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THE USE OF INDICATOR GROUPS FOR MEASURING BIODIVERSITY AS RELATED TO COMMUNITY STRUCTURE AND FUNCTION [1]

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RESUMEN

En este trabajo se discuten las razones para utilizar grupos indicadores en la medida de la biodiversidad a nivel de especies (diversidad organismal de Harper y Hawksworth). Se profundizan nuestras propuestas anteriores para el uso de los escarabajos del estiércol de la subfamilia Scarabaeinae (Insecta: Coleoptera) como grupo indicador para estudiar los tipos de comunidades que conforman los bosques tropicales y formaciones derivadas, especialmente por la acción antrópica. Se plantea cómo obtener una información cuantificable que permita realizar estudios comparativos, así como un análisis de los efectos de la acción humana al alterar, fragmentar y destruir las comunidades naturales. Aunque el énfasis se pone en el grupo indicador y las comunidades escogidas, se plantea este análisis de la biodiversidad para ser utilizado con otros grupos y en diferentes tipos de comunidad. Aunque todo lo que planteamos como argumentos para el análisis a través de grupos indicadores puede aplicarse a distintos enfoques del estudio de la biodiversidad a nivel de especies, este trabajo se concentra en presentar la metodología adecuada para el análisis ecológico. Es decir, para el estudio de la biodiversidad puntual como elemento para la interpretación de la estructura y función de las comunidades.
Palabras Clave: Biodiversidad. Grupos indicadores. Scarabaeinae.

ABSTRACT

In this study we discuss the reasons for using indicator groups to measure biodiversity at the species level ("organismal diversity" *sensu* Harper and Hawksworth). We further explore our previous proposals for the use of dung beetles belonging to the subfamily Scarabaeinae (Insecta: Coleoptera) as an indicator group for studying the types of communities found in tropical forests and derived formations, particularly those created by human activity. We present a method for obtaining quantifiable information that allows comparative studies to be done, as well as an analysis of the effects of human activities that result in the alteration, fragmentation and destruction of natural communities. Although emphasis is placed on the indicator group and the communities selected, we propose that this analysis of biodiversity can be used with other groups and in different community types. The arguments we present for the use of indicator groups can be applied to different ways of studying biodiversity at the species level, however this study focuses on presenting appropriate methodology for ecological analysis; that is, for the study of local biodiversity as an element for the interpretation of community structure and function.
Key Words: Biodiversity. Indicator groups. Scarabaeinae.

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INTRODUCTION

Since the 1980s, in both the scientific community and in the general public, there has been an increasing awareness of the effect of human activities on biological diversity. The current loss of species has stimulated the analysis of conceptual frameworks about the origin and function of biological diversity in order to make operative proposals for conservation (of the abundant recent literature see: Wilson, 1988; Solbrig, 1991; Ricklefs & Schluter, 1993; Hawksworth, 1995). During this century, the perception of species diversity has evolved from being considered the result of an historical process that reflects the accumulation and extinction of species through time (a perspective derived from taxonomy and paleontology, predominant at the beginning of this century), to being studied almost exclusively as the result of ecological interactions, primarily competitive, in small areas and habitats (the ecological perspective of the 60s and 70s). The current position (since the 1980s and particularly in the 90s) is that of reconciling both of these perspectives and of acknowledging that patterns in diversity are the result of a variety of ecological and evolutionary processes, of historical events and geographic circumstance, as well as ecological interactions. The recent book edited by Ricklefs and Schluter (1993) presents a brilliant synthesis of this new vision of biodiversity.

The analysis of biodiversity can be carried out from various fronts. We can make an ecological interpretation of local diversity of the species diversity that we find in a given ecosystem, as an important way of coming closer to understanding community structure and function (ecological focus of diversity). Another approach is to analyze the historical and geographical factors that have shaped a group of species at the landscape or regional level (biogeographical focus of biodivorsity). Lastly, we can analyze the species richness of a landscape or region and determine how it was formed, whether by high local diversity or through a notable turnover in species (strict analysis of biodiversity). This last focus is very similar to that which Hammond (1995) refers to as a "species richness assay". Each of these approaches treats the species as the unit of study, which Harper and Hawksworth (1995) refer to as the organismal level of biodiversity, distinguishing it from the genetic and ecological levels.

Regardless of the focus with which we approach our analysis, one conclusion that emerges is that if we cannot measure biodiversity on the same scale as that of the study, then we cannot predict the effects of changes imposed by humans with any degree of accuracy. The new biological discipline that is emerging addresses two key questions: Is biodiversity a measurable property? What is the most appropriate way of measuring biodiversity? (Harper and Hawksworth, 1995). The enormous difficulties of evaluating biodiversity, considering all organisms, whether at the local (alpha) scale, with respect to replacement (beta) or at the regional (gamma) scale, can be overcome by the use of groups of organisms that allow reliable relationships to be established between the information obtained in the field and global species richness, as well as between biodiversity and other characteristics of the ecosystem. In particular, the use of indicator groups allows one to follow up on what is happening to biodiversity by monitoring them. In recent years, there has been an increase in the search for indicators, the quantitative expression of which allow us to understand more clearly what is happening in the general community. Nevertheless, efforts for the selection of key groups in different types of ecosystems are still scarce (See Kremen, 1992, with respect to the selection of a group of indicator species. Regarding the measurement of biodiversity see: Magurran, 1988; Brown, 1988; Margalef, 1991; Toledo, 1994).

Although mammals, birds and flowering plants have been used as biodiversity indicators, there has recently been a strong tendency to consider insects and other arthropods for these types of studies (e.g. Webb, 1989; Brown, 1991; Coddington *et al.*, 1991a; Holloway & Stork, 1991; Kremen, 1992; Halffter *et al.*, 1992; Pearson & Cassola, 1992; Halffter & Favila, 1993; Kremen *et al.*, 1993; also see reference to the work of P.M. Hammond in Hammond, 1995; Finnamore, 1996). The most likely reason for this is that more than 80% of all the species in the world are insects, in addition to the fact that it is possible to establish simple systems for the capture of insects which provide quantifiable information.

There is no doubt that in complex ecosystems such as tropical forests, reliable information about total biodiversity can only be acquired after comparing the results for different groups of organisms obtained with different methodologies and even different theoretical approaches; in this way, findings can be corroborated. This is both desirable and possible in certain locales (see proposals in Coddington *et al.*, 1991b).

One of the types of ecosystems most threatened by human activity is tropical forest, which ranges from tropical rain forest to tropical deciduous forest. Tropical forests are the terrestrial ecosystems with the highest local species diversity (alpha diversity), the most complex ecological structure and tremendous spatial heterogeneity (beta diversity), but where knowledge of all these characteristics is more limited than for other vegetation types (Longino, 1994). Our objective in this article is to recapitulate and analyze our previous proposals (Halffter, 1991; Halffter *et al.*, 1992; Halffter & Favila, 1993) about the use of the guild of dung beetles of the subfamily Scarabaeinae (in the taxonomic sense followed by Halffter & Edmonds, 1982) as an indicator group for the study of basic aspects of biodiversity in tropical forests and for the evaluation and monitoring of the effects of anthropogenic alteration of these ecosystems. Although the arguments that we present for the selection of an indicator group can be applied to different approaches to the study of biodiversity as measured with species, this study proposes a methodology for an ecological analysis of biodiversity. That is, by using the Scarabaeinae as the material and tropical forest and derived ecosystems as the object of study, we offer an approximation of how the study of an indicator group can be used to measure and monitor the biodiversity of an ecosystem and its anthropogenic derivatives. Using the same reasoning for the selection of the indicator group, but with different analytical methods, it is possible to do biogeographical analysis of regional biodiversity (Halffter *et al.*, 1995) or the study of what we have referred to as biodiversity *per se.*

SCARABAEINAE AS AN INDICATOR FOR THE STUDY OF BIODIVERSITY

It is important to make an appropriate selection of the indicator group in order to justify its use as an indicator of modifications in the community or for the analysis of biodiversity. It does not necessarily follow that a group of organisms that works well in a given ecosystem will produce equally reliable results in other ecosystems.

For the same objectives and with characteristics very similar to those that we give to the indicator groups (Halffter & Favila, 1993, this text), Hammond (1995) proposes the use of "focal groups" and other authors also propose "indicator groups" (Pearson & Cassola, 1992; Prendergast *et al.*, 1993; Pearson, 1994, 1995; Margules *et al.*, 1994, Faith & Walker, 1996).

The function of the indicator group is to make possible the approximation of an answer to a complex and laborious problem, that of measuring and monitoring total biodiversity. The suitability of the selection made for a given community will only be ratified by the usefulness of the results and their agreement with results obtained with other indicator groups or by other estimates for measuring biodiversity.

A good indicator of biodiversity should have several characteristics, the most important of which are indicated below (see also Pearson, 1994 and 1995). We compare these characteristics with the information available about the group (Scarabaeinae) that we previously proposed as an indicator of biodiversity in tropical forests, not only in order to demonstrate that it has been correctly selected, but also to establish guidelines for the selection of other indicator groups for the same type of community or for others.

1) The indicator group should be comprised of a rich guild and be well defined in the type of community for which one wishes to evaluate biodiversity. This guild should be important in the structure and functioning of the entire ecosystem.

The Scarabaeinae, well represented in tropical areas, comprises a very well defined guild in both the functional and the taxonomic sense, as it is a clearly monophyletic group. The number of species ranges from 25 to 70 in tropical rain forests (see Halffter, 1991), with as many as 124 species in African savannas (Cambefort, 1985, 1986). The importance of this group in recycling excrement (and in forests of the Americas and southeast Asia the recycling of small carcasses and decaying fruit) makes it a key element in the dynamics of the ecosystem (Halffter & Edmonds, 1982; Hanski, 1989; Hanski & Cambefort, 1991; Halffter, 1991). In the forests of the Americas many species have adopted necro-coprophagic feeding habits, and even exclusive necrophagy, to compensate for the historical reduction (in the evolutionary sense) in the number of large mammals that generate excrement. In this same geographic area saprophagic species that feed on decaying fruit are also important (see Halffter & Matthews, 1966; Hanski, 1989; Hanski & Cambefort, 1991; Halffter, 1991).

2) There must be sufficient information available on the natural history and taxonomy of the proposed indicator group to allow for (a) the identification of species and (b) the ecological interpretation of the results obtained. When errors in identification occur or when there are gaps in the literature on the biology of the group, that group is not useful for our objectives. If we extend comparative studies in the geographic sense to include communities that correspond to the same type of ecosystem, but do not necessarily include the same species, the need for sound biological and taxonomic information becomes even more important.

In general terms, the biology, behavior and ecology of the Scarabaeinae have been thoroughly studied (see syntheses by Halffter & Matthews, 1966; Halffter & Edmonds, 1982; Hanski & Cambefort, 1991). This knowledge, which includes a number of seminal taxonomic monographs as well as local and regional faunistic studies, makes it possible for this group to be used by non-specialists with a reasonable amount of effort. Currently, there are several taxonomists who study Scarabaeinae in different parts of the world. It would be relatively easy to make field species identification keys and have regional reference collections for the rapid identification of species.

3) The organisms that make up the indicator group must be easy to capture. Capture method must be standardizable and it must be possible to repeat the capture method in different sites according to a pre-established program. Meeting these requirements will ensure that the results obtained can be compared, whether they come from geographic locales of the same ecosystem,

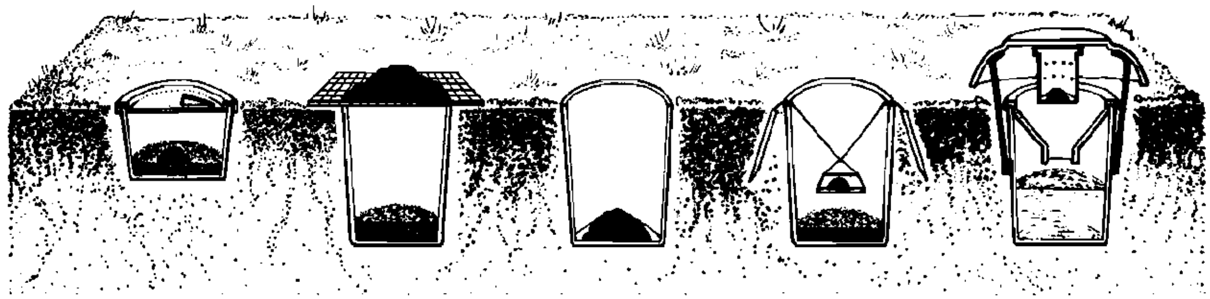
sites with different degrees of disturbance or sites that are biogeographically very different. It is important to remember that the usefulness of the indicator largely depends on the possibility of making comparisons of the data obtained, and consequently diagnoses and predictions. Coddington *et al.* (1991b) indicate that the sampling methods used for estimating species richness for a given area play a very important role in research on the loss of global biodiversity. In order to be useful, the methods should be rapid, as time is of the essence, and should also be reliable, simple and inexpensive.

The methodology for capturing Scarabaeinae has been standardized for quantitative sampling and is simple. Pit-fall traps are baited with excrement, carrion or decaying fruit and are buried at ground level (Fig. 1). The bait for coprophages is usually human or herbivore (cattle, mule or horse) dung. The most common bait for capturing necrophage beetles is a chunk of fish or squid. If, with the Scarabaeinae or other guilds, we wish to obtain a quantitative estimate for the purpose of analyzing and comparing the proportion of dominant, common and rare species, the relationship between species diversity, community complexity and other characeristics of communities, it is clear that we need collection methods that meet at least two requirements:

a) The results must be statistically comparable, implying that different samples are equivalent.

b) The specimens captured must statistically reflect the behaviour of the populations sampled. That is, we must emphasize a sampling design that allows us to estimate abundance and other measures of the different species that occur in the community with the number of specimens obtained in the sample.

There is ample evidence that pit-fall traps (Fig. 1) are appropriate for monitoring the abundance of dung beetles (Lobo *et al.*, 1988; Veiga *et al.*, 1989; Doube & Giller, 1990). However, the type of trap used can affect the results with ecological meaning (e.g. the relationship between the number of species and their abundance). Thus, it is preferable to use the same type of trap in the different study sites so that the results will be comparable. We have frequently used Trap A in Figure 1. This is a baited pit-fall trap with a hole in the lid that allows the volatile compounds of the bait to escape and the beetles to fall into the trap. A little soil is placed at the bottom of the box so that the beetles can bury themselves.



A B C D E

Figure 1
Types of traps commonly used for collecting coprophagous and necrophagous beetles (Halffter & Favila, 1993). The traps are buried level with the ground and a plastic top may be used to prevent rainwater from entering and sunlight from drying the bait. These traps are inexpensive and can be bought in any country.

The pit-fall traps are placed in the ground early in the day and collected, checked and rebaited at sunset in order to separate diurnal from nocturnal species. The use of soil in the trap instead of a compound that kills the insects allows the beetles to be released once they have been identified and eliminates any possible removal effect on the population in zones where the indicator group might have been affected by human activity. Specimens are only sacrificed for detailed taxonomic study where the coleopterofauna is poorly documented or in those cases where there is uncertainty about the identity of the species captured.

Sampling with pit-fall traps is the most appropriate approach for studies that have as their objective the ecological analysis of biodiversity because it is efficient, inexpensive and simple. However, for cases where it is necessary to obtain information about "all" the species in an area (analysis of biodiversity, *per se*), other complementary sampling regimes must be used (see Hill, 1996).

The simplicity and low cost of the sampling system, as well as the possibility of applying the method universally, makes the Scarabaeinae an ideal group for comparative studies of a given ecosystem found in different geographic locations. The necessity and importance of these studies has been emphasized by di Castri and Younès (1990). Sampling methods that are simple and not labour intensive make it possible to establish continuous, long term sampling programs because they do not require special equipment or specialized personnel. A useful estimate can be obtained by comparing unmodified forests or those with a low degree of modification with landscapes exhibiting different degrees of transformation, as long as one is working within an area that is biogeographically coherent, in the interest of reducing the noise that faunistic and taxonomic variations can introduce (see Halffter *et al.*, 1992). Another estimate can be obtained by comparing capture data collected before and after disturbance occurs. A simple monitoring program can determine the accuracy of the predictions made. These predictions and comparisons can be used for a global interpretation of changes in biodiversity.

We wish to emphasize the importance of having a sound statistical design for monitoring, to analyze the behaviour of the relationship between effort and species accumulation. Soberón y Llorente (1993) propose stochastic models for understanding the relationship between the collection time span and the number of species accumulated, since the longer a trap is in position, the greater the likelihood that more specimens will be caught. According to these authors this analysis gives more weight to faunistic and floristic studies and permits, among other things, (1) the quantitative comparison of lists of species, (2) the planning of collection activities in the field when the models predict that the maximum number of species has not been collected, and (3) their use as a predictive tool for the conservation and study of biodiversity. See the discussion of the use of accumulation curves and non-parametric estimates in Colwell and Coddington (1994, 1995).

4) The indicator group must be one for which collection and other necessary activities can be carried out without jeopardizing the conservation of the group.

On comparing different trap models used in Spain, Lobo *et al.* (1988) and Veiga *et al.* (1989) found that the traps tested reflected the taxonomic composition of the site well and did not result in a loss of species. Very few studies have been carried out in tropical regions (Hill, 1996; Santos, 1995) with the goal of comparing the efficiency of different trap models and systems for trapping, or for detecting the possible effects of removal on local populations. However, our extensive experience in the field leads us to believe that the repercussion of these samplings on natural populations is not considerable. Caves, mountain tops and similar sites in which populations consist of a reduced number of specimens are exceptions where livetrapping is strictly recommended. Beetles can be collected from the traps live and liberated after identification.

5) Capture data must provide enough ecological information to determine the composition and structure of the guild and its interaction with the rest of the community.

Scarabaeinae are an abundant group that is well represented in the tropical forests of the Americas as well as in other ecosystems such as the African savannas and open cattle ranching systems of the Mediterranean. Their role as the principal processors of the excrement of medium to large sized mammals makes them quite sensitive to changes in the composition and structure of a given community. Scarabaeinae are very sensitive to changes in vegetation. Numerous studies, especially those done in the tropics, have demonstrated that they are stenotopic with regard to vegetation cover (Howden and Nealis, 1975; Klein, 1989; Halffter *et al.*, 1992).

What follows is a list of the main variables which must be determined in order to reach an ecological interpretation of biodiversity.

To analyze guild diversity:

(a) Species richness: the number of species in each community.

(b) Indices of diversity and evenness. We propose the use of indices based on the proportional abundance of species: Shannon, Simpson, Hill. The last set of indices (Hill's numbers) seems to be the most appropriate (see below).

(c) An analysis of relative species abundance using importance curves (number of individuals or biomass per species).

To analyze guild structure:

(d) Trophic diversity: In the case of the Scarabaeinae, one of the following categories would be assigned to each species: generalist, strict coprophagous, necrophagous or saprophagous.

(e) Temporal diversity in activity. The separation of daily activity (diurnal, nocturnal and crepuscular species) and annual activity (changes in the species composition and abundance over the course of a year).

(f) Spatial segregation. In the case of Scarabaeinae, the relocation of food sources (in the case of digger and roller beetles) as well as the spatial separation of species due to external factors that affect resource availability (e.g. microclimactic variations and the spatial distribution of mammals) should be considered.

Of these points only the first, (a) species richness, provides the basis for a comparison of biodiversity in different tropical forests or modified ecosystems, if there are one or two well studied areas which facilitate the interpretation of other sites. Point (b) refines the ecological interpretation of alpha diversity. Point (c) is very useful for the analysis of changes in species/dominance relationships and allows us to evaluate the contribution of rare species, which exert a great influence on the shape of importance curves. The niche of the guild in natural and modified ecosystems is analyzed with points (d), (e) and (f), either by comparing different sites within a particular ecosystem or between different biogeographical regions. We stress here the importance of understanding the group's natural history, as this will permit the selection of those niche dimensions that must be analyzed in biodiversity studies. Multivariate methods of classification and ordenation are easily applied to the data matrix in the search for patterns of species which relate to gradients or environmental patches, e.g., the forest-clearing-edge-pasture-crop sequence.

6. The indicator group must not only provide information about the intact community, but also serve to measure decreases in biodiversity resulting from different causes: the reduction in area or available resources owing to human activity or environmental changes, different degrees of disturbance, management or other anthropogenic activity (Noss, 1990).

Studies by Halffter and Matthews (1966), Howden and Nealis (1975), Kohlmann and Sánchez-Colón (1984), Klein (1989), Halffter *et al.* (1992) and Hill (1996) show that the composition and organization of the Scarabaeinae species within tropical forests are different from those found outside forests. This allows us to speak of two guilds, one inside the forest and the other in the deforested surroundings. Transitional fauna, with its own ecological structure, is found in the ecotones. Here, we refer to landscapes in which tropical forest has been, or still is, the dominant community type. Under these conditions for native species of the Americas, Southeast Asia, and Australia, but not of Africa, in areas without dense arboreal cover, the Scarabaeinae guild is generally less rich than the guild found in the forest interior.

In each geographical area of the Americas, the existence of a series of very marked differences between Scarabaeinae guilds inhabiting the forest and in the immediate outskirts makes this taxon an excellent instrument for measuring the effect of change or partial transformation of tropical forest ecosystems on biodiversity (Halffter *et al.*, 1992). It is a group which clearly reflects the changes brought about by human actions such as ecosystem fragmentation, the depletion of fauna, simplification of the ecosystem and the effects of the introduction of cattle, among others.

HOW TO PROCESS THE INFORMATION

The short term consequences of forest destruction: changes in species diversity and modifications within the guild

Klein (1989), one of the first to document the effects of forest fragmentation on insects in the tropics, used the Scarabaeinae to show the effects of forest fragmentation and destruction on biodiversity. In fragments of 10 ha and 1 ha, the guild of these beetles is different from that found in continuous forest (Manaos, Brasil). This, despite the short lapse of time over which fragmentation occurred (2-6 years) and despite the short distance between the fragments (- 300 m). Upon comparison with the small deforested fragment, the change in the guild is almost complete; four species not found in either the 10 ha fragment or the continuous forest appear as dominant species. This study shows not only the change in the frequency with which each species is represented but also a modification in the composition of the guild itself (in species, biomass, and trophic structure). This change becomes drastic in the deforested area.

Using Scarabaeinae, Halffter *et al.* (1992) analyzed the short term (in Palenque, Chiapas) and long term (comparison of forests in the area of Laguna Verde, Veracruz, see below) effects of forest destruction and modification in Southeastern Mexico. In Palenque, they followed the methodology outlined herein to analyze the short term effect of deforestation by using capture data from 1965, for inside the forest (at the time largely undisturbed), on the forest edge and for nearby land with no arboreal cover, the latter characterized by horses, mules, some local inhabitants and visitors. In 1993, captures were repeated for the same sites, and these had changed in that there was a much greater human presence in deforested areas and along the forest edge, as well as greater proximity to the pastures created by cattle ranching (Data from 1993 is being processed).

Halffter *et al.* (1992) found that 11 of the 27 forest species were captured on the forest edges and only 5 in the deforested area (Table 1). Thus, 44% of the species expanded their distribution area to the edges but only 19% invaded the deforested area. All species found in the deforested area were also captured at the edge of the forest. This coincides with Klein's findings (1989).

Table 1
An analysis of the diversity of the Scarabaeinae guild in the Palenque, Chiapas forest and a recently deforested area in 1965 (data from Halffter, Favila & Halffter, 1992).

	Forest	Forest Edge	Pasture
Richness	27	11	5
Diversity (Shannon)	2.5	2.12	1.01
Evenness (Shannon)	0.76	0.88	0.62

The dominance-diversity curves which are based on the number of individuals (Fig. 2A) show that the distribution of abundance was more balanced in the forest than on the edge or in the cleared area, where a limited number of species were dominant. When dominance data were analyzed taking into account biomass (Fig. 2B), it became clear that there was a tendency toward a more balanced use of resources both in and around the forest, while the clearing showed a geometric distribution reflecting the dominance of a few species that are characteristic of harsh environments.

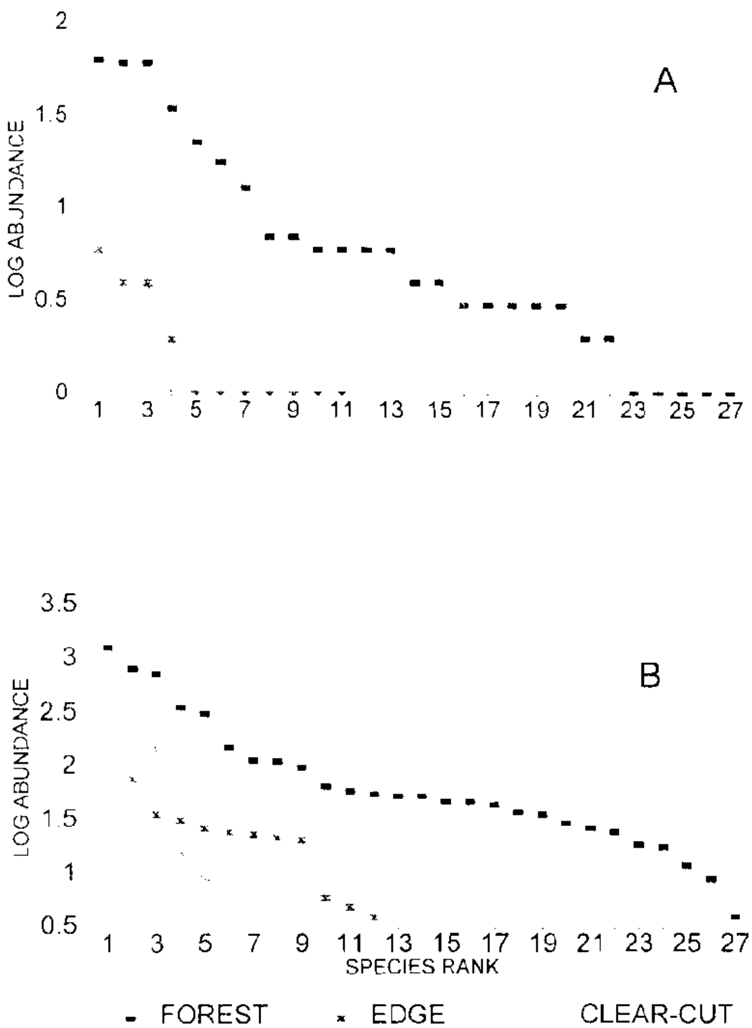


Figure 2
Dominance-diversity curves for three zones in Palenque, Chiapas. A. Number of individuals. B. Biomass.

With regard to guild structure, there was a greater proportion of non-roller than roller species in the three zones, but dominance of non-roller species lessened nearer to the clearing (Fig. 3A). As for trophic diversity (Fig. 3B), 52% of the forest species were generalists, 44% coprofagous and 4% necrophagous. At the edge of the forest, 73% were generalists and 27% coprophagous; there were no strictly necrophagous species. In the deforested area, 80% of the species were generalists and 20% coprophagous. With regard to activity period (Fig. 3C) in the forest and the edges, nocturnal species dominated notably. In the deforested area, however, there was a drastic change in guild composition: 80% of the species were diurnal and 20% nocturnal. Beetle size in the forest and edges ranged from 4 to 27 mm, but in the clearing from 4 to only 13 mm. This reduction is clearly related to the much greater importance of diurnal fauna, which are, on average, smaller in size.

The examples from Manaos (Klein, 1989) and Palenque (Halffter *et al.*, 1992), using Scarabaeinae as an indicator group in the same way that we propose in this study, show a drastic reduction in species as a short term result of forest destruction or fragmentation. They also illustrate changes in the structure and function of the guild. With deforestation, the proportion of small-sized, trophic generalist and diurnal species increases. In Manaos and in Palenque, both Neotropical areas originally covered by forest, a new guild appears. This new guild is much poorer in species and has a different structure than the forest guilds. What follows is a brief description of information that Scarabaeinae as an indicator group can provide about the long-term effects of forest destruction, fragmentation and change to pastures or other systems.

Analyzing diversity with the indicator group

Research which adopts the ecological focus for one or more sites included in analysis at this scale, using the same indicator group, will provide us with the means to interpret how the indicator group is integrated structurally and functionally, and will also allow us to predict how the group will respond to ecological changes. In addition, the ecological study of biodiversity, through monitoring programs, proves very valuable for the detection of small and intermediate changes.

A fundamental issue to be addressed in any study of biodiversity is that of scale. For example, the megadiversity index is a numerical way of referring to biodiversity and has been widely used in recent years. This index indicates the number of species per country for the most well-known groups of organisms (Mittermeier, 1988, 1990).

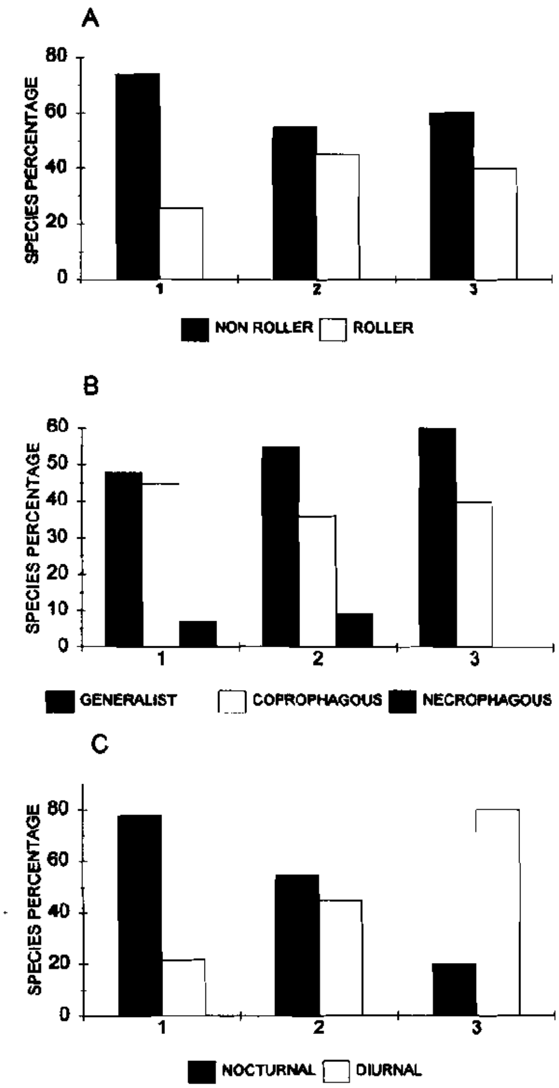


Figure 3
Ecological niche segregation of the Scarabaeinae guild in three zones in Palenque, Chiapas. 1. Forest, 2. Forest edge, 3. Open ground. A. Method of food relocation. B. Trophic segregation. C. Temporal segregation (data from Halffter, Favila & Halffter, 1992).

Although useful to indicate which countries have the greatest biodiversity on a global scale, it does not allow for the comparison of sites belonging to the same type of ecosystem or to different ecosystems. Nor can the megadiversity index serve as a basis for monitoring programs. In general terms, this occurs with any index that only takes into account the number of species belonging to one or several groups in extensive areas. In reality, these numerical expressions provide a sum total of the species found in different places and under different geographical conditions, the limits of which are rarely defined by nature as they are, most often, borders between countries or state lines.

Pielou's recent proposal (1991) is interesting, as it uses different strategy in the search for an all inclusive index of biodiversity; that is, one which takes into account all groups of organisms present in a given space. Pielou suggests the application of a diversity vector which, to be useful, must possess two properties: it must be formulated using information easily obtained from the field, and it must be easily understood by non-specialists.

In ecology, the variety of diversity indices is surprising. Why this growth in indices? Biological diversity has its own meaning when considered as the result of historical processes (evolutionary and geographical) and as a result of ecological processes; but it is also an element of ecological structure. In the sixties and seventies, ecologists were not interested in biodiversity *per se* but rather as a characteristic of the community which helped them to interpret how environmental resources and energy were distributed throughout biological systems. This led to the application of different methods of analysis which arose from systems theory. Thus, the study of biodiversity with an ecological perspective is a measure of the heterogeneity of a system, and this heterogeneity can be analyzed by focusing on different properties: balance, dominance, number of rare species, etc. This is why various indices of biodiversity are used in ecology, and why each has its own limitations (Ludwig and Reynolds, 1988).

According to ecologists, species diversity has two main components: species richness and the abundance of each of those species in a particular community (Magurran, 1988). Indices for measuring diversity generally incorporate these two components in a single value, which led Peet (1974) to call them heterogeneity indices. He recommends the use of indices which are easy to apply and interpret ecologically. The series of indices proposed by Hill (1973) meets these requirements well. He applies a family of diversity indices known as Hill's numbers. These measure the apparent number of species in one sample, and their units are given in number of species instead of bits, probabilities or other units of uncertain ecological value (Peet, 1974). With the exception of *N0*, Hill's indices are independent of size and number of sample units and, as a parametric family *et al.*, 1993). The family of diversity indices proposed by Hill in the form of an equation is:

$$NA = \sum_{i=1}^{s} (p_i)^{1/(1-A)}$$

where p_i is the proportion of individuals (biomass or other importance value), corresponding to the i th species and A is the order of the diversity index. Hill showed that the A = 0, A = 1 and A = 2 orders coincide with the most important measures of diversity (see Hill, 1973 for an explanation of this equation when A = 1). In this way, **N**0 is equal to the total number of species present in a sample; **N**1 is equal to the exponential of H', where H' is Shannon's index:

$$H' = \sum_{i=1}^{s} (pi \ln pi)$$

and **N**2 is the reciprocal of Simpson's index (i.e., $1/p^2_1 + 1/p^2_2 + \ldots + 1/p^2_n$). Explicitly, **N**0 is the number of species in the sample (regardless of abundance), **N**1 the number of abundant species in the sample, and **N**2 the number of very abundant species. **N**1 is more sensitive to changes in rare species, while **N**2 is more sensitive to changes in the very abundant species (Peet, 1974).

Using Hill's indices for three Mexican forests located in Boca de Chajul and Palenque in the state of Chiapas and for Los Tuxtlas in the state of Veracruz, as well as for a one-hundred year old pasture with forest fragments located in Laguna Verde, Veracruz, we found, that the number of species of Scarabaeinae (**N**0) collected in the forests was greater than in the pasture (Table 2). Only five of the species present in the pasture were also present in the forest, and all of these lived in fragments of surviving forest (Halffter *et al.*, 1992). Proportionally, **N**1 (abundant species) and **N**2 (very abundant species) tended to represent a greater percentage of the Laguna Verde pasture guild than in the forests. **N**1 and **N**2 represent a smaller proportion in Chajul compared to Palenque and Los Tuxtlas, which have similar values. Thus, the common characteristic of forests is the greater abundance of rare species, which in Boca de Chajul make up 51% of the total. This is not true for the pasture, where rare species account for only 2% of the total.

Hill's numbers tell us much about how biodiversity is affected by the ecological simplification of a complex community such as tropical forest. However, other diversity indices can be better measures in particular cases (Beav & Penev, 1995).

Currently, our research group at the Instituto de Ecología, A.C. is making comparisons among different types of tropical forest and pastures that result from deforestation and the introduction of exotic grasses and cattle. We are also comparing tropical forests and nearby coffee plantations, as well as tropical forests with different degrees of disturbance caused by clearing, the introduction of cattle or fragmentation. With the data from these studies for a given region, we can establish predictive models that indicate what will happen to the diversity of Scarabaeinae under different environmental conditions. The comparison of these results with data for other indicator groups will provide a quantitative approximation of how biodiversity is affected by anthropogenic changes.

Table 2

Diversity values using Hill's series for three tropical forests in southeastern Mexico. B. de Chajul (Morón *et al.*, 1985), Palenque, Chiapas (Halffter *et al.*, 1992), Los Tuxtlas, Veracruz (Morón, 1979) and for a pasture with remnants of tropical forest at Laguna Verde, Veracruz (Halffter *et al.*, 1992). Percent species in parenthesis.

Hill's Indices	B. de Chajul	Palenque	Los Tuxtlas	L. Verde
N0	27 (100)	27 (100)	24 (100)	18 (100)
N1	8.16 (30)	12.00 (44)	10.30 (43)	9.96 (55)
N2	5.25 (19)	8.00 (30)	7.24 (30)	7.66 (43)

One of the most pertinent questions which the ecological view of biodiversity addresses is the function of rare species (see Halffter and Ezcurra, 1992). Lovejoy (1988) presents two basic ideas about the origin and function of rare species in communities. 1) A community's rare species may have been important in the past but have been "marginalized" by the presence of other more competitive species. 2) Rare species may become important if the community undergoes change. In this way, the species that accumulate in an ecosystem as a consequence of historical events also provide the ecosystem with the capacity to respond to changing conditions.

In this context an important application of local ecological studies is their use as points of reference for "calibrating" the indicator group and the strategy for its use in the analysis of biodiversity *per se* at the landscape scale. If, within a given ecosystem, we compare two locales with different degrees of anthropogenic change, we find that the number of rare species is lower in the more modified locale. A drop in the number of species, which affects mainly the rare species, occurs at a local (alpha diversity) but not necessarily at a regional level. Over an extensive landscape, a certain degree of modification and fragmentation of human origin can result in an increase in the global number of species (gamma diversity), although within remnants of the original vegetation, local diversity may be lower than that found in an untransformed landscape (Gonzalo Halffter and Lucrecia Arellano, a study of the biodiversity of Scarabaeinae in Central Veracruz, personal communication).

One of the fundamental questions relating to the conservation of biodiversity concerns the degree to which can forests can be fragmented and patch size reduced (both the results of human intervention) before there is a drastic reduction in the number of species in the landscape unit. The answers will undoubtedly vary greatly depending on the indicator group selected.

The range which a particular species occupies within the importance curve of the indicator group provides an interesting approximation of the comparison between different locales (or with different degrees of modification) in one type of ecosystem. For example, *Canthon cyanellus cyanellus* LeConte is a copronecrophagous species of Scarabaeinae with an average abundance within the tropical forests of Mexico. While not truly rare, it is not one of the most important species found within the forest. By changing the ecological scenario and generating a landscape in which a vegetation mosaic dominates (pasture-forest fragments), this species acquires a very important role (Fig. 4). One possible explanation for its success in this type of modified environment is that *C. cyanellus* prefers to occupy the edges of tropical forest. As patches of forest vegetation are conserved in a mosaic landscape, the population density of this species increases (see Halffter *et al.*, 1992) because forest fragments are more similar to the forest edges in terms of the microclimactic conditions that they generate.

DISCUSSION

The practical difficulties in evaluating biodiversity, both at a local and regional level, lead to the search for strategies which yield results and can lead to recommendations in reasonable lapses of time. Of these, the most promising seems to be the use of indicator groups, also called focal groups. Through the use of indicator groups, we intend to establish reliable relationships between the information obtained in the field and the global richness of species, as well as between biodiversity and other characteristics of the community. Perhaps the most attractive aspect of using indicator groups is that it can provide an instrument for follow-up programs to monitor how biological diversity changes as natural communities are altered, fragmented or destroyed.

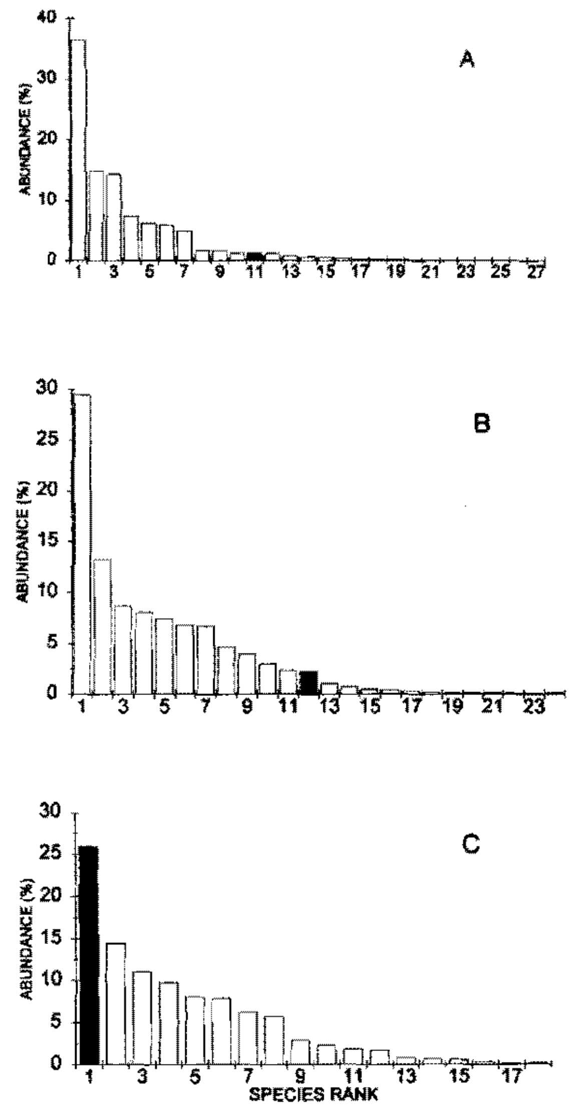


Figure 4

An example of changes in the position of *Canthon cyanellus cyanellus* (black rectangle) in relation to the dominance-diversity of the Scarabaeinae guild in: **A.** tropical forest in Chajul, Chiapas. **B.** tropical forest in Los Tuxtlas, Veracruz. **C.** pasture with remnants of tropical forest at Laguna Verde, Veracruz.

We have discussed the possibilities which indicator groups offer for the evaluation of biodiversity, using Scarabaeinae as an indicator group for tropical forests. We want to stress that not all groups of organisms are useful as indicators of biodiversity. Furthermore, a group that is adequate for one type of community is not necessarily appropriate for a different type of community. Scarabaeinae, because of their direct relationship to the excrement of large mammals (among them humankind and cattle, two rapidly expanding species), are thus of great ecological importance in a wide range of communities, but are only useful indicators in tropical forests and savannahs and in temperate, Mediterranean-type ecosystems.

This requires us to be diligent about keeping in mind one of the crucial attributes necessary in an indicator group: it must play a vital role in the type of community selected for study. If we are guided by this criterion when making our selection, we can avoid the controversy over evaluating the role of biological diversity in the community. The concern is over which is more important, one or several species (key species) that play a very specific role in the economy of a community, or a group of species found in a given place as a result of historical processes (and which may include redundant species).

The conditions which we have proposed here for the selection and use of indicator groups allow us to address this controversy. On one hand, the role of key species is made clear while the importance of the group of species, including rare species, is also considered.

When talking about biodiversity, we are not simply referring to the heterogeneity of a thermodynamic system in which efficiency is a basic requirement. Rather, we refer to the result of biological evolution, a process in which the redundance and the appearance of alternatives (i.e. species) occur with surprising frequency, even when these species do not appear to be ecologically important. It is this explosion of alternatives which determines the capacity for change and for adaptation to variable and often critical environmental conditions throughout geological time, as well as to present scenarios of drastic modification.

We do not view biodiversity as solely a response to the heterogeneity of the environment. It is also a consequence of historical processes such as the evolution of biota and of the earth. The survival and spatial coexistence of species which results from these processes has and will continue to be modeled by ecological determinants. But these, considered alone, do not explain the entire complexity of biological diversity.

In this paper we hope to have shown the virtues of using indicator groups as a strategy for measuring biodiversity. This strategy is effective both for analysis carried out from an ecological perspective and for a biogeographical interpretation of biodiversity. It is also effective for analysis which, at a local or regional level, attempts to evaluate biological diversity as a characteristic in its own right. From this last point of view, comparisons and syntheses based on results obtained with different groups make the strategy especially promising. Using this strategy to analyze the different ways in which anthropogenic activity affects biological diversity will permit the leap from postulating from a weak quantitative base to representative numerical estimations which can be compared and verified.

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