

**HABITAT MODIFICATION IN ANDEAN FOREST: THE RESPONSE
OF GROUND BEETLES (COLEOPTERA = CARABIDAE) ON THE
NORTHEASTERN COLOMBIAN ANDES**

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Trabajo de grado para optar al título de Biólogo

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To my family by its support.

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ABSTRACT

Habitat modification in Andean forest: the response of ground beetles (Coleoptera = Carabidae) on the northeastern Colombian Andes *

Juan Carlos Rey Velasco †

Keywords: Carabids, Diversity, Disturbances, Andes

Forestry practices, mainly the clear-cutting and establishment of young plantations, are two main drivers that increase fragmentation and change forest structure in many tropical forests. In the northeastern Colombian Andes, we studied changes in the composition and diversity of carabid assemblages in four different types of plant coverages affected by disturbance. We found a considerable change of carabid composition, diversity, and abundances among types of plant coverage. We found that carabid diversity and abundance were higher in the regenerating forests as the oak forest and gallery forest than in the natural forest as the undisturbed forest. Stenotopic species were associated with undisturbed forest, in contrast, eurytopic species were more abundant and associated with the oak forest. Therefore, the disturbance caused by the logging involved a loss of specialist species and an increase of generalist species in the disturbed areas. The local patterns caused by the disturbance might be related to the regional distribution of carabids species. Due to strongly association of some species with particular habitats, the regional distribution of specialist and generalist species might be determined by abiotic and biotic conditions as a results of differents events that lead the dispersal of carabids species.

*Proyecto de Grado: Habitat modification in Andean forest: the response of ground beetles (Coleoptera = Carabidae) on the northeastern Colombian Andes

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RESUMEN

Un ejemplo de modificación de hábitat: la respuesta de los carábidos (Coleoptera = Carabidae) en el nororiente de los Andes colombianos *

Juan Carlos Rey Velasco †

Palabras clave: Carabidos, Diversidad, Perturbación, Andes

Las prácticas forestales, principalmente la tala y la reporestación, son dos principales factores que aumentan la fragmentación y la estructura de los bosques y el cambio de muchos bosques tropicales. En el noreste de los Andes colombianos, se estudiaron los cambios en la composición y diversidad de los ensambles de carábidos en cuatro diferentes tipos de coberturas vegetales afectadas por la perturbación. Encontramos un cambio considerable de la composición de carábidos, la diversidad y abundancia. Se encontró que la diversidad de carábidos y la abundancia fue mayor en los bosques jóvenes regeneración como el bosque de roble y bosque de galería que en el bosque no perturbado. Las especies estenotópicas se asociaron con los bosques no pertrubados, por el contrario, las especies euritópicas fueron más abundantes y se asociaron con el bosque de robles. Por lo tanto, la perturbación causada por la tala implicó una pérdida de especies especialistas y un aumento de especies generalistas en las áreas perturbadas. Los patrones locales causados por la perturbación podrían estar relacionados con la distribución regional de las especies de carábidos. Debido a la fuerte asociación de algunas especies con hábitats particulares, la distribución regional de especialistas y las especies generalistas podría ser determinada por las condiciones abióticas y bióticas que permiten la dispersión de las especies de carábidos.

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AUTHOR SUMMARY

Carabids are a suitable group to detect changes in habitats affected by disturbance, mainly due to its important regulative role as predatory on ecosystems. To examine these changes in carabid diversity and composition, we conducted surveys in different habitats affected by the logging on the northeastern Colombia Andes. Our results indicated that carabids composition, abundances and diversity changed among the habitats. Carabid diversity was higher in the regenerated forest than in the mature forest. In addition, we found that the local distribution of carabids may be related with their habitat preferences and regional distribution. We postulate that habitat heterogeneity caused by the logging is the critical factor in structuring Andean carabids communities.

INTRODUCTION

Habitat fragmentation caused by selective logging is one of the most important factors that could influence the loss of biodiversity and landscape transformation [1–3], due mainly to the traditional reforestation strategies, that cause changes in microclimatic, abiotic and biotic conditions of the ecosystems [4]. Therefore, the disturbance regulates species diversity through the generation of habitat heterogeneity, which might induce changes in the community dynamics, and the ecological structures of the communities [1, 5].

Although ground beetles are a diverse group with a worldwide distribution, carabids species tend to consort specific habitats, since carabids are often affected by soil type, plant coverages, and microclimate [4, 6–8]. Consequently, carabids diversity and composition, make them suitable organisms to study impacts on habitat alteration and changes in terrestrial communities [9]. The taxon provides substantial ecological information about the functioning and the status of ecosystems [10], given by the high frequency and abundance in the ecosystems of low intervention [11], and the vital role as predators [12, 13].

Particularity in South America, the highest ground beetle species richness occurs in low lands, e.g. at a western Amazonian site, Erwin [14] collected a total of 569 species in an area of approximately 4000 hectares. Moreover, along eastern slope of the Andean Cordillera; where these species tend to have very restricted ranges [15]. Moret [16] reported an exceptionally high diversity of ground beetles in the Ecuadorian paramo, about 94% of the survey (191 species) were endemic.

Previous studies has been conducted on carabid diversity along an altitudinal gradient [17, 18]. However, data from Andes concerning disturbance caused by the logging effects on carabids communities are rather limited.

Overall, there are three fragmentation-related issues on ground beetles communities [9]:

1) species composition changes although species number may remain unchanged [19], 2) species abundance changes (increasing or decreasing) in some but not in all species [20, 21], and 3) specialist species decline and open habitat species increase [22, 23]. Therefore, one of the consequences of habitat fragmentation or disturbance of forests, is the increase of diversity. Heterogeneous landscapes enclose higher species diversity levels than homogeneous areas, since structurally complex habitats provide more habitats and ways to resource exploitation [24–27]. However, the effects of habitat disturbances on carabids are ambiguous. Indeed, previous research on coniferous plantation in Europe [26, 28, 29], suggested that species richness and diversity of carabid assemblages were lower in the coniferous plantations than in the adjacent deciduous forests. But some findings in boreal forests [23, 30] point out that species richness and abundance of carabid assemblages were much higher in young regenerating forests than in mature forests. This ambiguity may be the result of the different responses of individuals, their particular habitat requirements, and the different forest types studied [9, 21].

The aim of this study was to test the effects of disturbances caused by logging on carabid beetle communities in an area known as “La sierra” inside the Santuario de Fauna y Flora Guanentá, Alto Río Fonce at the northeastern Colombian Andes. There is no preliminar hypothesis to predict the pattern of overall carabid abundance at forest affected by the logging compared to undisturbed forest, as several authors record increases [23, 30] or decreases [26, 28, 29] of the abundance.

Initially, we expected little change in the number of species, i.e. species richness, between the disturbed forests and the undisturbed forest, as open habitat species may be abundant at the disturbed forest and forest specialists could be abundant in the undisturbed forest.

In terms of individual species, habitat generalists are expected to be little influenced by disturbance, while forest specialist species are expected to be negatively influenced. Open habitat species are expected to be more abundantly collected at disturbed forests than undisturbed forest. We also expect a greater diversity at the disturbed than undisturbed forests, since disturbed forests are more heterogeneous with open and dry areas in the same forest. Undisturbed forest are more homogeneous in terms of environmental conditions such as temperature, moisture and darkness.

RESULTS AND DISCUSSION

We collected altogether 1081 specimens of ground beetles belonging to four subfamilies, nine genera and twenty-four species (Table S1). These species of ground beetles were distributed in seven stands within four types of plant coverages: Open area (OP), Gallery forest (GF), Oak forest (OF) and Undisturbed forest (UF).

Nonparametric estimators ICE, Jackknife1, Jackknife2, and Chao2 suggested that the actual diversity of ground beetles at “La sierra” could be between 27 and 31 species. Therefore, we collected approximately 68-88% of the expected species for the area.

Rarefaction curves showed that the stands fell into four general categories (Figure 1). The first category, the species accumulation curve rose gradually but never leveled off (OP stands = pink curve). The second category, the species accumulation curve rose gradually with increasing subsample size (OF stands = blue curves). The third category, the species accumulation curve rose initially, and then rapidly leveled off (UF-2 stand = gray curves). The fourth category, the species accumulation curves increased more rapidly initially and then leveled off slightly whereas subsample size increased (GF and UF stands = yellow, green and red curves). Despite of the species accumulation curves showed a structure in relation to the types of plant coverages, where the stands were grouped by the rate of species accumulation, there was little interpretable differences in the species richness values (Table 3). OP stand had the lowest accumulation rate, even when is taking into account the size of the sample (the vertical line indicates a subsample size of 18 individuals). Therefore, the differences among the stands, is due to mainly the characteristics of the habitats and not for the sampling efforts.

CARABIDS COMPOSITION

According to the results obtained by the cluster and ordination analyses, there were differences in terms of carabid species composition among the afore mentioned plant coverages. These analyses showed four clusters, the first cluster is conformed by the OP stand, the second cluster is conformed by the GF-1 stand, the third is conformed by the OF-1, OF-2 and GF-2 stands, and the fourth conformed by the UF-1 and UF-2 stands (Figure 2 and 3). Despite of the low similarity between the OP and the GF-1 stands, the GF-1 stand was the site that shared more species with the OP stand (Table 3). On the other hand, the GF-2 and OF stands shared more species with each other than with the GF-1 stand (Table 3).

The GF stands might be considered as a distinguishable mosaic in terms of carabids composition, as GF had elements of the OP and OF stands. Therefore, cluster and ordination analyses indicated that the structure of carabids communities changed markedly among the disturbed plant coverages (OP, GF and OF stands) and undisturbed plant coverages (UF stands). Thus, from the four areas initially considered, the ground beetles composition recognized three groups of areas. Two disturbed plant coverages (OP and OF stands) and one undisturbed plant coverage (UF stands). These differences among the plant coverages were more apparent when the habitat preferences of carabids were considered. The responses of individual species provide a deeper understanding of the dynamics of carabid populations and the potential processes that lead the extinction or persistence of the carabids species in fragmented landscapes.

SPECIES ASSOCIATION

According to the indicator species analysis [31], only two species showed a significant indicator value ($p < 0.05$), *Dyscolus trapezicollis* (Putzeys, 1878) and *Glyptolenoides azureus* (Chaudoir, 1859). *D. trapezicollis* with an indicator value of 100, was strongly associated with the undisturbed plant coverages. *D. trapezicollis* that occurred in only one habitat, might be deemed as a mature forest specialist (stenotopic species) [32]. Probably, the distribution of *D. trapezicollis* is associated with its preference for ma-

ture forests, thus limiting a more widespread distribution in the Andes, as it is evident by its restricted distribution in the northeast of the Andes (Colombia and Venezuela) between 1750 - 2200 m altitude [33, 34] (Figure 4). On the other hand, *G. azureus* with an indicator value of 54 was significantly associated with the disturbed and undisturbed plant coverages (GF, OF and UF stands). These results suggested that, *G. azureus* was a generalist species that occurred in a wide variety of habitats (eurytopic species) [32]. This result was also comparable with the widespread distribution of *G. azureus* in montane cloud forests between 1800-3300 m of altitude in intertropical Andes from Venezuela to Bolivia [16, 33, 35] (Figure 4). Therefore, the local distribution of a generalist species as *G. azureus* might be given by its regional distribution habitat preferences in the Andes. These results post a possible relation between local habitat characteristics and the regional distribution of carabids species.

Previously, we considered habitat association of rare species. However, disturbance may favor the widespread and abundant species [19, 36]. The incrementation of common species in plant coverages affected by the logging was taken into consideration as shown below.

SPECIES ABUNDANCE

In the same way that the species composition was structured by the disturbance, the species abundances of ground beetles communities also changed among the stands (Table 4). There were statistically significant differences in carabid species abundances (Kruskal-Wallis test $p < 0.05$) among the different stands, where the species abundance was higher in the OF stands than in the remaining stands. Particularly, *Dyscolus physopterus* (Chaudoir, 1878) and *Dyscolus subreflexus* (Chaudoir, 1878) were twice more abundant in the OF stands than in the remaining stands. The abundance structure was illustrated clearly by the rank-abundance curves constructed for each stand (Figure 5).

These results are inconsistent with Gray's [36] prediction of the opportunistic species. The species abundance was concentrated on a small number of carabid species in the undisturbed plant coverages (UF stands). Pielou's evenness index presented higher

values for the disturbed plant coverages (GF and OF stands), and demonstrated a more homogeneous distribution of individuals per species in these stands (Table 4). Several studies had reported similar reductions in the dominance, as a response to the disturbance caused by logging [22, 30, 37–39]. Therefore, the increase of ground beetles diversity caused by the disturbance, might follow a general pattern that probably is related to the habitat heterogeneity, being this a characteristic of the young forests such as the oak forest [4, 21].

Rare species and common species showed a particular pattern that is defined by the species abundances structure. e.g. Rare species as *G. azureus* and *D. trapezicollis* showed habitat preferences (as the indicator species analysis showed above). And in common species as *D. physopterus* and *D. subreflexus*, the abundance was higher in moderately disturbed stands as the OF stands. Despite of the small number of species associated with specific habitats, the distribution and abundances of carabids showed differences. Therefore, the dynamic of the ground beetles populations might be associated with abiotic and biotic factors related an event of disturbance [13, 40].

SPECIES DIVERSITY

The pattern presented by species abundance was also shown by species diversity index (represented by Inverse Simpson index). The carabid diversity was higher in the OF stands than in the remaining stands (Table 4). Although in this study, the disturbance was considered as a categorical variable, our results showed a pattern that might agree with the Intermediate Disturbance Hypothesis (IDH) [24]. These results were consistent with previous researches in boreal forests [22, 23, 30, 38], spruce-fir forest in Maine [37] and oak forests in the U.S. [39]; where the species diversity and the abundance of carabids were higher in young regenerating forests than in mature forests. However, some findings reported in coniferous plantation in Europe [26, 28, 29, 36] and China [41], contradict the IDH. Since the species richness and diversity of carabids were lower in the coniferous plantations than in the adjacent deciduous forests. The high carabid diversity in the OF stands is probably attributable to the generally high biological productivity and small-scale habitat diversity of moderately human-modified habitats as the oak forest [12, 20, 22]. Particularly, among the several abiotic and biotic environ-

mental factors that affect the diversity and the distribution of carabids [42], the habitat heterogeneity -that leads to the increasing of coverage of the vascular plants- is one factor that might structure the communities of carabids [25–27]. Since the microclimatic conditions in heterogeneous habitats are more favorable for the development of the herb cover, the carabid abundance is affected by the increasing of the herbivorous invertebrate preys [13, 19, 27]. Therefore, the change in the carabid diversity may be parallel to the change in plant coverages, and the disturbance caused by the selective logging might structure carabid diversity directly (herbivorous carabids) or indirectly (carnivorous species). Some studies had reported that the arboreal characteristics and the structural heterogeneity of the vegetation affect carabid beetle species diversity [43–47]; e.g. the significant positive correlation between the diversity of carabids and the cover of herbs [4, 21]. Thus, the lower temperature and light levels, and higher relative air moisture prevailing under the dense canopy of the unmanaged plantation would have an impact on insect faunas [45].

The higher carabid diversity in the OF stands might be attributed to the large heterogeneity, in terms of diversity and composition of plants reported by Galindo *et al.* [48] in “La sierra”. Subsequently, Gutierrez-Lamus *et al.* [49] using Anura as taxon proved that in “La sierra” there were two types of plants coverages (the oak forest and undisturbed forest) and species diversity was higher in the oak forest than in the undisturbed forest. In fact, both studies suggest that the high diversity in “La sierra” is mainly due to the habitat heterogeneity as a result of the disturbance caused by the logging.

Although, plants, anurofauna and carabids species showed parallel results, the causes of these results might differ. The relations between the different taxa affected by the disturbances and the degree to which changes in carabid communities reflect the response of other species may be ambiguous. e.g. Lawton *et al.* [50] using different taxonomic groups found that the disturbance has an effect on the diversity of taxa, but this effect is hardly comparable between taxa. This is mainly due to the habitat preferences and the roles of the taxa in the ecosystems. There may be no correlation between species groups with different ecological requirements [51]. However, some correlation can be expected between species depending on the same ecological factors, e.g. moisture, soil quality, and dead wood [50, 51].

SPECIES RICHNESS

The species richness by itself, did not showed significant differences among the stands (Kruskal-Wallis test $p > 0.05$). Overall, theses results showed that carabid richness remain unchanged. Similar results have been found in correlative studies of carabids in *Eucalyptus* forest in Australia and old coniferous forest in southern Finland. In these studies [19,38], the results were attributed to the immigration and emigration rates from the high richness area to low richness area. In addition, the distances among the areas was another factor that influenced this result, since one individual can covered short distances (some hundreds of meters) among areas [38]. Thus, independent fluctuation of local populations might provide an explanation of the heterogeneous occurrence of carabid in the sites.

The simple counting of the number of species provides no information on the effect of disturbances in the sites. However, if species identities are considered, it can be seen that there has been some changes in species composition due to the disturbances [19] as our results showed (Table 3). In addition, the use of richness as a measure of biological conservation value, may be misleading because disturbances may allow the occurrence of the widespread and abundant species, leading to an incrementation in richness. In contrast, making the analysis of the responses of individual species is more likely to provide an understanding of the processes that lead to extinction or persistence in fragmented landscapes [9, 19].

Finally, the results of this study showed that carabid composition, abundance and diversity can vary within a relatively small geographic area, and small habitat fragments can support diverse and distinctive carabid communities. One of the most interesting results of this study, is the comparison that can be made between generalist and specialist species in a local area versus the widespread distribution and restricted distribution in a regional level. Therefore, the poorly dispersing species to regional level (for example *D. trapezicollis*) have low abundances and are associated with a particular area at a local level. Thus, stenotopic species may be considered as the restricted regional distribution species. Well-dispersing species to regional level (as *Glyptolenoides azureus*) are highly abundant and are associated with several stands in local level (eurytopic species may be deemed the same as the widespread distribution species). Therefore, the regional distribution of species might be related with disturbances conditions such

as long-time (geological, glaciations, natural disturbance regime) or small-time (forests fragmentation, agriculture, forestry practices and others). Studying these species can uncover carabid fauna ecology and behavior in the Andes ecosystems.

CONCLUSIONS

Data presented here suggested that the disturbance caused by the logging has structured the composition, diversity and abundance of ground beetle communities in the different types of plant coverages sampled. Thus, the habitat heterogeneity as a result of the disturbance caused by logging is the critical factor in structuring Andean carabids communities. Nevertheless, the species richness did not exhibit significant differences among the plant coverages. Moreover, our findings showed that diversity of ground beetles was higher in the disturbed plant coverages, where eurytopic species were significantly associated. Therefore, the disturbance caused by the logging involved a loss of specialist species and an incrementation of widespread species in areas affected by disturbance.

Future efforts should be directed to quantify the effect of the forest fragmentation to regional level and assess whether the intermediate disturbance hypothesis and/or the opportunistic species hypothesis might be considered as the general pattern in the ground beetles communities in the Andean ecosystems. And to fully understand the disturbance effects on carabid beetle communities, it should be included physical variables such as the incidence of light into the forest, moisture soil and temperature, canopy cover; chemical variables as pH and chemical soil composition and biological variables as the presence and distribution of competitors.

MATERIALS AND METHODS

STUDY AREA

This research was conducted in "La sierra" (between the departments of Boyacá and Santander), a "rainy montane forest" (bh-MB) [52] located in the western slope of the eastern Colombian mountain ridge. The studied sites were located at an elevation of 2300-2700m. These sites have a mean annual temperature of 10.4°C. The rainfall shows a bimodal pattern with two peaks of high precipitation in April (233.2 mm) and in October (233.6 mm), and a low peak in July (75.1 mm) and the annual average rainfall was 1851 mm. Three field trips were conducted in July 2001, January 2002, and September 2002 with a total sampling of 18 days in seven stand Open area (OP), Gallery forest (GF-1 and GF2), Oak forest (OF-1 and OF-2) and Undisturbed forest (UF-1 and UF-2) (Table 1) within four different plant coverages (Table 2).

SAMPLING METHODS

Carabid populations in each plot were sampled using pitfall, McPhail and Malaise traps. We used to collect carabid beetles unbaited and baited (dung and tuna) pitfall traps that consisted of plastic cups with a small plastic cup as bait receptacle, the mouth inserted flush with ground level, with a plastic roof anchored by nails over the opening to prevent rain water from entering. Each trap was filled with ethanol 70 % as a preservative and a small amount of soap to minimize surface tension. 20 pitfall traps were placed in each stand (ten traps unbaited pitfall trap, five tuna-baited pitfall trap, and five dung-baited pitfall trap), except in OP stand, due to that is a small area where we placed six unbaited pitfall traps, three tuna-baited pitfall trap and three dung-baited pitfall trap; for a total of 132 pitfall traps. Five Macphail traps were placed close to

each Pitfall transect. Macphail traps were placed in a random fashion, each one about 2 m above the ground, and baited with sugar cane juice. Two Malaise traps were placed in each transect. The traps had the collector recipient 1.5 m about the ground. In addition, we used two types of active sampling (beating sheets and sweeping net). In the Table 2 shows the sampling effort for each stand. The specimens were stored in vials with ethanol 85 % and deposited at the Entomological Collection of Universidad Industrial de Santander (Colombia).

ANALITICAL METHODS

All analysis were done in R version 2.10.1 (2009-12-14) [53]. We used non-metric multi-dimensional scaling (NMDS) ordination and with the Bray-Curtis dissimilarity measure. Dimensionality of the solution was determined by adding dimensions (up to a maximum of 6) as long as they reduced the final stress by at least 5%. Results were compared to 100 runs of randomized versions of the data, and compared via a Monte Carlo test. We used the vegan package [54] to perform the analyses.

We conducted a cluster analysis to depict relationships and the structure among assemblages in different stand types. We used Jaccard similarity coefficient as the measure of similarity. To perform the analyses we used R packages ade4 and ape [55].

We compute indicator values of species within clusters of sites. IndVal index combines a species mean abundances and its frequencies of occurrence in the groups. A high indicator value is obtained by a combination of large mean abundance within a group compared to the other groups (specificity) and presence in most sites of that group (fidelity) [31]. The groups of sites were defined by k-means partitioning. The statistical significance of the species indicator values is also evaluated by IndVal using a randomisation procedure. We used the R package labdsv [56] to perform the analyses.

We used Kruskal-Wallis non-parametric analysis to assess differences in species richness and abundance of carabid assemblages among the stands. We assessed carabid diversity and abundance using: species richness (S), species abundances, Pielou's evenness and the Inverse Simpson index. We investigated carabid dominance structure by constructing

rank-abundance plots for each stands.

Finally, We employed individual-based rarefaction and rank abundance plots to describe species richness and abundance of the total sample. We used individual-based rarefaction method to compare species richness, to correct for uneven catch rates, this method estimated the number of species expected in a subsample drawn randomly from the entire sample. Therefore rarefaction estimates of species richness were obtained from non-standardized data for each transect with the rarefaction function [57] based on the vegan package [54].

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TABLES

Table 1. Coordinates of the study sites in the SFF Guanenta alto del rio Fonce

Stand	Plant coverages	Coordinate
(OP)	Open Area	N 6°00' 42" W 73°9' 2"
(GF-1)	Gallery forest	N 6°00' 25" W 73°8' 58"
(GF-2)	Gallery forest	N 6°00' 50.7" W 73°5' 13.5"
(OF-1)	Oak forest	N 6°00' 34" W 73°9' 11"
(OF-2)	Oak forest	N 6°00' 37.5" W 73°9' 14.2"
(UF-1)	Undsiturbed forest	N 6°00' 33.8" W 73°8' 58.2"
(UF-2)	Undsiturbed forest	N 6°00' 51" W 73°9' 2"

Table 2. Study sites in the SFF Guanenta alto del rio Fonce in for different vegetative stands

Plant coverages	Habitat characteristics
Open Area (OP)	It is a small extension (ca 150m) of grasses and shrubs (Melastomataceae and Mirtaceae of no more than 5 m height).
Gallery forest (GF)	Shows a rocky topography, and it is characterized by the presence of oaks <i>Quercus humboldtii</i> , Melastomataceae, Araceae, ferns, hepatics, and mosses of the family Dicranaceae and Polytrichaceae.
Oak forest (OF)	It is characterized by the presence of <i>Q. humboldtii</i> (trees with 20m height on average) and <i>Cecropia sp.</i> (Cecropiaceae). According to [48] this is a rainy forest with dense understory and abundant epiphytic vegetation.
Undisturbed forest (UF)	It is a mature forest, with trees over 20 m in height that provide a large percentage of coverage. It is characterized by native trees of <i>Q. humboldtii</i> , arborescent ferns <i>Cyathea</i> spp., and epiphytes [48]. In the dry season, this forest in contradistinction to the oak forest, keeps leaf litter and soil much wetter (198.34 g and 81.67 g of moisture-average in 500 g soil, respectively) [49].

Table 3. Carabid composition in the stands. On the diagonal are the values of species richness for each stand, above the diagonal the number of shared species and below the diagonal Jaccard similarity index.

(S)	OP	GF-1	GF-2	OF-1	OF-2	UF-1	UF-2
OP	5	5	2	2	2	2	2
GF-1	0.236	12	8	8	7	8	7
GF-2	0.065	0.272	13	10	9	10	9
OF-1	0.074	0.317	0.465	11	9	10	9
OF-2	0.087	0.293	0.445	0.574	9	9	8
UF-1	0.069	0.293	0.423	0.520	0.5	12	11
UF-2	0.069	0.233	0.339	0.402	0.380	0.608	12

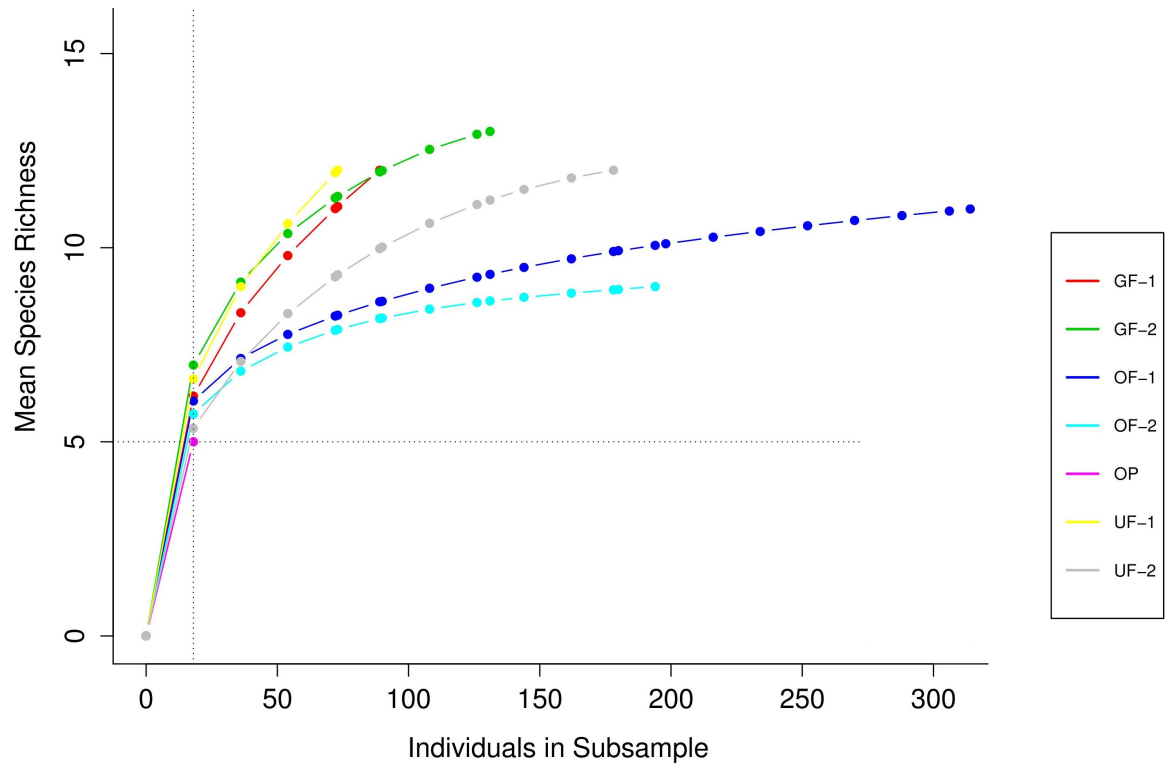
Table 4. Comparison of index values per stands location from carabids collected.

Stands	Abundances	Richness	InvSimpson	Pielou's evenness
OP	18	5	3.60	0.86
GF-1	89	12	3.26	0.67
GF-2	131	13	5.05	0.76
OF-1	314	11	5.20	0.76
OF-2	194	9	4.66	0.78
UF-1	73	12	4.00	0.72
UF-2	178	12	3.67	0.65

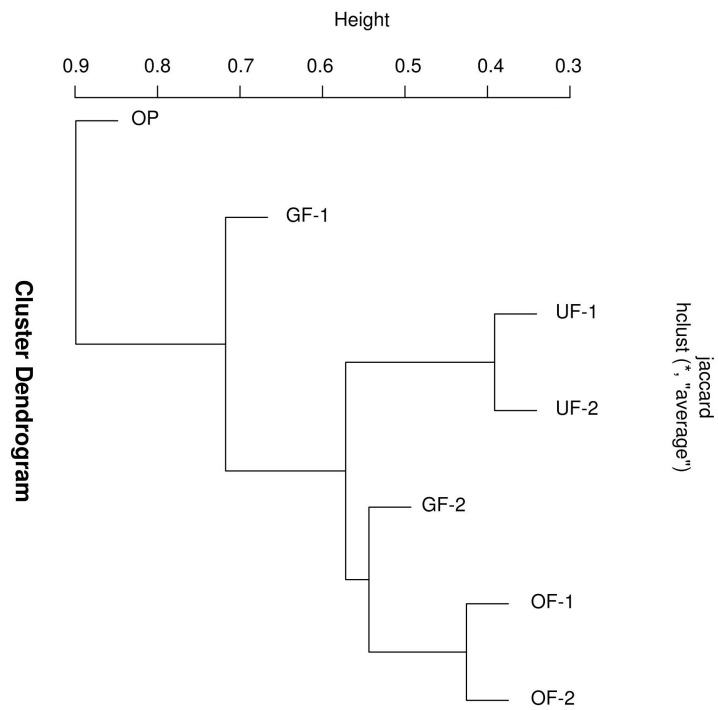
Table 5. Sampling effort for each kind of trap. sampling effort was calculated from two components (trap number x time period, in units of trap hours or trap-hours)

Stand	Pitfall	McPhail	Malaise	Beating	Net	Free search
OP	5184	2160	432	108	108	108
GF-1	8640	2160	864	108	108	108
GF-2	8640	2160	864	108	108	108
OF-1	8640	2160	864	108	108	108
OF-2	8640	2160	864	108	108	108
UF-1	8640	2160	864	108	108	108
UF-2	8640	2160	864	108	108	108

FIGURES



Figures 1. Rarefaction-estimated number of species in a series of subsamples of varying size, for each of seven subunits. Vertical line indicates a subsample size of 18.



Figures 2. Results of cluster analysis (UPGMA method) similarities based on Jaccard, comparing ground beetles communities collected in seven stands of the plant coverages.

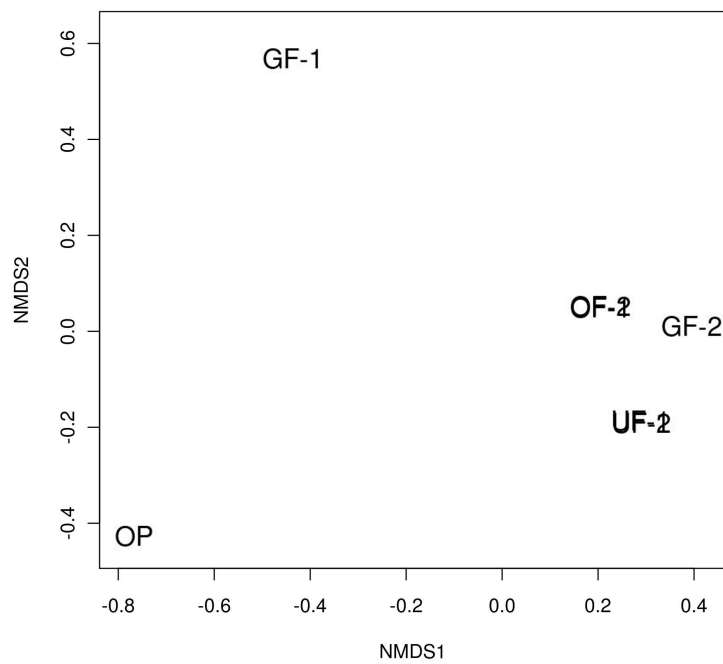
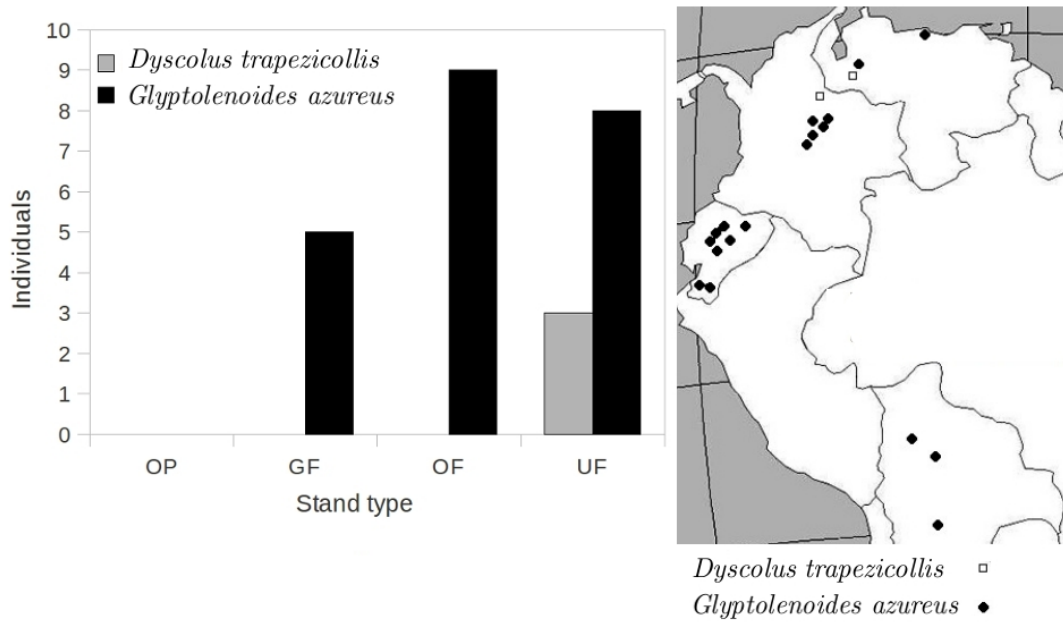
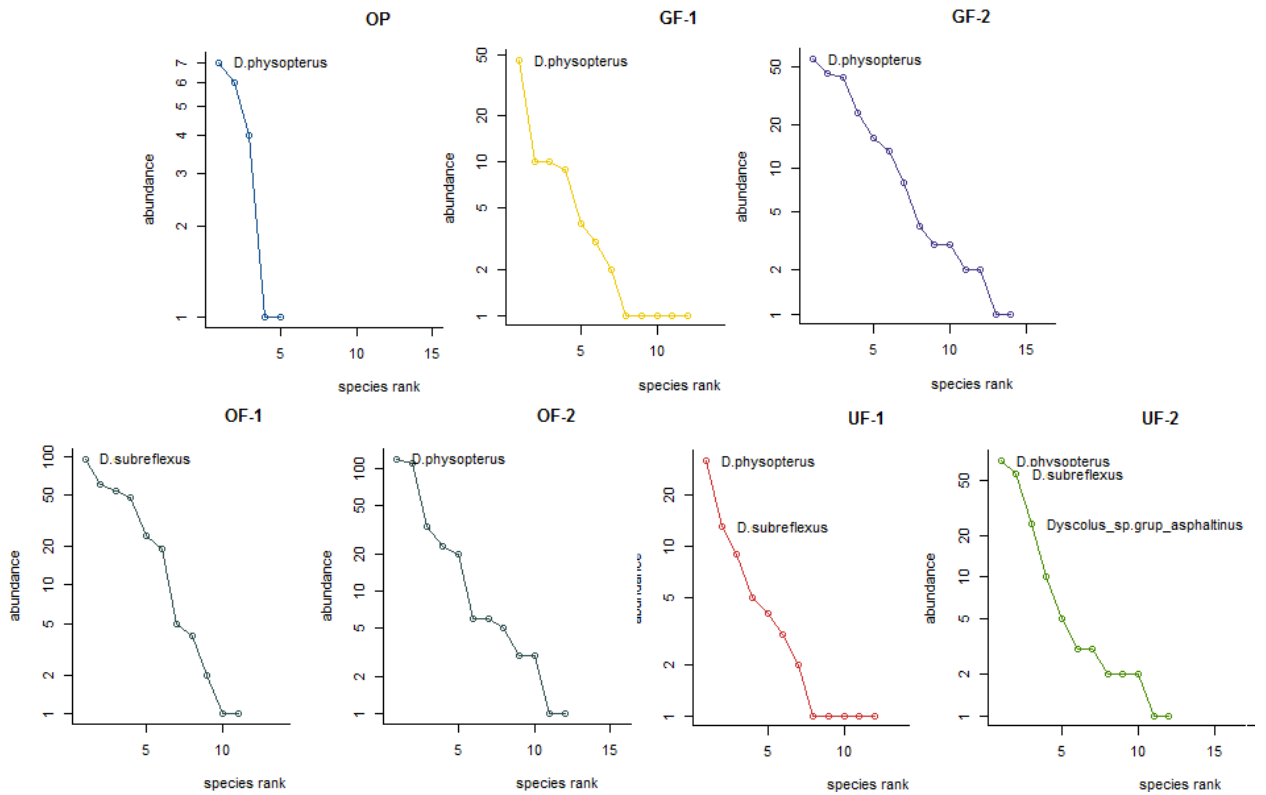


Figure 3. Nonmetric multidimensional scaling (NMDS) ordination, showing differences in ground beetle communities collected in seven stands of the plant coverages. Final stress of $6.7e-05$ and $p\text{-value} = 0.009$



Figures 4. Local distribution vs global distribution. Only indicator species with significant indicator values. Data from regional distribution of the species were taken from [16,33–35]



Figures 5. Rank abundance curves of individual at subunits sampled. Note the variation in rare species among the subunits. Abbreviations: OP, Open area; GF, Gallery forest; OF, Oak forest; UF, Undistrubed forest. Rank-abundance