

LEAF BEETLES (CHYSOMELIDAE) RICHNESS AND ABUNDANCE IN SAN LORENZO PROTECTOR TROPICAL RAINFOREST REMNANT, PANAMA

RIQUEZA Y ABUNDANCIA DE ESCARABAJOS DE LAS HOJAS (CHYSOMELIDAE) EN UN REMANENTE BOSCOSO EN EL BOSQUE PROTECTOR SAN LORENZO, PANAMÁ

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Recepción: 3 de junio de 2022

Aprobación: 22 de agosto de 2022

Abstract

Chrysomelidae constitutes one of the most abundant and diverse groups of Coleoptera. As well as any other group of insects, leaf beetles respond to factors such as habitat heterogeneity. For this reason, the modification of forest structure and composition has a direct impact on the leaf beetle communities and alters their diversity. Leaf beetle species abundance, richness, and community structure were characterized and compared between three different habitat types (Late Secondary Forest, Coffee-Growing Zone, Disturbed Forest) in a forest remnant of the San Lorenzo Protector Tropical Rainforest, Panama. Samples were collected every two weeks, using three Malaise traps in each habitat over one year, from October 2015 to October 2016. In total, 72 samples (24 per trap) which contained 347 individuals of leaf beetles were collected. These were identified to 77 species, 55 genera, in 7 subfamilies of Chrysomelidae. The greatest insect abundance and species richness occurred in the Late Secondary Forest. The differences among the three habitat types on the distribution of leaf beetle assemblages is likely to correspond to the structural characteristics

of those habitats and complexity and affect leaf beetle's richness and abundance associated. However, further studies are required to determine the causes of differences in species composition among each sites.

Key Words: Tropical rainforest, habitat heterogeneity, leaf beetle communities, Achiote, Panama

Resumen

Chrysomelidae constituye uno de los grupos de Coleoptera más abundantes y diversos. Al igual que cualquier otro grupo de insectos, los escarabajos de las hojas responden a factores como la heterogeneidad del hábitat. Por ello, la modificación de la estructura y composición del bosque tiene un impacto directo sobre las comunidades de escarabajos de la hoja y altera su diversidad. La abundancia, riqueza y estructura de la comunidad de especies de escarabajos de la hoja se caracterizaron y compararon entre tres tipos de hábitat diferentes (Bosque Secundario Tardío, Zona de Cafetal, Bosque Perturbado) en un remanente de bosque dentro del Bosque Tropical Protector de San Lorenzo, Panamá. Las muestras se recolectaron cada dos semanas, utilizando tres trampas Malaise en cada hábitat durante un año, desde octubre de 2015 hasta octubre de 2016. En total, 72 muestreos (24 por trampa) se realizaron, colectándose 347 individuos de escarabajos de las hojas. Se identificaron 77 especies, 55 géneros, en 7 subfamilias de Chrysomelidae, presentándose la mayor abundancia de insectos y riqueza de especies se presentó en el Bosque Secundario Tardío. Es probable que las diferencias entre los tres tipos de hábitat en la distribución de los conjuntos de escarabajos de la hoja se correspondan con las características estructurales de esos hábitats y la complejidad, afectando la riqueza y abundancia. Sin embargo, se requieren más estudios para determinar las causas de las diferencias en la composición de especies entre cada sitio.

Palabras Clave: Bosque Tropical, Heterogeneidad de hábitat, comunidad de escarabajos de las hojas, Achiote, Panamá

INTRODUCTION

Tropical forests host most of the Earth's plant species and simultaneously drive the insects' abundance and species richness. Several factors can affect the structure and diversity of insects (biotic and abiotic conditions, dispersal behavior, anthropogenic changes, habitat size and resource acquisition and quality) (Schowalter 2006). One of those factors is habitat heterogeneity which is subject to environmental variables such as the composition of plants (Teles et al. 2019); for herbivorous insects, plants diversity is crucial (Jolivet 1988; Novotny et al. 1999; Farnum & Murillo 2019).

A group of insects whose diversity and richness are tightly linked to plant diversity is Chrysomelidae, one of the most abundant and diverse groups of Coleoptera, commonly known as leaf beetles, with around 36000 described species grouped in 12 subfamilies and with over 2000 genera (Bouchard et al. 2017).

As a group, the leaf beetles show strong associations with their host plants (Mitter et al. 1991; Ambruster 1992; Jolivet & Hawkeswood 1995) and respond to factors such as the

quality of the environment and habitat heterogeneity (structure of the habitat and vegetable composition) (Teles et al. 2019). Chrysomelidae are mainly phytophagous, feeding primarily on leaves (Bieńkowski 2010) but also fruits (Janzen & Nishida 2016), roots (Pokon et al. 2005) seeds (Johnson 1983, Romero-Nápoles et al. 1996), flowers (Bienkowski 2010) herbaceous stalks and shrubs (Teles et al. 2019).

Their phytophagous nature means they have a very close relationship with the composition and floristic diversity of a habitat which may influence the insects' vertical stratification (Kirnse & Chaboo 2018) and spatio-temporal diversity (Basset et al. 2003; Baselga & Jiménez-Valverde 2007; Charles & Basset 2005; Kuchenbecker et al. 2021; Rěhounek 2002; Şen & Gök 2009). Hence, the modification of their forest has a direct impact on the leaf beetle communities and alters their richness and abundance (Richards & Coley 2007; Wasowska 2004).

This study aimed at characterizing the richness and abundance of leaf beetles (Coleoptera: Chrysomelidae) in a portion of tropical rainforest and comparing them among three different habitat types. Previous studies (Wagner 2000; Ohsawa & Nagaike 2006; Thormann et al. 2016; Teles et al. 2019) have shown that the habitat type contributed to the dynamics of Chrysomelidae, as well as the richness of species at the sites in which their research was conducted.

MATERIALS AND METHODS

The study was conducted in the San Lorenzo Protector Forest, Panama, over a 1-year period, October 2015 to October 2016, under permit SE/A-3-2015 and SE/A-4-2016 from Ministerio de Ambiente de Panamá.

Study Area

The San Lorenzo Protector Forest is one of the most important protected areas in the Caribbean side of Panama (Centro de Estudios y Acción Social Panameño 2006). El Tropic trail ($9^{\circ}11'52''N$, $79^{\circ}58'47''W$) is a portion of Tropical Moist Forest, located on Achote road (Chagres district), in the south part (Fig. 1). Two trails, which together consisted of 950 m, traversed the area sampled in this study.



Figure 1. Location of the Chagres district; the arrow and star symbol marks the area of study. Source: Own data (2020).

The first trail was characterized by the absence of slopes and comprised 600 m. The second trail's area consisted of 350 m with a + 30 ° slope (Centro de Estudios y Acción Social Panameño 2006). Herein we describe each one of the habitats studied in this research:

Habitat descriptions

- i. Late Secondary Forest (Fig. 2A): it's an 80 years old forest composed of trees reaching 25 m in height or higher, where plants grow such as the Royal Palm (Arecaceae: *Attalea butyracea* (Mutis ex L.f.) Wess.Boer), Yellow Mombin (Anacardiaceae: *Spondias mombin* L.), Guácimo (Malvaceae: *Guazuma ulmifolia* Lam.), Indio Desnudo (Burseraceae: *Bursera simaruba* (L.) Sarg.) and Tachuelo (Rutaceae: *Zanthoxylum ekmanii* (Urb.) Alain). The shrubs layer consists of palms as Pacaya (Arecaceae: *Chamaerodera tepejilote* Liebm. ex Mart. whereas the ground layer is covered by ferns (Pteridaceae: *Pityrogramma calomelanos* (L.) Link). Herbaceous vines and woody lianas are abundant, meanwhile herbaceous coverage was sparse and less diverse. It shows a dense canopy cover, a shady understory (0.4416 ± 0.1059 lux) and a substantial number of understory trees with a considerable amount of deadwood as well.
- ii. Coffee-Growing Zone (Fig. 2B): a small coffee plantation (Rubiaceae: *Coffea canephora* L.) and other crops such as bananas (Musaceae: *Musa sapientum* L. and *Musa paradisiaca* L.) showed an opened canopy without shade (20.18 ± 1.1685 lux). The area was used as a banana-growing farm between 1938 and 1953 and then for coffee cultivation in the 1990s. The ground layer is covered by herbs such

as Milkweed (Euphorbiaceae: *Chamaesyce hirta* (L.) Millsp.), Hierba de Toro (Asteraceae: *Tridax procumbens* L.) and Pega-Pega (Amaranthaceae: *Achyranthes aspera* L.).

- iii. Disturbed Forest (Fig. 2C): signs of human activities could be observed, such as the construction of Achioite internal road section near the forest, the vegetation included medium-size trees such as caimito (Sapotaceae: *Chrysophyllum cainito* L.), Balso (Malvaceae: *Ochroma pyramidalis* (Cav. ex Lam.) Urb.) some shrubs such as plantain (Musaceae: *Musa*), Cow Itch (Urticaceae: *Myriocarpa longipes* Liebm.) numerous herbaceous plants such as *Calathea* (Marantaceae), *Heliconia* (Heliconiaceae), Pokeberry (Phytolaccaceae: *Phytolacca rivinoides* Kunth & C.D.Bouché) and ferns (Tectariaceae: *Tectaria incisa* Cav., Lygopodaceae: *Lygodium venustum* Sw., and *P. calomelanos*). Its canopy showed some gaps (luminosity level near 17.75 ± 0.8966 lux) due to the road construction activities near the trail.

The shaded and unshaded condition of those habitats was measured with a Weston Master Universal Exposure Light meter model 715.

Sampling Design

Chrysomelid samples were collected from October 2015 to October 2016. We selected three sampling sites taking into account the predominant plant association. Once the sites were delimited, we placed three terrestrial Malaise traps measured approximately 1.8 m in height and 1.2 m in width (Fig. 2D).



Figure 2. Habitats sampled and method used in this study: A) Late Secondary Forest, B) Coffee-Growing Zone, C) Disturbed Forest, D) Malaise trap in field

We monitored the trap's every 14 days (consistency of sampling was sometimes marred by occasional delays in changing bottles due to bad weather). Although Malaise traps are not generally used for collecting Chrysomelidae, this method can be very productive (Flowers & Hanson 2003; Furth et al. 2003). Beetle samples are deposited at the Insect Collection of the Biology School of Universidad de Panamá, Centro Regional Universitario de Colón, where samples were separated, assembled, and labeled with the corresponding information. Also, we made floristic assessments (species list) in our sampling sites following the methodology proposed by Mendieta & Farnum (2012) (Appendix 1).

The material collected was identified to the generic-specific level, through the use of keys available, and specialized bibliography (summarized in Van Roie et al. 2019 (Chrysomelidae s. str.); Windsor et al. 1992; Morrison & Windsor 2017 (Cassidinae); Flowers 2004; Maes et al. 2016; Benítez-García et al. 2017 (Chrysomelinae); Vencl 2004 (Criocerinae); Flowers, 1996; Jolivet & Verma 2008; Moseyko et al. 2013 (Eumolpinae); Derunkov et al. 2015; Rodrigues & Mermudes 2016 (Galerucinae-Luperini); Scherer 1962, 1983; Furth 1996, 2006, 2017, 2019 (Galerucinae-Alticini); Sekerka 2014; Staines & Garcia-Robledo 2014 (Hispinae); Jacoby 1878; Monrós 1956, 1958 (Lamprosomatinae). Provisional Tortoise and Hispine beetle's genera and species identifications were made using the online Borowiec & Świętojańska (2021) photographic catalog of Cassidinae of the World and online Staines

(2015) photographic catalog of Hispines of the World. Some information included here have been published (Lanuza-Garay et al. 2020).

In cases where specimens showed some sexual dimorphism, we revisited the works of Mohamedsaid & Furth (2011) and Prado (2013) and compared the beetles collected with local insect collections of the School of Biology at the Centro Regional Universitario de Colón (CRUC), the Graham Bell Fairchild Museum of Invertebrates of Universidad de Panamá (MIUP), and Smithsonian Tropical Research Institute (STRI). We follow the Bouchard et al. (2011) taxonomic classification of Chrysomelidae includes the Bruchidae family as a subfamily.

Data Analysis

The Chrysomelidae assemblage we sampled was characterized regarding the number of individuals (abundance) and species (richness) collected. We then categorized our sampled species into classes according to Teles et al. (2019): [1] singleton (only one specimen), [2] doubleton (two specimens) [3] rare (3 to 10 specimens), [4] common (11 to 30 specimens) and [5] very common (more than 30 specimens). Regarding the species richness, we used the number of species collected from each habitat type. To express the dominance of beetle communities, abundance range curves were plotted by habitat type codifying each species, aided with GraphPad Prism 8 (Graphpad Software, 2020), where the level of curvature, whether more horizontally or vertical, indicates the similarity or dominance of specific communities

In addition, we performed species accumulation curves to estimate the effectiveness of the samplings by habitat type. These curves were made using the “Sobs” value, based on the number of individuals captured using the *Estimates 9.01* statistical package, selecting 100 randomizations (Colwell 2013). Also, leaf beetle communities in the studied sites were compared using the parameters of species composition and total abundance.

Results

In the one-year sampling period, we collected 72 Malaise trap samples (24 per trap) which contained 347 individuals of Chrysomelidae. They were identified to 77 species, 56 genera in 7 subfamilies (Table 1)

Relative abundance

Throughout the study 347 specimens of Chrysomelidae were collected in three habitats (Late Secondary Forest = 215 individuals, $X = 2.19$, $\sigma = 6.420259608$; Coffee-Growing Zone = 88 individuals, $X = 1.0114$, $\sigma = 8.85820728$; Disturbed Forest = 44 individuals, $X = 0.5057$, $\sigma = 3.797772627$) (Fig. 3) within this forest remnant, belonging to a total of 10 subfamilies, where three of them have greater frequency representativeness: Galerucinae (271 ind. = 77 %), Cassidinae (37 ind. = 11 %) and Eumolpinae (27 ind. = 9 %) (Fig. 4f).

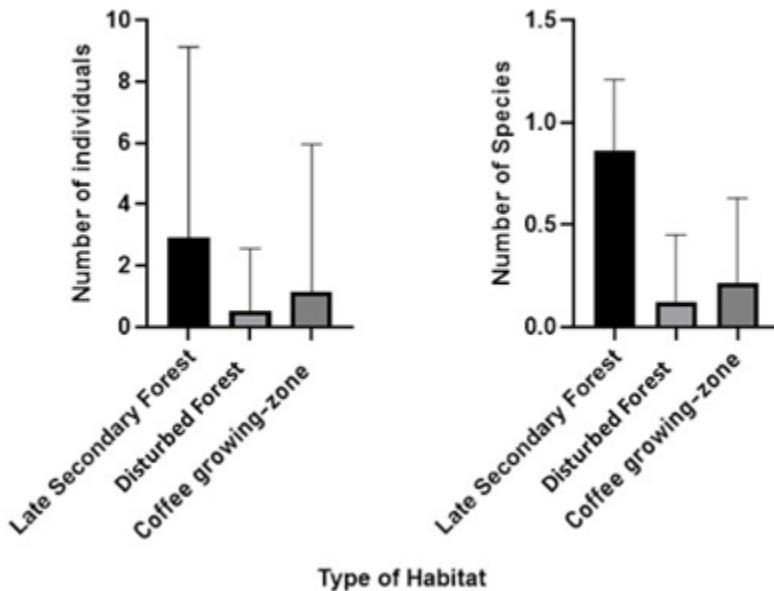


Figure 3. Number of individuals and species for Chrysomelidae communities in different habitat types (Mean \pm standard deviation).

On the other hand, when documenting the fauna composition (abundance and richness) of species present in the different plant associations, a total of 78 species are registered, 65 of them distributed in the Late Secondary Forest, followed by the Coffee-Growing Zone with 20 species and finally the Disturbed Forest with 9 species, among them, 10 species were found in more than one habitat type (Table 1), where Galerucinae was present in all studied sites. In total, only 5 species comprised more than 10 individuals (6.6%), while 60.5 % of species were singletons ($n = 46$), 14.4% were doubletons ($n = 11$) and 18.4% were rare ($n=14$).

Among the latter, *Diabrotica* Chevrolat in Dejean, 1836 (157 individuals = 41%), *Eccoptopsis* Blake, 1966 (37 individuals = 10%) (Galerucinae: Luperini), *Systema* Chevrolat in Dejean, 1836 (26 individuals = 7%) (Galerucinae: Alticini) and *Rhabdopterus* Lefèvre 1885 (26 individual=7%) (Eumolpinae: Eumolpini) are the most representative in the study (Fig. 4e); *Diabrotica mitteri* (M22), was the most abundant species in all study sites (together with M20)(Fig. 4a) and the Late Secondary Forest habitat with 20% of the observed species (Fig. 4b), whilst *Diabrotica godmani* (M20) was in the coffee-growing zone with 40% (Fig. 4c); for its part, *Systema variabilis* (M58) contributed to 33% of the species observed in the disturbed forest habitat (Fig.4d).

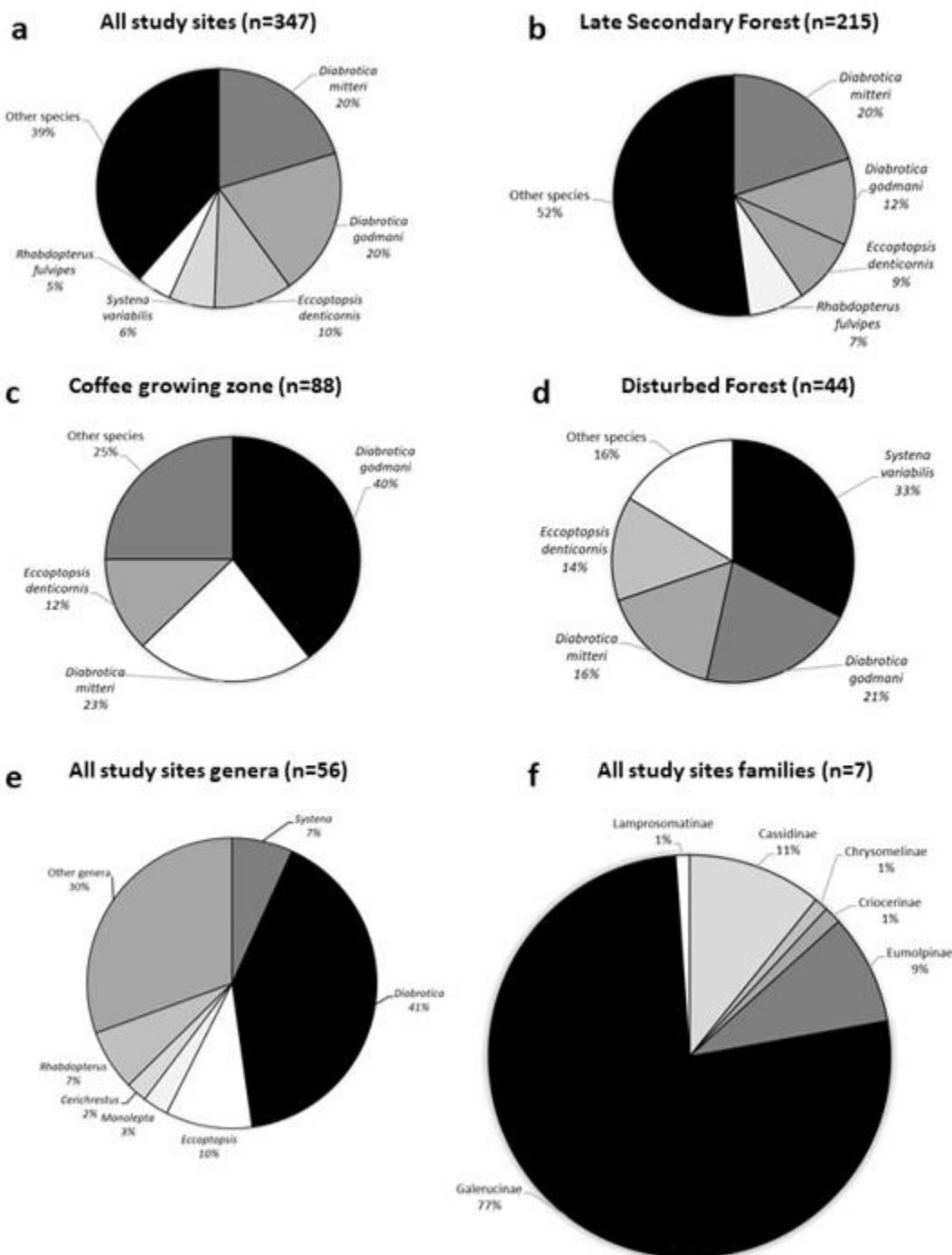


Figure 4. Community structure of Chrysomelidae taken in Malaise traps at Trogon trail, shown as percentages of individuals. **a**. All study sites; **b**. Late secondary forest; **c**. Coffee-growing zone; **d**. Disturbed forest; **e**. all genera treated; **f**. all families treated. Subfamilies such as Bruchinae that present less than 1% not shown.

The abundance range curves show different patterns (Fig. 5A–C). Coffee-Growing Zone and the Disturbed Forest have curves downward, indicating that both were dominated by few species. In contrast, Late Secondary Forest produced more abundant and rare species, in addition to singletons and doubletons. In the same way, species richness is significantly different between habitats, based on confidence interval curves, when the same number of individuals are considered (Fig. 5D). The Late Secondary Forest contributes a greater number of species; however, it has not managed to reach the asymptotic curve during the study, suggesting a high community diversity of leaf beetles in this remnant of forest, predictable by the large number of unique and rare species in the sample.

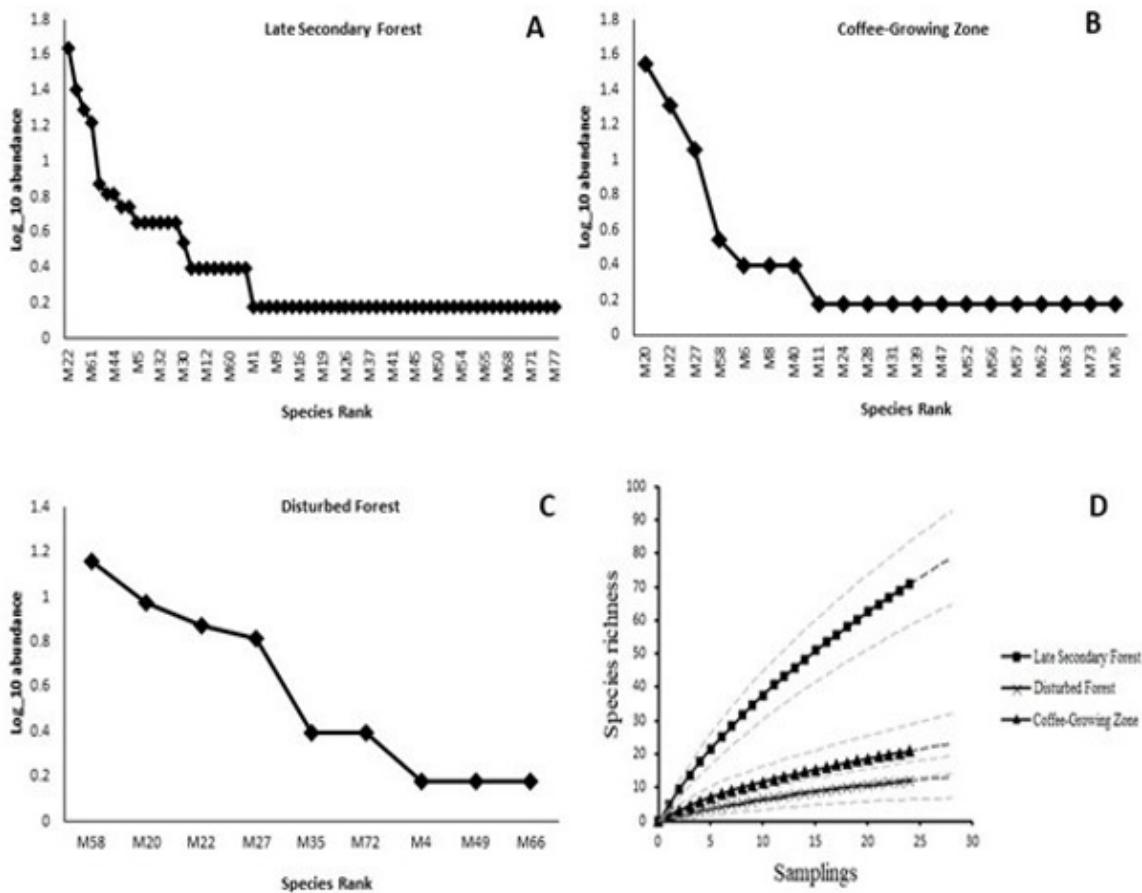


Figure 5. A–C. Rank-abundance of Chrysomelidae communities in three habitats in a tropical rainforest remnant, D. Cumulative species curve based on the number of individuals collected in habitat types. Note: The dotted lines represent the confidence interval limit (95%) for the estimated number of species. The interrupted lines following the solid lines represent extrapolations (24 + 4 samples).

DISCUSSION

This research shows that 84% of the species composition is found in the Late Secondary Forest when compared to the other types of habitat studied here. The differences among the

three habitat types on the distribution of leaf beetle assemblages is likely to correspond to the structural characteristics of those habitats and complexity (plant diversity, forest maturity, canopy coverage, height and light exposure) (Basset et al. 2001; Borer et al. 2012; Campos et al. 2006; de Cauwer et al. 2006; Neves et al. 2013; Novotny et al. 2006; Schowalter 2017) and affect leaf beetle's richness and abundance associated (Fig. 6). Compared with Coffee-Growing Zone and Disturbed Forest, the coverage of herbaceous in Late Secondary Forest was sparse and less diverse, dominated especially by plant species such *Heliconia* and *Calathea*, meanwhile the coverage of trees, lianas and palms are similar between both Late Secondary Forest and Disturbed Forest. When considering habitats such as Disturbed Forest, we expected that their complexity rate would be similar to the Late Secondary Forest; however, due to anthropogenic changes in recent decades, the richness of plant species has been reduced.

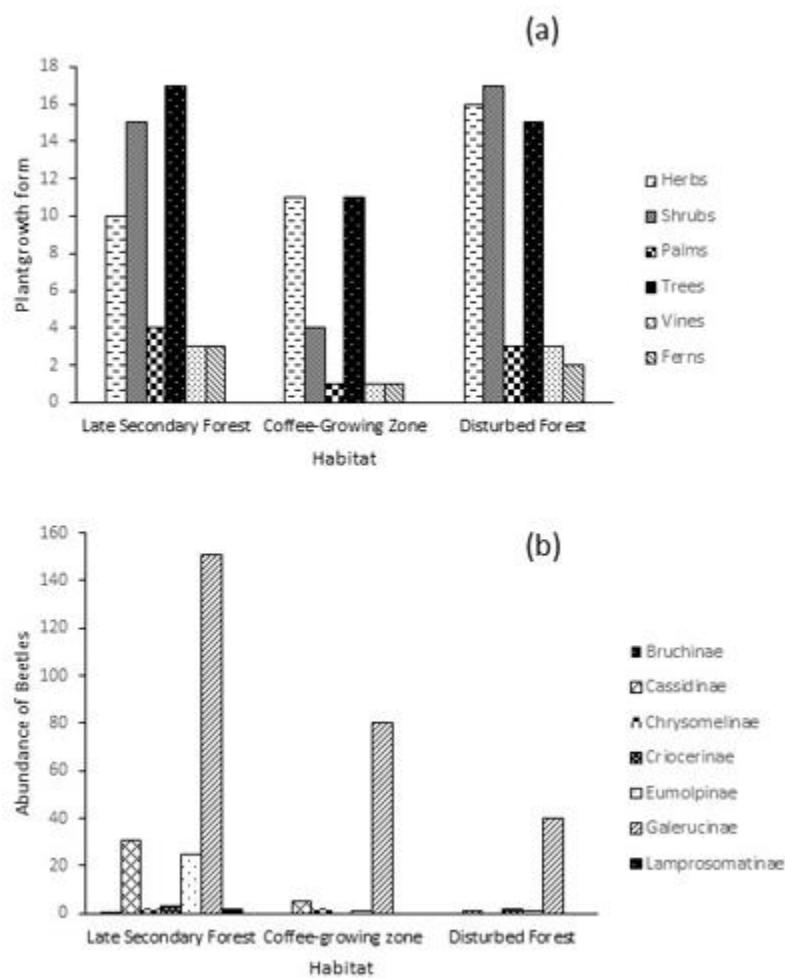


Figure 6. Leaf beetle species structure and plant growth form associated with three types of habitat in a forest remnant in Panama: (a) different plant growth forms assessed, (b) most

representative leaf beetle families sampled. In all three habitats, Galerucinae (+Alticini) are the most abundant.

The dominance of different species in different habitats may also indicate the influence of the vegetation structure on the distribution of leaf beetles, such as in the case of some species feed on plants that were distributed in more than one habitat, for example, *Acalymma separatum*, *Eccoptopsis denticornis*, *Diabrotica mitteri*, and *Diabrotica godmani* due to their polyphagous ability to feed on different plants and available plant resources, maintaining a large distribution in their habitat (Jolivet et al. 1994, Basset 2001). Nevertheless, this distinct ability is not exclusively of Galerucids—e.g. Cassidinae prefer sunny places and certain plant families such Heliconiaceae, meanwhile, Cassidinae spines are miners associated with monocots such palms and *Heliconia* (Farrell & Mitter 1993; Novotny et al. 2000); whereas Eumolpines have subterranean larvae, so they will be richer in certain soils without pesticides (Jolivet 1988; Jolivet et al. 2014).

In the case of Flea beetles (Galerucinae: Alticini), authors such as Jolivet (1988), Williams, 1990, Konstatinov & Tishechkin (2004), and Aslan & Ayvaz (2009) indicate that these beetles have broad nutritional habits and can take advantage of non-woody stems of some plants. In addition, Alticini was the group that was more representative (= 45% of registered species of the 36 species are registered in Galerucinae) in this study because their population develops closer to the ground. However, *Monomacra* prefers aerial plants such as lianas, which promote interconnectivity between the canopy and the undergrowth (Basset et al. 2001; Basset & Samuelson 1996). In contrast, *Monolepta* prefer lianas (Flowers & Janzen 1997) and shrubby forms (Young 1988), therefore, it is valid to argue the richness and diversity of leaf beetles are influenced by the structural characteristics and complexity of this small patch of tropical forest. Nevertheless, empirical evidence of such a relationship between forest structure, plant diversity, and Chrysomelidae is rare, suggesting that further studies need to be carried out about plant composition and the structural attributes of forest remnant areas (Teles et al. 2019).

Another factor to analyze is the presence of a high number of singletons or rare species in the sample (60.5%). Although these kinds of species are common in the tropics, a large representation of insect species with low abundance may be due to collection methods (passive collection traps, such as Malaise traps, can capture many transitional species), eating habits of species, or since they are genuinely rare species (with low population levels) (Novotný & Basset, 2000). Thus, additional sampling techniques such as sweep-net sampling and beating could improve inventory efficiency.

Acknowledgment

We thank Annette Aiello (Smithsonian Tropical Research Institute) and Roberto Cambra (G. B. Fairchild Invertebrate Museum, U. P.) for access to the insect collections of both institutions; David Furth (Smithsonian National History Museum) and Shawn Clark (University of Utah) for confirmation of the species *Isotes serraticornis*; Yorielis Salazar for support with the fieldwork; Salomón Aguilar (University of Panama), Orlando Ortiz

(University of Panama) and Loraine Pérez (Universidad Autónoma de Chiriquí) for their collaboration in the identification and taxonomic elements of plants; and the Biofuture Association of Panama for the donation of the Lightning Photo Shoot Box EMART (14.0 x16.0 in) to photo-document the beetles treated in this research project. We also thanks to Roberto Alex Arroyo, Albert Thurman (Mississippi Entomological Museum, Mississippi State University), Dumas Galvez (Universidad de Panamá) and Rob Westerduijn for useful comments and review in English.

Conflicts of Interest: The authors declare no conflict of interest.

Author contributions “Conceptualization, A.L.G., F.F.C and L.C.; methodology, A.L.G. and A.S.M.; software, A.S.M.; formal analysis, A.L.G., F.F.C. and A.S.M.; collecting resources, A.L.G. and A.S.M.; specimen curation, A.L.G. and L.C.; sites characterization and plant survey, V.M.G; writing—original draft preparation, A.L.G.; writing—review and editing, A.S.M., F.F.C., L.C., V.M.G.; English translation, C.A.; supervision, A.L.G.; project administration, A.L.G., A.S.M. and F.F.C. All authors have read and agreed to the published version of the manuscript.”

Funding: This research received no external funding.

Institutional Review Board Statement: The authors declare no omitted or violated any legal or ethical statement in this research.

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Appendix 1. List of plant species observed in the different habitats present in the remnant of tropical humid forest studied. Note: LSRF = Late Secondary Forest, CGZ = Coffee-Growing Zone, DF = Disturbed Forest.

Plant	Late Secondary Forest	Coffee Growing Zone	Disturbed Forest	Family	Plant growing form
<i>Justicia secunda</i> Vahl		1		Acanthaceae	Herb
<i>Justicia grandiflora</i>		1		Acanthaceae	Vine
Dum.Cours					
<i>Achyranthes aspera</i> L.	1	1	1	Amaranthaceae	Herb
<i>Anacardium excelsum</i>	1		1	Anacardiaceae	Tree
(Bertero ex Kunth)					
Skeels					
<i>Spondias mombin</i> L.	1	1		Anacardiaceae	Tree
<i>Annona spraguei</i> Saff.			1	Annonaceae	Tree
<i>Guatteria amplifolia</i>		1		Annonaceae	Tree
Triana & Planch.					
<i>Lacistema panamensis</i>	1	1		Apocynaceae	Tree
(Woodson) Markgr.					
<i>Thevetia ahouai</i> (L.) A.			1	Apocynaceae	Shrub
DC.					
<i>Anthurium ochrantium</i>				Araceae	Herb
K. Koch					
<i>Dieffenbachia</i> sp.		1		Araceae	Herb
<i>Attalea rostrata</i> Oerst.	1	1	1	Arecaceae	Palm
<i>Bactris major</i> Jacq.			1	Arecaceae	Palm
<i>Calyptrogyne ghiesbreghtiana</i> (Linden & H.Wendl.) H.Wendl.	1		1	Arecaceae	Palm
<i>Chamaedorea tepejilote</i>	1			Arecaceae	Palm
Liebm. ex Mart.					
<i>Socratea exorrhiza</i>	1			Arecaceae	Palm
(Mart.) H.Wendl.					

<i>Mikania micrantha</i>	1	1	Asteraceae	Vine
Kunth				
<i>Sphagneticola trilobata</i>	1		Asteraceae	Herb
(L.) Pruski				
<i>Tridax procumbens</i> L.	1	1	Asteraceae	Herb
<i>Vernonanthura patens</i>	1	1	Asteraceae	Shrub
(Kunth) H. Rob.				
<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	1	1	Boraginaceae	Tree
<i>Cordia bicolor</i> A. DC.	1		Boraginaceae	Tree
<i>Aechmea magdalenae</i> (André) André ex Baker.		1	Bromeliaceae	Herb
<i>Bursera simaruba</i> (L.) Sarg.	1	1	Burseraceae	Tree
<i>Protium panamense</i> (Rose) I.M. Johnst.	1		Burseraceae	Tree
<i>Clusia pratensis</i> Seem.	1		Clusiaceae	Tree
<i>Ipomoea indica</i> (Burm.) Merr.		1	Convolvulaceae	Vine
<i>Costus villosissimus</i> Jacq.	1		Costaceae	Herb
<i>Carludovica palmata</i>	1		Cyclanthaceae	Herb
Ruiz & Pav.				
<i>Cyperus luzulae</i> (L.) Rottb. ex Retz.		1	Cyperaceae	Herb
<i>Dioscorea mexicana</i> Scheidw.	1		Dioscoreaceae	Vine
<i>Euphorbia hirta</i> (L.) Millsp.	1	1	Euphorbiaceae	Herb
<i>Hura crepitans</i> L.		1	Euphorbiaceae	Tree
<i>Inga cocleensis</i> Pittier			Fabaceae	Tree
<i>Desmodium adscendens</i> (Sw.) DC	1	1	Fabaceae	Herb
<i>Zygia longifolia</i> (Willd.) Britton & Rose		1	Fabaceae	Tree
<i>Chrysothemis friedrichsthaliana</i> (Hanst.) H.E. Moore	1	1	Gesneriaceae	Herb
<i>Xiphidium caeruleum</i> Aubl.	1		Haemodoraceae	Herb
<i>Heliconia latispatha</i> Benth.	1		Heliconiaceae	Herb
<i>Lacisterna aggregatum</i> (P.J. Bergius) Rusby		1	Lacistemataceae	Shurb

<i>Aegiphila panamensis</i>	1		1	Lamiaceae	Tree
<i>Moldenke</i>					
<i>Gustavia superba</i>	1	1	1	Lecythidaceae	Tree
(Kunth) O.Berg.					
<i>Lygodium venustum</i> Sw.	1			Lygodiaceae	Fern
<i>Apeiba tibourbou</i> Aubl.			1	Malvaceae	Tree
<i>Ceiba pentandra</i> (L.)	1			Malvaceae	Tree
Gaertn.					
<i>Herrania purpurea</i>			1	Malvaceae	Shrub
(Pittier) R.E. Schult.					
<i>Luehea seemannii</i>	1		1	Malvaceae	Tree
Triana & Planch					
<i>Luehea speciosa</i> Willd.	1	1	1	Malvaceae	Tree
<i>Ochroma pyramidalis</i>			1	Malvaceae	Tree
(Cav. ex Lam.) Urb.					
<i>Sterculia apetala</i> Jacq.			1	Malvaceae	Tree
H. Karst.					
<i>Calathea similis</i> H.	1		1	Maranthaceae	Herb
Kenn.					
<i>Calathea lasiostachya</i>	1		1	Maranthaceae	Herb
Donn. Sm.					
<i>Miconia argentea</i> (Sw.)	1		1	Melastomataceae	Shrub
DC.					
<i>Guarea glabra</i> Kunth	1			Meliaceae	Tree
<i>Trichilia pleeana</i> (A.		1		Meliaceae	Tree
Juss.) C. DC.					
<i>Ficus insipida</i> Willd.	1		1	Moraceae	Tree
<i>Ficus popenoei</i> Standl.	1			Moraceae	Tree
<i>Poulsenia armata</i>	1		1	Moraceae	Tree
(Miq.) Standl.					
<i>Sorocea affinis</i> Hemsl.	1			Moraceae	Shrub
<i>Musa paradisiaca</i> L.		1	1	Musaceae	Herb
<i>Musa sapientum</i> L.		1	1	Musaceae	Herb
<i>Virola surinamensis</i>	1			Myristicaceae	Tree
(Rol.) Warb.					
<i>Stylogyne turbacensis</i>	1		1	Myrsinaceae	Shrub
(Kunth) Mez					
<i>Neea laetevirens</i> Standl.			1	Nyctaginaceae	Herb
<i>Passiflora biflora</i> Lam.	1		1	Passifloraceae	Vine
<i>Hieronyma</i>	1		1	Phyllanthaceae	Shrub
<i>alchorneoides</i> Allemão					
<i>Phytolacca rivinoides</i>	1		1	Phytolaccaceae	Shrub
Kunth & C.D.Bouché					
<i>Piper umbellatum</i> L.	1	1	1	Piperaceae	Shrub

<i>Pityrogramma calomelanos</i> (L.) Link.	1	1	1	Pteridaceae	Fern
<i>Coffea arabica</i> L.		1	1	Rubiaceae	Shrub
<i>Coussarea curvigemmia</i> Dwyer		1		Rubiaceae	Shrub
<i>Faramea occidentalis</i> (L.) A. Rich.	1		1	Rubiaceae	Shurb
<i>Genipa americana</i> L.	1		1	Rubiaceae	Tree
<i>Pentagonia macrophylla</i> Benth.	1		1	Rubiaceae	Shrub
<i>Psychotria deflexa</i> DC.	1			Rubiaceae	Shrub
<i>Psychotria marginata</i> Sw.	1		1	Rubiaceae	Shrub
<i>Psychotria poeppigiana</i> Müll. Arg.	1		1	Rubiaceae	Shrub
<i>Zanthoxylum panamense</i> P.Wilson	1		1	Rutaceae	Tree
<i>Cassearia guianensis</i> (Aubl.) Urb.	1		1	Salicaceae	Shrub
<i>Cupania rufescens</i> Triana & Planch.	1		1	Sapindaceae	Shrub
<i>Manilkara bidentata</i> (A.DC.) A.Chev.	1			Sapotaceae	Tree
<i>Solanum hayesii</i> Fernald	1		1	Solanaceae	Shrub
<i>Tectaria incisa</i> Cav.	1		1	Tectariaceae	Fern
<i>Cecropia obtusifolia</i> Bertol.		1		Urticaceae	Shrub
<i>Cecropia peltata</i> L.		1		Urticaceae	Tree
<i>Myriocarpa longipes</i> Liebm.			1	Urticaceae	Shrub
<i>Lantana camara</i> L.			1	Verbenaceae	Herb

Table 1. List of Chrysomelidae species collected in the different plant associations present in the remnant of tropical humid forest studied. Note: LSRF = Late Secondary Forest, CGZ = Coffee-Growing Zone, DF = Disturbed Forest.

Taxon	Code	LSRF	CGZ	MF	Total	%
Subfamily Cassidinae						
Tribe Mesomphalini Hope, 1840						
<i>Botanochara ordinata</i> (Bohemian, 1850) (Fig. 25)	M1	1	0	0	1	0.3

Tribe Cassidini Gyllenhal, 1813

<i>Acromis sparsa</i> (Boheman, 1854) (Fig. 9)	M2	2	0	0	2	0.6
<i>Charidotella sexpunctata</i> (Fabricius, 1781) (Fig. 20)	M3	1	0	0	1	0.3
<i>Chelymorpha alternans</i> (Boheman, 1854) (Fig. 7–8)	M5	4	0	0	4	1.2
<i>Ischnocoidia annulus</i> (Fabricius, 1781) (Fig. 21)	M6	1	2	0	3	0.9
<i>Deloyala fuliginosa</i> (Olivier, 1790) (Fig. 19)	M7	2	0	0	2	0.6
<i>Microctenochira reticularis</i> (Degeer, 1775) (Fig. 17)	M8	0	2	0	2	0.6
<i>Microctenochira fraterna</i> (Boheman, 1855) (Fig. 22)	M9	1	0	0	1	0.3
<i>Microctenochira lugubris</i> (Boheman, 1862)	M10	1	0	0	1	0.3
<i>Microctenochira infantula</i> (Boheman, 1862) (Fig. 23)	M11	0	1	0	1	0.3
<i>Microctenochira vivida</i> (Boheman, 1855) (Fig. 18)	M4	0	0	1	1	0.3
<i>Agroinconota propinqua</i> (Boheman, 1855) (Fig. 25)	M12	2	0	0	2	0.6

Tribe Imatidiini Hope, 1840

<i>Imatidium thoracicum</i> Fabricius, 1801 (Fig. 10)	M13	1	0	0	1	0.3
<i>Aslamidium semicirculare</i> (Olivier, 1808) (Fig. 11)	M14	4	0	0	4	1.2

Tribe Spilophorini Chapuis, 1845

<i>Calyptocephala brevicornis</i> Boheman, 1850 (Fig. 13)	M15	7	0	0	7	2.0
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<i>Spilophoroides marginatus</i> (Weise, 1910) (Fig. 12)	M16	1	0	0	1	0.3
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Tribe Prosopodontini Weise, 1910

<i>Prosopodonta dorsata</i> (Baly, 1885) (Fig. 14)	M17	1	0	0	1	0.3
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Tribe Chalepini Weise 1910

<i>Oxychalepus normalis</i> (Chapuis, 1877) (Fig. 15)	M18	1	0	0	1	0.3
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<i>Sceloenopla scherezeri</i> (Baly, 1858) (Fig. 16)	M19	1	0	0	1	0.3
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Subfamily Galerucinae

Tribe Luperini Gistel 1848

<i>Diabrotica godmani</i> Jacoby, 1887 (Fig. 26)	M20	25	35	9	69	20.1
<i>Diabrotica championi</i> Jacoby, 1887 (Fig. 27)	M21	2	0	0	2	0.6
<i>Diabrotica mitteri</i> Derunkov, Prado, Tishechkin, Kostantinov, 2015 (Fig. 28)	M22	43	20	7	70	20.3
<i>Diabrotica hartjei</i> Derunkov, Prado, Tishechkin, Kostantinov, 2015 (Fig. 29)	M23	1	0	0	1	0.3
<i>Diabrotica brevilineata</i> Jacoby, 1887 (Fig. 30)	M24	0	1	0	1	0.3
<i>Diabrotica tessellata</i> Jacoby, 1887	M25	1	0	0	1	0.3
<i>Neobrotica caeruleofasciata</i> Jacoby, 1887	M26	1	0	0	1	0.3
<i>Eccoptopsis denticornis</i> (Jacoby, 1887) (Fig. 31–32)	M27	19	11	6	36	10.5
<i>Acalymma separatum</i> (Baly, 1886) (Fig. 38)	M28	1	1	0	2	0.6

<i>Paratriarius adonis</i> (Baly, 1859) (Fig. 33)	M29	4	0	0	4		1.2
<i>Chthonoëis jansoni</i> Jacoby, 1879 (Fig. 40)	M30	3	0	0	3		0.9
<i>Isotes puella</i> (Baly, 1886) (Fig. 34)	M31	0	1	0	1		0.3
<i>Isotes serraticornis</i> (Baly, 1886) (Fig. 35)	M32	4	0	0	4		1.2
<i>Monolepta bipartita</i> (Jacoby, 1888) (Fig. 37)	M33	5	0	0	5		1.5
<i>Monolepta panamensis</i> (Jacoby, 1888)	M34	6	0	0	6		1.7
<i>Phyllobrotica</i> sp.	M35	0	0	2	2		0.6
<i>Gynandrobrotica ventricosa</i> Jacoby 1878 (Fig. 36)	M36	1	0	0	1		0.3

Tribe Galerucini Latreille, 1802

<i>Coelomera godmani</i> Jacoby 1879 (Fig. 41)	M37	1	0	0	1		0.3
<i>Dircema cyanipenne</i> Bechyne, 1951 (Fig. 39)	M38	1	0	0	1		0.3

Tribe Alticini Newman, 1834

<i>Acanthonycha championi</i> Bechyné, 1959 (Fig. 45)	M39	1	1	0	2		0.6
<i>Cerichrestus clarki</i> Jacoby, 1886 (Fig. 42)	M40	5	2	0	7		2.0
<i>Cerichrestus freidbergi</i> (Furth, 2019) (Fig. 43)	M41	1	0	0	1		0.3
<i>Rhinotmetus trifasciatus</i> (Bowditch, 1815) (Fig. 44)	M42	1	0	0	1		0.3
<i>Alagoasa decemguttatus</i> (Fabricius, 1801) (Fig. 60)	M43	1	0	0	1		0.3

<i>Alagoasa godmani</i> (Jacoby, 1880) (Fig. 59)	M44	6	0	0	6	1.7
<i>Alagoasa bipunctata tritaenioides</i> (Harold, 1876) (Fig. 56)	M45	1	0	0	1	0.3
<i>Alagoasa bipunctata perennis</i> (Harold, 1876) (Fig. 57)	M46	1	0	0	1	0.3
<i>Alagoasa montana</i> (Jacoby, 1886) (Fig. 58)	M47	0	1	0	1	0.3
<i>Diphaulaca aulica</i> (Olivier, 1808) (Fig. 52)	M48	1	0	0	1	0.3
<i>Disonycha trifasciata</i> Clark, 1865 (Fig. 54)	M49	0	0	1	1	0.3
<i>Hydmosyne inclyta</i> Clark, 1860 (Fig. 46)	M50	1	0	0	1	0.3
<i>Monomacra chiriquensis</i> (Jacoby, 1884) (Fig. 48)	M51	1	0	0	1	0.3
<i>Monomacra perplexa</i> (Jacoby, 1884) (Fig. 49)	M52	0	1	0	1	0.3
<i>Omophoita albicollis</i> (Fabricius, 1787) (Fig. 53)	M53	1	0	0	1	0.3
<i>Omophoita clerica</i> (Erichson, 1848)	M54	1	0	0	1	0.3
<i>Physimerus antennarius</i> Harold, 1875 (Fig. 77)	M55	1	0	0	1	0.3
<i>Stegnea chiriquensis</i> (Jacoby, 1885) (Fig. 47)	M56	2	1	0	3	0.9
<i>Systema oberthuri</i> Baly, 1878 (Fig. 50)	M57	0	1	0	1	0.3
<i>Systema variabilis</i> Jacoby, 1884 (Fig. 51)	M58	4	3	14	23	6.7
<i>Heikertingeria</i> sp. (Fig. 55)	M59	4	0	0	4	1.2

Subfamily Eumolpinae

Tribe Eumolpini Hope, 1840

<i>Rhabdopterus uncotibialis</i> (Blake, 1976) (Fig. 65)	M60	2	0	0	2	0.6
<i>Rhabdopterus fulvipes</i> (Jacoby, 1882) (Fig. 66)	M61	16	0	0	16	4.6
<i>Percolaspis rugosa sculpta</i> (Jacoby, 1890) (Fig. 64)	M62	2	0	0	2	0.6
<i>Percolaspis</i> sp. (Fig. 63)	M63	0	0	0	1	0.3
<i>Allocolaspis grandicollis</i> (Blake, 1976) (Fig. 62)	M64	2	1	0	3	0.9
<i>Deuteronoda suturalis</i> (Lefrevre, 1878) (Fig. 67)	M65	1	0	0	1	0.3
<i>Cayetunya consanguinea</i> (Blake, 1976) (Fig. 61)	M66	1	0	0	1	0.3

Tribe Megascelidini Chapuis, 1874

<i>Megascelis puella</i> Lacordaire, 1845 (Fig. 68)	M67	1	0	1	2	0.6
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Subfamily Lamprosomatinae Lacordaire, 1848

Tribe Lamprosomatini Lacordaire, 1848

<i>Lamprosoma inornatus</i> Jacoby, 1878 (Fig. 79)	M68	1	0	0	1	0.3
<i>Oomorphus</i> sp. (Fig. 78)	M69	1	0	0	1	0.3

Subfamily Criocerinae Latreille, 1804

Tribe Lemini Gyllenhal, 1813

<i>Lema chiriquensis</i> Jacoby, 1888 (Fig. 74)	M70	1	0	0	1	0.3
<i>Lema subapicalis</i> Baly, 1879 (Fig. 76)	M71	1	0	0	1	0.3
<i>Lema</i> sp. (Fig. 75)	M72	1	0	0	1	0.3
<i>Oulema</i> sp.	M73	0	0	2	2	0.6

Subfamily Chrysomelinae

Chrysomelini Latreille Tribe, 1802

<i>Stilodes fuscolineata</i> Stål, 1865 (Fig. 71)	M74	0	1	0	1	0.3
<i>Platyphora ligata</i> Stål, 1858 (Fig. 69)	M75	1	0	0	1	0.3
<i>Calligrapha argus</i> Stål, 1859 (Fig. 70)	M76	1	0	0	1	0.3
<i>Leptinotarsa undecimlineata</i> Stål, 1859 (Fig. 72)	M77	0	1	0	1	0.3

Subfamily Bruchinae Latreille, 1802

Tribe Pachymerini Bridwell, 1929

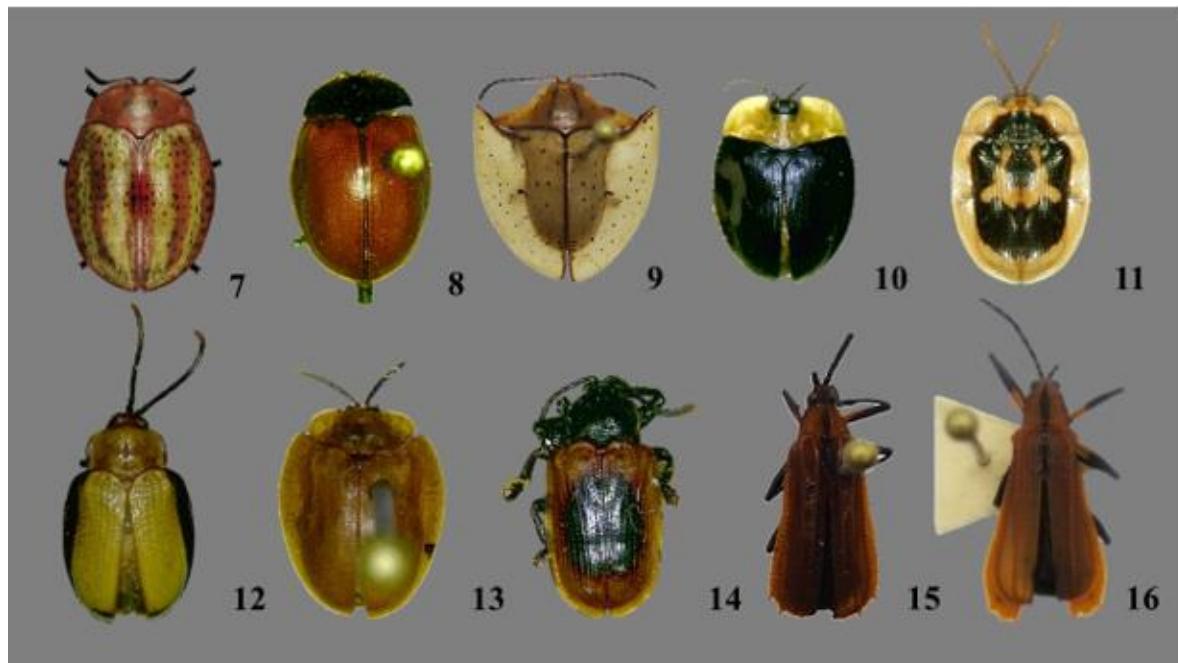
<i>Pachymerus cardo</i> (Fåhraeus, 1839) (Fig. 73)	M78	1	0	0	1	0.3
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Total Individuals	215	88	44	347	100
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Total Species	65	20	9
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Table 2. Summary of Malaise trap catches of Chrysomelidae from Trogon Trail sampling sites. Code: LSRF = Late Secondary Forest, CGZ = Coffee-Growing Zone, DF = Disturbed Forest, TroT=Trogon trail total, Ind=individuals, Sp= species.

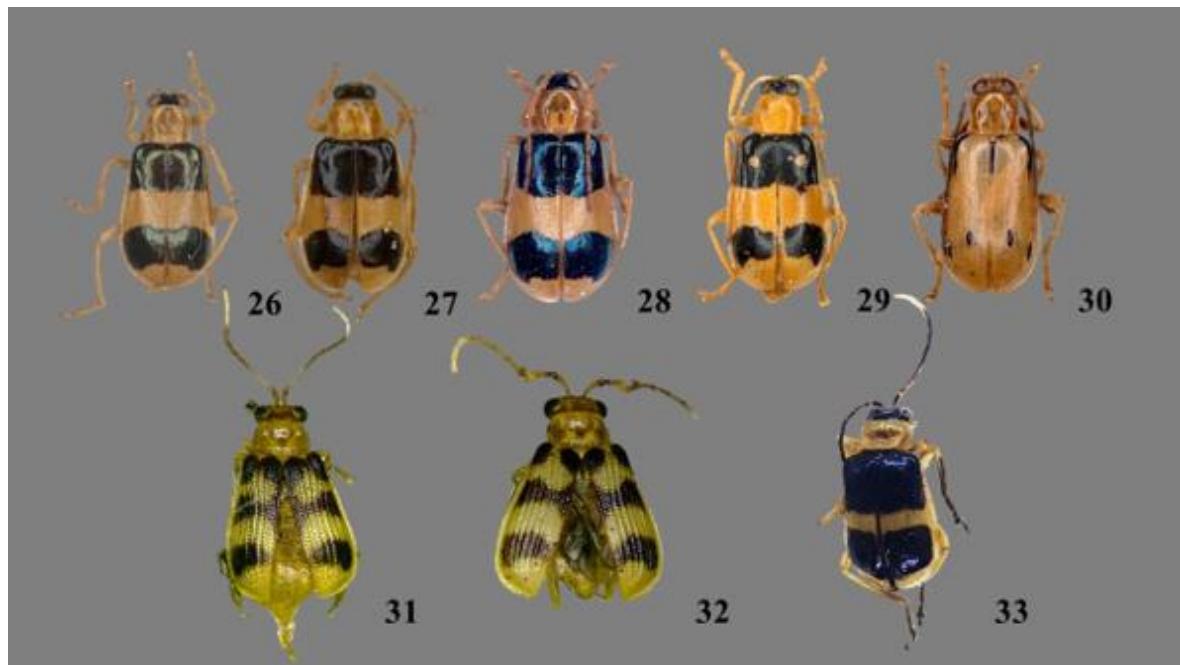
	Ind	Sp	Singletons	Doubletons	Rare	Common	Very Common
LSRF	215	65	40	7	12	3	1
CGZ	88	20	12	3	1	2	1
DF	44	9	3	3	3	1	0
TroT	347	77	46	11	14	2	3



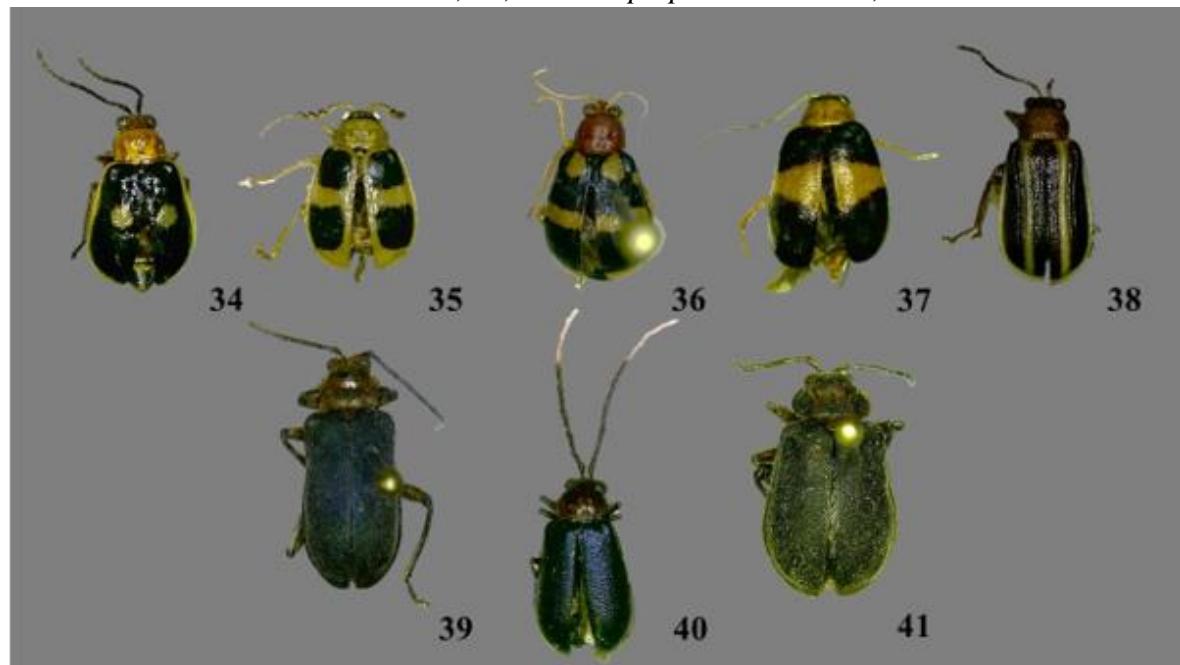
Figures 7–16. Dorsal view of Chrysomelidae Cassidinae: 7,8 *Chelymorpha alternans*, 9. *Acromis sparsa* 10. *Imatidium thoracicum*, 11. *Aslamidium semicirculare*, 12. *Spilophoroïdes marginatus*, 13. *Calyptocephala brevicornis*, 14. *Prosopodonta dorsata*, 15. *Oxychalepus normalis*, 16. *Sceloenopla scherezeri*.



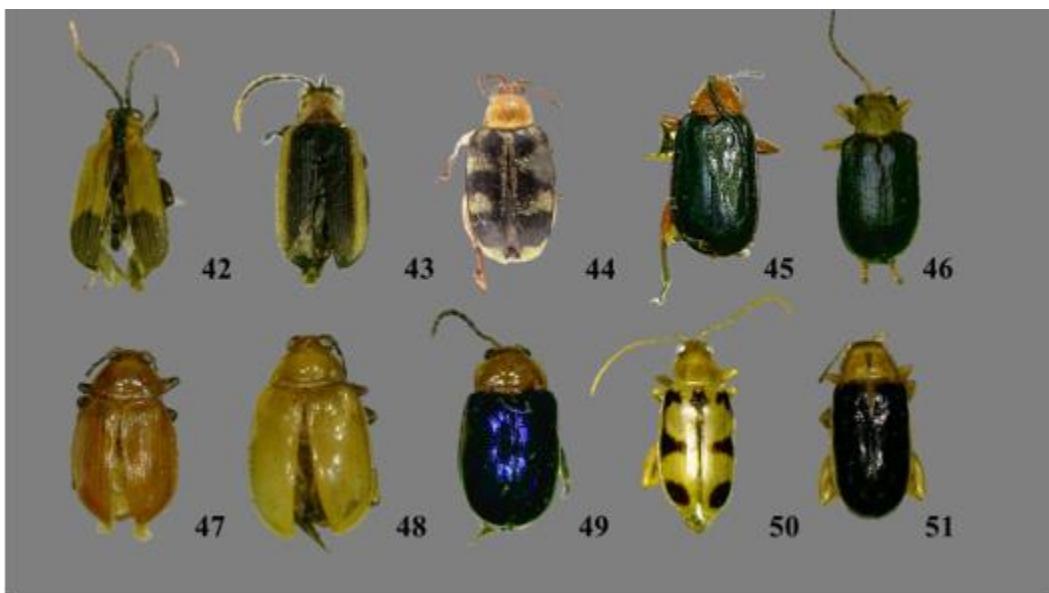
Figures 17–25. Dorsal view of Chrysomelidae Cassidinae: 17, *Microctenochira reticularis*, 18. *Microctenochira vivida* 19. *Delyuala fuliginosa*, 20. *Charidotella sexpunctata*, 21. *Ischnocodia annulus*, 22. *Microctenochira fraterna*, 23. *Microctenochira infantula*, 24. *Agroinconota propinqua*, 25. *Botanochara ordinata*.



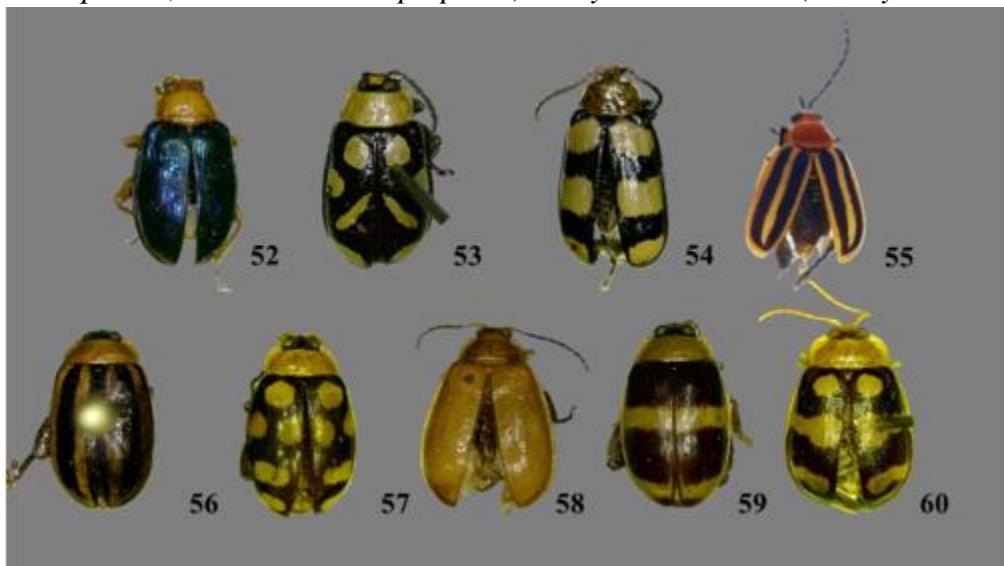
Figures 26–33. Dorsal view of Chrysomelidae Galerucinae: Luperini: 26. *Diabrotica godmani*, 27. *Diabrotica championi*, 28. *Diabrotica mitteri*, 29. *Diabrotica hartjei*, 30. *Diabrotica brevilineata*, 31, 32. *Eccoptopsis denticornis*, 33. *Paratriarius adonis*



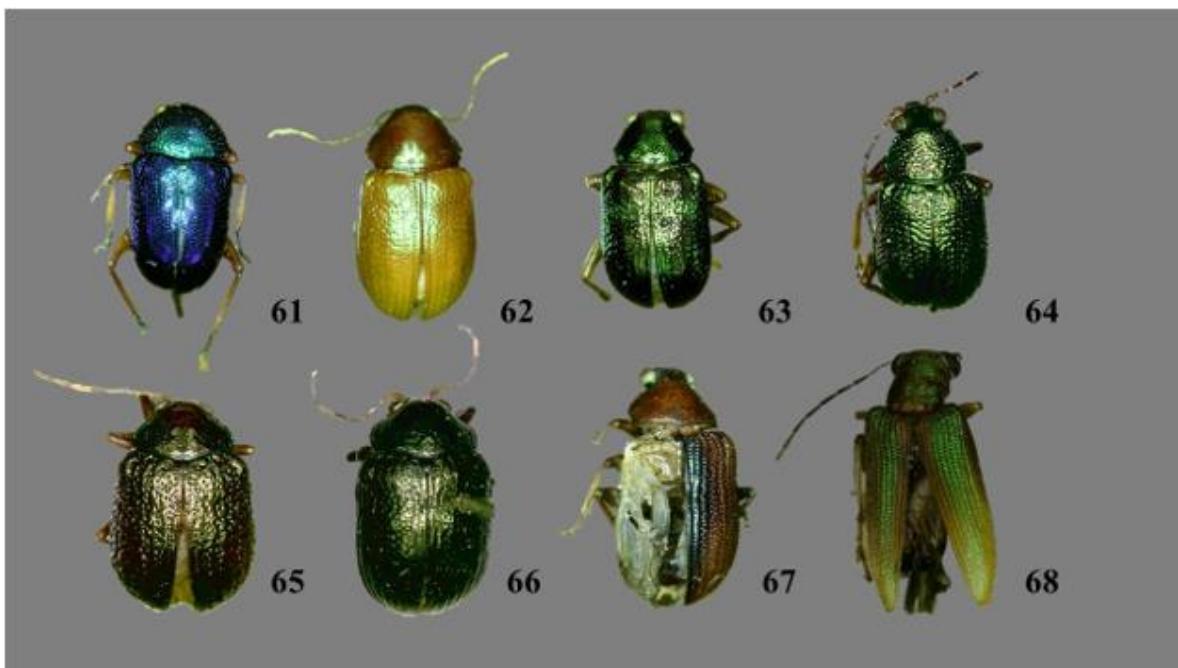
Figures 34–41. Dorsal view of Chrysomelidae Galerucinae: Luperini + Galerucini: 34. *Isotes puella*, 35. *Isotes serraticornis*, 36. *Gynandrobrotica ventricosa*, 37. *Monolepta bipartita*, 38. *Acalymma separatum*, 39. *Dyrcema cyanipenne*, 40. *Chthonoës jansoni*, 41. *Coelomera godmani*.



Figures 42–51. Dorsal view of Chrysomelidae Galerucinae: Alticini: 42, *Cericrestus clarki*, 43. *Cericrestus freidbergi*, 44. *Rhinotmetus trifasciatus*, 45. *Acanthonycha championi*, 46. *Hydmosyne inclita*, 47. *Stegnea chiriquensis*, 48. *Monomacra chiriquensis*, 49. *Monomacra perplexa*, 50. *Systena oberthuri*, 51. *Systena variabilis*



Figures 52–61. Dorsal view of Chrysomelidae Galerucinae: Alticini: 52, *Diphaulaca aulica*, 53. *Omophoita albicollis*, 54. *Disonycha trifasciata*, 55. *Heikertingeria* sp., 56. *Alagoasa bipunctata tritaeniodes*, 57. *Alagoasa bipunctata perennis*, 58. *Alagoasa montana*, 59. *Alagoasa godmani*, 60. *Alagoasa decemguttata*.



Figures 61–68. Dorsal view of Chrysomelidae Galerucinae: Eumolpinae: 61, *Cayetunya consanguinea*, 62. *Allocolaspis grandicollis*, 63. *Percolaspis sp.*, 64. *Percolaspis rugosa*, 65. *Rhabdopterus uncotibialis*, 66. *Rhabdopterus fulvipes*, 67. *Deuteronoda suturalis*, 68. *Megascelis puella*



Figures 69–76. Dorsal view of Chrysomelidae Chrysomelinae: 69, *Platyphora ligata*, 70. *Calligrapha argus*, 71. *Stilodes fuscolineata*, 72. *Leptinotarsa undecimlineata*, Bruchinae: 73. *Pachymerus cano*, Criocerinae: 74. *Lema chiriquensis*, 75. *Lema sp.*, 76. *Lema subapicalis*



Figures 77–79. Dorsal view of Chrysomelidae Galerucinae: Alticini: 77. *Physimerus antennarius*, Lamprosomatinae: 78. *Oomorphus* sp., 79. *Lamprosoma inornata*.