5).

Mountain landscape
There is a high degree of species exchange between the pasture and fir forests (>79%) or pine forests (>63%). This exchange is a consequence of the rich copronecrophagous fauna that is characteristic of treeless places (see Table 5); of which only a very small proportion enter the forest.

GAMMA DIVERSITY

We have seen how gamma diversity for the three landscapes is determined by the relationship between alpha and beta diversity. However, gamma diversity does have its own value, a historical value, on which the number and composition of species found in a landscape depends.

In the tropical landscape, the richness of the indicator group is primarily a result of the Scarabaeinae which are characteristic of the tropical forest, although there is a group of species associated with open conditions. In contrast, for the mountain landscape, the most important element is comprised of the species of the indicator group that are associated with open areas. In the transition landscape the species associated with the cloud forest dominate.

In the tropical and transition landscapes, the dominant fauna corresponds to the natural community that was most extensive before human intervention. The fact that there are more species in the grasslands of the mountain landscape, even though this is not the dominant natural community, is related to the thermophilous and heliophilous characteristics of the Scarabaeinae. (These beetles are not abundant in other cool, temperate forests of the rest of the world).

In the three landscapes that we have studied, the fragmentation of the natural communities does not appear to have caused the loss of species (see Closing Remarks below). In the tropical landscape the fragmentation of the tropical forests has favoured the expansion of species from open areas. These heliophilous and coprophagous species include two recent invaders (*Digitonthophagus gazella* and *Euoniticellus intermedius*) which are very abundant in some pastures. Fragmentation has also favoured the expansion of ubiquitous

species, or those that take advantage of the edges of communities, such as *Canthon (Glaphyrocanthon) leechi* and *Canthon (C.) cyanellus*. In contrast, fragmentation has resulted in a contraction in the distribution of specialists such as *Canthon (Glaphyrocanthon) femoralis* that exploit the excrement of arboreal mammals, especially that of monkeys. For now, as far as we can determine, no species has disappeared. This has to do with the topography of the landscape and the type of deforestation that has occurred. Gorges with steep slopes help the narrow strips of tropical forest to survive. The majority of the pastures are not totally denuded of trees since gorges, living fences with trees and trees in the pastures help to maintain the connectivity of the landscape (Guevara *et al.* 1998).

In a tropical landscape such as that of central Veracruz the deciduous or semi-deciduous tropical forest has alternated between forest and open areas over centuries. Hence, the heliophilous species are more numerous than in the parts of Tropical America that were originally covered with tropical rainforest. In the latter, the effects of deforestation are much more drastic (Howden & Nealis 1975, Klein 1989, Turner 1996, Laurence & Bierregard 1997, Estrada *et al.* 1998). Nevertheless, even where rainforest completely dominates, there are some heliophilous species (those of the gaps or edges) that respond favourably to forest fragmentation (for related information on the butterflies of the Amazon, see Tocher *et al.* 1997).

In the transition landscape there are no species that are characteristic of the pasture. *Phanaeus amethystinus* which shows a consistent affinity for open conditions, is more abundant on the lower levels of the mountain landscape. Although *Onthophagus incensus, Copris incertus* and *Ontherus mexicanus* are found more often in the pastures, unlike in the tropical landscape, there is not a clear separation between the fauna of the pastures and that of the forest. Under these conditions the coffee plantations with polyspecific shade provide an important connection between the surviving fragments of cloud forest. These plantations occupy a wide area and, as qualitatively and quantitatively shown in this research, are an example of the ideas of Víctor M. Toledo and colleagues (Moguel & Toledo 1999, Toledo *et al.* 1994) with respect to how diversified agro-silvicultural exploitation can help conserve biodiversity.

The absence of a group of fauna characteristic of the pasture in the transition landscape is confirmed by the lack of an ecological group: the roller beetles (see Alpha Diversity), and also by the good number of cow pats that go unexploited. The latter is emphasized by the unequal development of the grasses.

It is evident how fragmentation and the change of communities can reduce the number of species that are found in a landscape. On losing the conditions that are favourable for a given population, it disappears. But, how can a certain degree of fragmentation and landscape modification result in an increase in the original number of species? For this to happen, two conditions must be met. First, the fragments of the original community that persist must be of a sufficient size and there must be adequate interconnection so that populations are not lost. The required size and degree of connectivity varies greatly from one species to the next. See below for a discussion of species that can adapt to a metapopulation dynamic.

Second, the new conditions created by the change open opportunities. They allow colonization by species that were previously outside of the landscape, and not necessarily in contiguous places. This occurs in the three landscapes that we analyzed. In the tropical landscape, deforestation creates or expands pastures and this allows heliophilous species and those that prefer cow dung to extend their distribution. Deforestation in the transition landscape permits heliophilous species at both higher and lower altitudes to move downwards or upwards. And finally, in the mountain landscape deforestation creates conditions that are more favourable for the penetration of some tropical species, but especially the heliophilous species of the Mexican High Plateau. It is evident that the altitudinal gradient favours these types of displacement associated with the modification communities that previously were the most continuous and wooded.

An idea of the relative richness of each landscape is given by the mean alpha diversity by landscape (that is, the mean of all the alpha diversity values found in all the communities of a given landscape). These values are 10.25 species for the tropical landscape, 8.45 species for the transition landscape and 3.37 for the mountain landscape. These data are notably influenced by the richness of the main component of the indicator group: the Scarabaeinae, which is much more abundant in species in the tropical landscape.

Complementarity among landscapes

Species composition is very distinct in the three landscapes and so complementarity is greater than 79%. The proportion of species exclusive to each landscape are 70.97% in the tropical, 47% in the mountain, and 43% in the transition landscape; the latter sharing the most species with the other two (Table 6).

Complementarity between landscapes was calculated with and without Aphodiinae species. Complementarity between the tropical and transition landscapes is $C_{12} = 82.69$ (with Aphodiinae) and 77.11 (without), and between the tropical and mountain landscapes it is $C_{13} = 97.87$ and 94.81, indicating totally different fauna (only one species is shared). Between the transition and mountain landscape complementarity is $C_{23} = 79.49$ and 35.00. Here, the marked change that occurs on including Aphodiinae is the result of this subfamily having many species that are shared between this last pair of landscapes.

CLOSING REMARKS
1. As far as our data allows us to speculate, the effects of human activity (deforestation, changes in landscape use to pastures or crops, alteration and/or fragmentation of the forests) has not affected the total number of species of the indicator group in any of the three landscapes. We do however have doubts about the cloud forest which is the foundation of gamma diversity in the transition landscape. These doubts can only be resolved by a comparative study of a well preserved and biogeographically equivalent cloud forest with the cloud forest of central Veracruz (see Appendix 4).

It is interesting that disturbance by human activity appears to have been overcome by the beetles of the indicator group for different reasons in each landscape. In the tropical landscape it is a result of the heliophilous fauna, for which the number of species has even increased with the recent arrival of two invaders. This fauna also complements the tropical forest fauna that lives in the remnant fragments, and a small proportion of it is adapted to the pastures. This is why the pasture fauna is not poor in species, as might be expected in a landscape once dominated by deciduous tropical forests (see Montes de Oca 2001 for an analysis of pasture fauna in Los Tuxtlas, southern Veracruz and its relationship to the forest and forest remnants). In the transition forest, where we feel the impact on the forest has been greater, the coffee plantations with polyspecific shade have mitigated anthropogenic effects by creating a matrix that connects the fragments of cloud forest. In the mountain landscape the indicator group is not naturally species rich in the cool temperate forests. The expansion or creation of grasslands has increased the availability of conditions favourable for heliophilous species.

It remains to be seen whether these findings can be applied to other groups of animals and plants. We do not expect all biota to have the same capacity for homeostasis in the face of anthropogenic changes as the indicator group of beetles we have studied. From the work done by our research group Julián Bueno-Villegas (pers. com.) has found 23 species (preliminary data) of Diplopoda in the cloud forest and only 2 in coffee plantations, with only one species shared between the two communities. Diplopods are very sensitive to the loss of forest cover and the introduction of agricultural and animal husbandry practices (Bueno-Villegas & Rojas 1999).

An interesting sign is that throughout the sampling of our indicator group we have not detected any extinctions (aside from our doubts about the cloud forest). This, in spite of the disappearance or big decrease in birds, medium-sized and large fauna (often as a direct result of hunting). Here, we refer to extinction at the landscape level since it is evident that at the local level, the number of species can be greatly affected by anthropogenic modifications. The homeostasis of the landscapes is an unexpected result of the topographic heterogeneity of central Veracruz, and of the previously mentioned factors which, to a certain degree, buffer the effects of anthropogenic changes. It is important to remember that for the Scarabaeinae, the most abundant of our indicator group, the main change has not occurred recently, but rather from the time of the 16th century when cattle, sheep and horses were introduced to Mexico. Additionally, in recent years evidence has been published (along with models for its analysis) indicating that some species can survive as metapopulations, even in highly fragmented landscapes (Wahlberg 1996, and literature cited therein).

It is important to note that in the tropical and transition landscapes (Scarabaeinae are poor indicators for mountain forests), there is the feeling that in the type of forest that originally dominated (i.e. the main "container" of species richness) fragmentation and alteration are very close to or have passed sustainable limits. This is especially apparent for the cloud forest, where the composition and richness of the indicator group is very similar to the values found

for the coffee plantations with polyspecific shade. This, added to the visual impression of alteration, makes us aware of the fact that it has not been possible for us to work with intact cloud forest, but rather only with remnants which are all in some way simpler than the original community. We used the word "feeling" above because we recognize that an analysis of the fragments that takes into consideration its size and shape, as well as the number of species, is required for the three landscapes. This would allow us to predict the point beyond which the number of species decreases dramatically.

Klein (1989) has published the only study to date regarding the number of copronecrophagous Scarabaeoidea (essentially Scarabaeinae) species and forest fragment size. This study was done in Manaos, Brazil and has been repeatedly cited to illustrate the catastrophic effects of deforestation and demonstrate the loss of species from tropical evergreen forest that occurs as fragment size decreases. However the landscape, even in the Amazon, has other components. Klein mentions that four species of *Canthon (Glaphyrocanthon)* appear in a gap of the forest. They are heliophilous species that are dominant at the edges and in gaps, just as *Canthon (Gl.) leechi* is in our study.

As our study shows for the tropical landscape, heliophilous species can even be found in regions originally dominated by tropical forest. The transformation of forest to pastures and the new availability of cattle dung allows these species to become more abundant and evident. (An analysis of the richness of dung beetle fauna in a highly fragmented landscape of southern Veracruz that has rainforest remnants, plantations and pastures can be found in Estrada *et al.* 1998.)

Thus, a question arises: Can the analysis of the species richness of a forest or of the dominant community allow us to predict what is happening to the diversity and species composition in the entire landscape? Our answer is no, although we must remember that we are working in a very heterogeneous region where there is obvious complementarity between the different communities of the landscape.

Smith *et al.* (1997) propose a reevaluation of the role of ecotones in the generation and maintenance of the biodiversity of tropical forests. Davis *et al.* (2000) show, for the conditions of Borneo, how forest species that live in more exposed conditions (edges, riverbanks) are more adaptable than those of the forest interior to anthropogenic conditions, such as forest plantations.

2. The title of this study reflects our interest in the relationships between the three expressions of biodiversity: alpha, beta and gamma. Gamma diversity depends on the biogeographical history of the landscape and is the most stable expression of biodiversity. It is also that which has greater homeostasis in the face of human activities. The value of alpha diversity depends on the biogeographical and historical events, but even more on the assemblage of the community being studied. In this study we have tried to see whether the characteristics of regional species richness (gamma) depend mainly on local richness (alpha) or on the exchange between communities (beta). Ricklefs (2000) also addresses this question with a different focus in his analysis.

It is important to understand the double sense in which the relationships between local diversities and landscape diversity manifest. The alternatives are: how many, and which species depend on the historical biogeographical

phenomena that have acted both on the biota and on the landscape. The value is expressed as gamma, but gamma is "constructed" from different values of alpha. This is why we say that gamma diversity is a determinant of alpha and beta diversity, but at the same time is also conditioned by the values of alpha and beta.

In the tropical landscape, gamma largely depends on the species richness of the community that was originally dominant (alpha): deciduous (or semi-deciduous) tropical forest. There is a notable degree of complementarity with the heliophilous fauna of the pasture that results in gamma (30 species) being higher than the cumulative richness for the deciduous forest (22 species) or the pastures (21 species, see Table 3). In the transition landscape, cloud forest had the highest richness and was most responsible for gamma diversity, though anthropogenic modification (i.e. deforestation) allows some species to ascend from the tropical landscape and others to descend from the mountain landscape. These species add to the gamma richness. In the mountain landscape the total number of species (17) is close to the cumulative richness of the pastures (13), but very different from that of even the richest forests (7 species). The creation or expansion of the grasslands creates the right conditions for the addition of a rich heliophilous fauna.

So, the relationship between the cumulative richness of the community that originally was the most important and the gamma diversity is different for each of the three landscapes, and these differences depend on whether or not there was an ecologically distinct species assemblage during the original conditions, and on the response of that assemblage to changes introduced by humans. We return to the title of our study and our central question: What is the order of importance of the factors that determine the diversity of a landscape? And our answer varies with the biogeographical history of the landscape. In the three landscapes, the species exchange between forested areas and their corresponding grasslands results in a value for gamma diversity that is superior to the highest recorded value of alpha diversity. Hence beta diversity is also very important to the gamma diversity of coprophagous beetles.

Moreno & Halffter (2001) did a study of bats in a valley of the tropical landscape with the same objectives as those of this study. They found that of the 20 species that comprised the gamma diversity, 18 were found in the richest community (subdeciduous tropical forest) and the remaining two were found in the riparian vegetation. In bats, the landscape's species richness depends on that of the richest community to a greater extent than it does in beetles.

In a study of frogs in the cloud forests, coffee plantations and pastures of the transition landscape, the expression of the components of diversity of beetles and frogs (two taxonomically and biologically distinct groups) is similar for parts of the landscape with similar characteristics (E. Pineda, pers. com.). Gamma diversity for the frogs is 21 (22 for beetles), and mean alpha diversity is 8.16 species for the frogs (9 for beetles). Species exchange between sites for both beetles and frogs is high and greater than between communities, suggesting that in this mosaic spatial heterogeneity is linked to the heterogeneity inherent to groups of species and that differences in the degree of conservation of each site lead to differences in the composition of the indicator groups.

3. Alpha diversity is one of the most frequently used values to characterize biodiversity. Although it is well defined in spatial terms, its large variation over time is not often considered. Along with Moreno and Halffter (2001), we distinguish the alpha diversity of a site or a community (which requires a varying amount of time to sample) from the cumulative species richness of a community (referred to as cumulative alpha diversity by Moreno and Halffter), which is the sum of all the species collected from a community during a given period of time. Taking into consideration the great variations that can occur between these two values (Table 3), it is interesting to ask which of these two values is most meaningful for the characterization of a community and its contribution to the biodiversity of the landscape (gamma).

The differences in the values of diversity are not constant. They are much greater in the communities that are the richest and most representative of each landscape, and in some communities the cumulative richness can be double the mean alpha diversity. These communities might be remnants of the natural vegetation or communities resulting from human activity. This is the case for the tropical forests and their neighbouring pastures in the tropical landscape, the cloud forests and coffee plantations with polyspecific shade in the transition landscape, and for the grasslands next to pine forest, as well as the pine forests themselves in the mountain landscape.

At the other extreme, in the poorest communities (including those on the rocky lava flows) cumulative richness and mean alpha diversity have approximately the same value. There is no evidence of species accumulation over time. This means that for the indicator group, and perhaps for many others, the communities that are richest in species have the greatest degree of species exchange over time. This conclusion is quite contrary to one's first impression. The communities that are richest in species correspond to the most complex assemblages: those where there should be fewer empty sites. How is it that under these conditions there are so many tourist species and even so much species exchange? One possible explanation is that the massive availability of herbivore and omnivore dung (cows, horses, pigs, sheep and even humans) is a new phenomenon across the entire gradient of landscapes, having occurred over the last 400 years for domestic livestock and several millennia for humans. The assemblage process has not finished; quite the contrary. Human activities such as deforestation, the introduction of livestock and the very presence of humans, have created new niches that have yet to be fully taken advantage of. In the transition landscape, this is quite clear in the unused dung piles that are abundant in the pastures.

An additional explanation exists. The richest communities are those that have the greatest number of rare species which, are the most likely to be missed during sampling. The number of species will be affected by both tourist species (occasional passersby) and individuals from the source populations. In both cases these beetles stay in these sites precisely because of the heterogeneity of the community which allows them to temporarily survive in the ecological spaces that are available.

Consistent with the importance of species exchange, the number of species exclusive to communities is low. The exception being the pastures next to pine forest in the mountain landscape where the highest absolute number of exclusive species was recorded. The pastures of the mountain landscape are a community

that was created or at least expanded by deforestation. The species of this community – even though they are exclusive in relation to the other communities of the same landscape (see Table 4) – represent a peculiar assemblage of species from distinct origins and come together in response to the open conditions and food availability (cattle dung).

The presence of exclusive species in communities of anthropogenic origin in the tropical and transition landscapes is the result of two invader species (only one of which is found in the transition landscape), and of the existence even in undisturbed conditions of a few species that prefer gaps (see comments in Closing Remarks 1).

The rocky lava flows have a drastic effect on the indicator group, especially the Scarabaeinae. In each of the three landscapes, the communities on this kind of soil are the poorest in species. In the transition and mountain landscapes the indicator group is only represented by the Silphidae that are less sensitive than the Scarabaeoidea to soil quality. In the tropical landscape the Scarabaeinae that are found on the rocky lava flows are the most abundant and ubiquitous of the landscape, but are always present in limited numbers (marginal specimens of nearby metapopulations). One exception is the abundance of *Canthidium puncticolle* and *Canthon (Gl.) leechi*, two species that are very small in size that were captured in a pasture on the rocky lava flows (see Appendix 3).

The comparison of the numeric values of mean alpha diversity by landscape or of the gamma diversity, disregards the very important replacement of species of different biogeographic origin that occurs in the indicator group (see Halffter *et al.* 1995, Lobo & Halffter 2000). In the tropical landscape, of 32 species, 31 are Scarabaeinae and one is Silphidae. In the transition landscape, of 30 species, 25 are Scarabaeinae, 1 is Geotrupinae and 4 are Silphidae. In the mountain landscape, of a total of 17 species, 11 are Scarabaeinae, 4 are Geotrupinae and 2 are Silphidae. Biogeographical replacement also occurs in the Aphodiinae. The genus *Ataenius* dominates in the tropical and transition landscapes, while *Aphodius* group of genera dominates in the mountain landscape (see Lobo & Halffter 2000).

4. The temporal and spatial dimensions of alpha diversity. Both this study and that of Moreno & Halffter (2001) demonstrate that alpha diversity has values that are far from fixed. Alpha diversity, that is the number of species that are found in a community, is one of the important characteristics and perhaps the most important in terms of reflecting the history of the community. It also contributes decisively to conditioning the structure and function of the community. These relationships between the number of species and structure and function require an in-depth review since, there does not appear to be confirmation of the linear, deterministic sequence that most authors have maintained to date.

If the community is an assemblage of species that varies in time and space, we should not be surprised that alpha diversity also varies in time and space. In this study we have explored spatial variation. What we call alpha diversity by site is the number of species found in a site when the sampling effort has resulted in the capture of at least 85% of the estimated number of species present. Mean alpha diversity of a community is the mean obtained by sampling the different sites that correspond to the same community in a landscape. This value does not take into consideration the spatial and stochastic variation among the samples (sites)

taken from an entity (community). The cumulative richness of species for a community is a cumulative value that ignores spatial and temporal variations within the sampling period.

We have not analyzed the differences in alpha diversity that the temporal dimension might cause, such as those resulting from the timing, duration and frequency of sampling, or how alpha diversity varies over the years and longer cycles of time.

This study clearly indicates that the expressions of alpha diversity we have studied, i.e. those associated with space, vary greatly depending on the type of community. If we consider the differences related to temporal variation, we believe that these too would depend on the type of community. The richest communities, such as the tropical forests exhibit a greater variation in alpha diversity over time owing to the low probability of capturing rare species. In simpler communities, such as those growing on the rocky lava flows in the tropical landscape, there is less variation in the number of species captured, since the species are more widespread.

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Appendix 1

The Aphodiinae species (Coleoptera: Scarabaeidae) of Central Veracruz, Mexico.The landscape in which the species are found in the Cofre de Perote Region of central Veracruz, Mexico. 1 = Tropical, 2 = Transition, 3 = Mountain. Sources for data collection are: A = occasional captures by Arellano and Halffter, B = captures made by Imelda Martínez and colleagues, C = data from Marco Dellacasa, as well as reports from the literature. Only one source is cited for cases where several authors report a species for a given location. Sources of bibliographic information are in Roman numerals: I = Lobo & Halffter (2000); II = Deloya (2000), III = Deloya & Lobo (1995), and IV = Deloya (1994). The local name of the site, its altitude and, where possible, the number of individuals captured or reported (ND = no data) are given. The taxonomic study used for the determination of Aphodiinae was Dellacasa *et al.* (2001) and for Eupariini, Deloya (2000).

Species	Landscape	Source	Site	Altitude (m asl)	No. ind.
Trichonotuloides glyptus Bates, 1887	3	A	San José Aguazuelas	2900	2
	3	I	Los Pescados	3000	19
	3	A	Estación Las Lajas	3000	1
	3	A	km 11 Cofre de Perote	3300	2
	3	C	El Triunfo	2600	6
	3	C	Tembladeras	3100	5
Agrilinus prope duplex LeConte, 1878	3	I	Los Pescados	3000	15
	3	I	El Conejo	3300	2
	3	A	km 11 Cofre de Perote	3300	42
Agrilinus azteca Harold, 1863	2	A	Barrio La Ermita	1900	1
	3	I	Chololoyan	2500	1
	3	A	Camino a Las Lajas	2900	7
	3	A	Estación Las Lajas	3000	3
	3	C	Cruz Blanca	2400	2
Chilotorax pumilio Schmidt, 1907	2	I	Ixhuacán	1900	10
	2	I	Acajete	2000	16
	3	I	Toxtlacoaya	2300	18
	3	I	Cruz Blanca	2400	57
	3	I	Chololoyan	2500	1
Chilotorax multimaculosus Hinton, 1834	3	I	Cruz Blanca	2400	4
Agrilinus lansbergei (Harold, 1874)	1	C	Palma Sola	4	2
Planolinus prope tenellus Say, 1823	3	I	San José Aguazuelas	2950	2
Blackburneus (sensu lato) guatemalensis ab scotinus (Bates, 1887)	2	C	Las Animas	1400	6
	2	C	El Fresno	1800	2
Trichonotulus perotensis Lobo y Deloya, 1995	3	III	Los Pescados	2900-3100	90
Platyderides pierai Lobo y Deloya, 1995	3	III	Los Pescados	2900-3100	36
Blackburneus (sensu lato) charmionus (Bates, 1887)	1	A	Otates	480	1
	3	C	Oxtlapa	2100	5
	3	C	2 km from Oxtlapa	2400	2
	3	C	San José Paso Nuevo	2300	1
	2	C	km 14.5 Xico-Oxtlapa	2050	5
Cephalocyclus hogei (Bates, 1887)	3	I	San José Aguazuelas	2950	23
	3	I	Cruz Blanca	2340	25
	3	A	Plan del Vaquero	2900	3
	3	A	Camino a Las Lajas	2920	26
	3	A	Estación Las Lajas	3000	78
Planolinus vittatus Say, 1825	2	B	Alto Lucero	1100	2
	2	I	Ixhuacán	1900	17
	3	I	Cruz Blanca	2400	10

Appendix 1 Continuation

Species	Landscape	Source	Site	Altitude (m asl)	No. ind-
Planolinus vittatus Say, 1825	3	B	Rancho Los Salazares	2450	21
	3	I	Chololoyan	2500	1
	2	C	Xalapa	1400	1
	3	C	El Triunfo	2600	2
	3	C	Los Laureles	2500	1
	3	C	Oxtlapa	2100	8
	3	C	2 km from Oxtlapa	2400	14
	3	C	San José Paso Nuevo	2300	75
	3	C	San José Aguazuelas	3000	2
	3	C	Tonalaco	2350	11
Gonaphodiellus opistius Bates, 1887	2	I	Acajete	2000	506
	2	C	El Fresno	1800	92
	2	C	La Joya	2000	7
	3	I	Cruz Blanca	2400	17
	3	I	San José Aguazuelas	2950	1
	3	I	Chololoyan	2500	570
	3	I	Ixhuacán	1900	2915
	3	C	Rancho Los Salazares	2450	35
	3	C	A 2 km de Oxtlapa	2400	2
	3	C	Tetelcingo	2200	50
	3	C	Km 14.5 Xico Oxtlapa	2050	1
Agrilinus sallei Harold, 1863	2	C	Las Animas	1400	2
	2	C	Alto Lucero	1100	4
	2	C	Parque Ecológico Clavijero	1360	2
	2	C	Quiahuistlán	60	88
	1	C	Palma Sola	5	2
	1	C	La Estancia, Palma Sola	10	2
	1	C	El Toche, Chavarrillo	600	3
	1	C	Los Lirios, Actopan	5	15
	1	B	La Mancha	0	17
	1	B	Rancho el Tajo, Actopan	5	23
	1	A	Cerro El Metate	30	3
	1	A	Barranca Grande	980	1
	1	A	Dos Rios	990	30
Nialaphodius nigrita Fabricius, 1801	1	B	Quiahuistlán	60	10
	1	B	Villa Rica	4	4
	1	A	Cerro El Metate	30	2
	1	A	Dos Ríos	990	2
	1	C	Palma Sola	5	5
	1	C	El Tajo, Actopan	5	30
	1	C	La Estancia, Palma Sola	10	12
	1	C	Los Lirios, Actopan	5	68
	2	B	Alto Lucero	1100	1
	2	C	Km 14.5 Xico Oxtlapa	2050	1
Labarrus pseudolividus Balthasar, 1941	1	B	Quiahuistlán	0	5
	1	B	Villa Rica	4	6
	1	B	Rancho Los Lirios, Actopan	5	3
	1	C	Palma Sola	5	1
	1	C	El Tajo, Actopan	5	54
	1	C	Quiahustlán	60	26

Appendix 1 Continuation

Species	Landscape	Source	Site	Altitude (m asl)	No. ind.
Labarrus pseudolividus Balthasar, 1941	1	C	La Estancia, Palma Sola	10	4
	2	B	Alto Lucero	1100	22
	2	A	El Fresno	1920	36
	2	C	Club Hípico, Las Animas	1400	5
	2	C	Las Animas	1400	66
	3	C	Los Laureles	2500	1
	3	C	Oxtlapa	2100	1
	3	C	Tembladeras	3100	1
Ataenius apicalis Hinton, 1837	1	II	Villa Rica	10	ND
	1	II	Actopan	200	ND
	1	IV	Cotaxtla	50	ND
Ataenius euglyptus Bates, 1887	3	A	Las Vigas	2450	1
Ataenius languidus Schmidt, 1910	1	II	Puente Nacional	6	2
	1	IV	Cotaxtla	50	2
Ataenius cibrithorax Bates, 1887	2	IV	Xalapa	1400	ND
Ataenius imbricatus Melsheimer, 1844	1	II	Cotaxtla	50	ND
	2	IV	Xalapa	1400	ND
Ataenius holopubescens Hinton, 1938	1	IV	Cotaxtla	50	ND
Ataenius abditus (Haldeman, 1848)	2	A	Rancho Briones	1360	ND
Ataenius sculptor Harold, 1868	1	IV	Cotaxtla	50	1
	2	A	Ixhuacán	1900	14
Ataenius strigicauda Bates, 1887	1	II	Cotaxtla	50	ND
	1	IV	Veracruz	5	ND
	2	IV	Xalapa	1400	ND
Ataenius jalapensis Bates, 1887	2	II	Xalapa	1400	ND
Ataenius liogaster Bates, 1887	1	II	Villa Rica	10	ND
	2	IV	Xalapa	1400	
Ataenius texanus Harold, 1874	1	IV	Puente Nacional	60	1
Ataenius glabriventris Schmidt, 1911	1	IV	Cotaxtla	50	4
Ataenius capitosus Harold, 1867	3	IV	Las Vigas	2400	ND
Ataenius figurator Harold, 1867	1	IV	Córdoba	900	ND
Ataenius rickardasi Hinton 1938	1	IV	Veracruz	5	ND
	1	IV	Cotaxtla	50	1
	2	IV	Huatusco	1250	2
	2	IV	Fortín de las Flores	1000	1

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Appendix 2
A list of the Scarabaeinae species found in Laguna Verde, Veracruz, Mexico.

Species	Community	
	tf	pt
Onthophagus batesi Howden y Cartwright, 1963	0	1
Onthophagus schaefferi* Howden y Cartwright, 1963	0	1
*Onthophagus hoepfneri** Harold, 1869	0	1
Digitonthophagus gazella (Fabricius, 1787)	0	1
Dichotomius amplicollis (Harold, 1869)	1	0
Dichotomius colonicus (Linneo, 1767)	0	1
Copris incertus (Say, 1835)	1	0
Canthidium puncticolle Harold, 1868	1	0
Copris lugubris Boheman, 1868	0	1
Phanaeus scutifer Bates, 1887	0	1
Phanaeus tridens Castelnau, 1840	0	1
Coprophanaeus pluto (Harold, 1863)	1	0
Sisyphus mexicanus Harold, 1863	0	1
Eurysternus mexicanus Harold, 1869	1	0
Euoniticellus intermedius Reiche, 1849	0	1
Canthon (Glaphyrocanthon) circulatus Harold, 1868	1	0
Canthon (G.) leechi (Martínez Halffter y Halffter,1964)	1	0
Canthon (G.) antoniomartinezi Rivera y Halffter, 1999	1	0
Canthon (C.) cyanellus Le Conte, 1859	1	0
Canthon indigaceus chevrolati, Harold, 1868	0	1
Deltochilum lobipes Bates, 1887	1	0
Deltochilum scabriusculum Bates, 1887	1	0
Alpha Diversity		

* Mario Zunino identified these species and recommends a taxonomic revision of this group of *Onthophagus.*

Appendix 3
The distribution and alpha diversity of Scarabaeinae, Geotrupinae and Silphidae species in sites with expected capture rates above 85%.

Community	tf						tfr		pt				ptr		svt	
Site	1	2	3	4	5	6	1	2	1	2	3	4	1	2	1	2
Species																
Onthophagus batesi Howden y Cartwrigt, 1963	1	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0
Onthophagus schaefferi Howden y Cartwrigt, 1963	0	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0
Onthophagus hoepfneri Harold, 1869	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1
Onthophagus igualensis Bates, 1887	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Digitonthophagus gazella (Fabricius, 1787)	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0
Dichotomius amplicollis (Harold, 1869)	1	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0
Uroxys boneti Pereira y Halffter, 1961	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
Canthidium puncticolle Harold, 1868	1	1	0	0	1	1	0	0	0	1	0	1	1	1	0	1
Dichotomius colonicus (Linneo, 1767)	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1
Copris incertus (Say), 1835	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1
Copris lugubris Boheman, 1868	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1
Phanaeus endymion Harold, 1863	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Phanaeus tridens Castelnau, 1840	1	1	0	0	1	0	0	0	0	0	1	1	1	1	0	0
Coprophanaeus telamon Harold, 1863	1	1	1	1	1	0	0	1	0	1	0	1	0	1	0	0
Coprophanaeus pluto (Harold, 1863)	1	1	0	0	0	1	1	0	1	0	0	0	1	0	0	1
Sisyphus mexicanus Harold, 1863	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Eurysternus mexicanus Harold, 1869	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Euoniticellus intermedius Reiche, 1849	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Canthon (Glaphyrocanthon) femoralis (Chevrolat,1834)	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Canthon (G.) leechi (Martínez Halffter y Halffter,1964)	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1
Canthon (G.) zuninoi Rivera y Halffter, 1999	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0
Canthon (G.) moroni Rivera y Halffter, 1999	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Canthon (G.) antoniomartinezi Rivera y Halffter, 1999	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Canthon (Canthon) indigaceus chevrolati Harold, 1868	0	1	1	1	1	0	0	0	0	1	1	0	1	0	1	1
Canthon (C.) cyanellus Le Conte, 1859	1	1	1	1	1	1	0	0	1	1	0	1	0	0	1	1
Deltochilum gibbosum Bates, 1887	0	0	1	1	1	1	1	1	1	1	0	0	0	1	0	1
Deltochilum lobipes Bates, 1887	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deltochilum scabriusculum Bates, 1887	0	1	1	0	1	0	0	1	0	1	0	1	1	0	1	0
Oxelytrum discicolle (Brullé, 1840)	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Alpha Diversity	10	14	15	8	10	11	5	4	11	11	9	14	12	7	13	10

Appendix 3 Continuation

												**Transition Landscape**												
Community	cf			of		ofr	por			pof	cm		cp		pc		prof	gc		svo	ppor			prpo
Site	1	2	3	1	2	1	1	2	3	1	1	2	1	2	1	2	1	1	2	1	1	2	3	1
Species																								
Onthophagus schaefferi Howden y Cartwright,1963	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Onthophagus hoepfneri Harold, 1869	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Onthophagus incensus (Say, 1835)	1	1	1	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1	1	1
Onthophagus cyanellus Bates, 1887	1	1	1	1	1	1	1	0	1	1	0	0	1	1	0	1	0	1	1	1	1	1	1	1
Onthophagus corrosus Bates, 1887	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Onthophagus nasicornis Harold, 1869	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Onthophagus mextexus Howden, 1879	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	1
Onthophagus subcancer Howden, 1973	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus aureofuscus Bates, 1887	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus chevrolati retusus Harold, 1869	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1
Onthophagus rhinolophus Harold, 1869	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Dichotomius amplicollis (Harold, 1869)	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Dichotomius colonicus (Say, 1835)	0	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0
Dichotomius satanas Harold, 1867	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	0	1	1	1	0	0	0	0
Ateuchus illaesum Harold, 1868	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Scatimus ovatus Harold, 1862	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Ontherus mexicanus Harold, 1869	1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	1
Copris incertus (Say, 1835)	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	0	1	0
Phanaeus endymion Harold, 1863	1	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0
Phanaeus amethystinus Harold, 1863	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Coprophanaeus telamon Harold, 1863	1	0	1	0	0	1	0	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0
Eurysternus magnus Castelnau, 1840	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
Euoniticellus intermedius Reiche, 1849	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Canthon humectus (Say, 1832)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0
Deltochilum mexicanum Burnmeister, 1848	1	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Onthotrupes nebularum (Howden, 1964)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Oxelytrum discicolle (Brullé, 1840)	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	1	1	0	1	1	1
Nicrophorus olidus Matthews, 1888	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	1	0
Nicrophorus mexicanus Matthews, 1888	0	0	0	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	1
Tanatophilus graniger (Chevrolat, 1833)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Alpha Diversity	10	13	12	10	8	9	6	6	5	8	8	5	13	12	10	7	6	6	8	7	9	5	11	11

Appendix 3 Continuation

		Montane Landscape														
Community		pf			pfr	ff	pa		gp			gf	gpa		hav	
Site	1	2	3	4	1	1	1	1	2	3	4	1	1	1	2	3
Species																
Onthophagus mextexus Howden, 1970	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Onthophagus aureofuscus Bates, 1887	0	1	1	1	0	0	1	0	0	0	1	1	0	0	0	0
Onthophagus chevrolati retusus Harold, 1869	1	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0
Onthophagus fuscus orientalis Zunino y Halffter, 1988	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Onthophagus lecontei Harold, 1871	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Onthophagus chevrolati chevrolati Harold, 1869	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Onthophagus hippopotamus Harold, 1869	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Copris armatus (Harold), 1869	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Ontherus mexicanus Harold, 1869	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Phanaeus amethystinus Harold, 1863	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Canthon humectus (Say), 1832	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Onthotrupes nebularum (Howden), 1964	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Halffterius rufoclavatus (Jekel), 1865	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
Onthotrupes herbeus (Howden), 1964	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ceratotrupes bolivari Halffter y Martínez, 1962	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0
Nicrophorus mexicanus Matthews, 1888	1	1	1	1	1	0	1	0	1	0	0	0	0	1	0	0
Tanatophilus graniger (Chevrolat), 1833	0	1	1	0	1	1	1	0	0	0	0	0	0	0	1	0
Alpha Diversity	3	5	3	2	2	3	5	6	7	7	3	5	2	1	1	0

Appendix 4
List of the cited species for the Cofre de Perote region, but not collected in this article.

In searching for information on the species that might have escaped our collection efforts in the three landscapes in the Cofre de Perote region, we have carried out a thorough review of both collections and the literature. The species that have cited in some way for the region, but not collected by us are listed here.

Nicrophorus marginatus Fabricius, cited by Peck and Anderson (1985) for Xalapa. We have not collected this species, nor have any of our colleagues who carry out studies in the area of Xalapa. *N. marginatus* is widely distributed in southern Canada, the majority of the United States of America, and enters northern Mexico (Coahuila, Durango) and extends to Mexico City D.F. and Puebla (in the centre of the Mexican High Plateau). According to Peck and Anderson's data (1985) this is the only record of this species for Veracruz State.

Copris laeviceps Harold is cited by Matthews (1965) for Xalapa, but was based on specimens collected by Hoege (British Museum). We are quite familiar with the distribution and ecological requirements of this species. It is associated with the rainforest and conditions that are more tropical than those of Xalapa. It is possible that this identification is the result of the erroneous labelling that frequently occurred in the 19th century.

Copris rebouchei Harold is a species from the Balsas River Basin. Matthews (1965) includes a site in Coatepec which would be the most eastern of its distribution area. Coatepec is within our study region and is not an impossible site for the collection of *C. rebouchei*. However, if the specimens on which Matthews bases the record correspond to this site, then it is totally marginal to its main area of distribution. The other site reported in Veracruz: Presidio, is clearly an error. Many years ago, one of the authors (G. Halffter) received from a collector who lived in Presidio material erroneously referenced to this location; and it is from there that the specimens labelled from Presidio come.

Phanaeus mexicanus Harold is cited by Edmonds (1994) for sites near our transect, but located either on the Pico de Orizaba volcano slope or in the most tropical and rainy region of Los Tuxtlas. *P. mexicanus* appears to have a vicariant distribution with *P. scutifer* which is found in the transect.

Phanaeus sallei Harold is cited by Edmonds (1994) for Banderilla, Xalapa and Cosautlán - all places that are located in our transect. We have not collected this species which tends to have the rest of its distribution in more tropical areas than the places cited. Even so, its presence as cited by Edmonds does not seem impossible since it has been collected in cloud forest in Chiapas State, in the Montebello Lagoons and in rainforest. Perhaps its present is restricted to the lowest parts of some ravines in our transect.

Literature Cited

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