



Biodiversity, conservation, and hotspot atlas of Costa Rica: a dung beetle perspective (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract

This paper is an analysis of the distribution of areas of high species richness and endemism based on dung beetles living in the different Holdridge life-zones of Costa Rica by using a geographic information system (GIS). Endemism was examined in relation to whether the species were shared with Nicaragua and/or Panama, or if they were strictly Costa Rican. The species composition of dung beetle distributions in the sampling areas and life-zones was evaluated. Species distribution was also analyzed in relation to altitudinal levels. The species richness and endemism maps served as a base for doing a gap analysis and defining four different levels of high priority conservation areas. We also investigated what percentage of these priority areas is under some type of protection or conservation scheme and which of these areas should be enlarged. Also considered is the feasibility that these areas under protection have for enlargement, considering possible problems and interactions with present land-use. We include a list of all the recorded dung beetle species for Costa Rica, as well as their presence in the different Holdridge life-zones and their endemism status. This study clearly demonstrates the need to include insects in biodiversity-endemism studies because different and more detailed results are obtained in relation to vertebrate and plant-based studies.

Key words: Biodiversity atlas, conservation, biodiversity areas, endemism areas, gap analysis, Costa Rica, dung beetles, Scarabaeinae

Resumen

En el presente trabajo se realizó un análisis de la distribución de áreas de alta riqueza específica y endemismo de escarabajos del estiércol en las diferentes zonas de vida de Holdridge en Costa Rica, utilizando un sistema de información geográfica (SIG). Los endemismos fueron particularmente analizados en relación a si se compartían con Nicaragua y/o Panamá, o si eran estrictamente costarricenses. Se evaluó la representatividad de las áreas de colecta y la cobertura de zonas de vida. Se analizó también la distribución de las especies con respecto a pisos altitudinales. Los mapas de riqueza específica y endemismo sirvieron de base para realizar un análisis de tipo Gap y definir cuatro zonas de conservación de alta prioridad. Se analiza también qué porcentaje de esas áreas prioritarias se encuentran actualmente bajo algún tipo de protección, y cuáles de estas zonas deberían aumentar su cobertura al respecto. Se analiza también la factibilidad de que se logren realizar estas extensiones de protección en relación a posibles problemas e interacciones con el presente sistema de uso de suelos. Se incluye una lista de todas las especies registradas de escarabajos del estiércol de Costa Rica, así como su presencia en las diferentes zonas de vida de Holdridge y su condición de endemismo o no. Este estudio demuestra claramente la necesidad de incluir a los insectos en estudios de biodiversidad y endemismo, se pueden obtener resultados distintos y con más detalle en relación a los estudios que se basan sólo en vertebrados y plantas.

Introduction

The distribution of biodiversity is not an even occurrence across the surface of the Earth. On the contrary, numbers vary and species composition present highs and lows in a very complex pattern. Many attempts have been undertaken to try to understand, map, and identify general spatial patterns, especially species richness and endemism of well-known groups, such as vertebrates and plants. However, very little information is available for highly speciose groups, such as insects (Gaston and Spicer 2004).

At the same time, global biodiversity is decreasing precipitously with innumerable species going extinct. No one knows for sure what the final effect of this crisis will be, but one thing is certain: first we must know how this biodiversity is spatially distributed. For this reason, Morrone and Espinosa (1998) have advocated the compilation of biogeographic atlases. A biogeographic atlas represents the synthesis of the distribution patterns of taxa for a country or a biogeographic area, represented by bioclimatic predictions, panbiogeographic analysis, cladistic biogeography, and areas of species richness and endemism (Nix 1989, Espinosa and Llorente 1993, Morrone et al. 1996, Lobo et al. 1997, Morrone 2000). Biogeographic atlases furnish information relevant for the identification of species richness and endemic areas, which in turn can be used for establishing conservation areas and developing sustainability policies. Because the present analysis concentrates primarily on the species richness and mapping endemism it should be considered foremostly as a biodiversity atlas.

Costa Rica is not a big country (Fig. 1). It has only 51,100 km² of land surface, representing only the 0.03% of the surface of the Earth (Ministerio del Ambiente y Energía 2000). In the ranking of world biodiversity, it occupies the 20th place, approximately. As such, it was not considered a megadiverse country by Mittermeier and Goettsch Mittermeier (1997), who gave this status only to the top twelve countries. However, what makes Costa Rica special is its species density (number of species per unit of area) (Obando 2002). Using this measure, Costa Rica ranks first in the world (Valerio 1999, Obando 2002). It is considered that Costa Rica possesses around 4% of the total world biodiversity and if we consider the total number of described species this number jumps then to 5.4 % (Jiménez 1995). To give a comparative idea, Costa Rica has 234.9 plant species per 1,000 km², whereas the second most species-dense country, Colombia, has 39.4 plant species per 1,000 km² (Obando 2002). In the same line of thought, Costa Rica has 16.9 bird species per 1,000 km², whereas Colombia has only 1.5 bird species per 1,000 km² (Valerio 1999, Obando 2002). Costa Rica's extreme biodiversity is now under protection by a world-class national system of protected areas, which was initiated in the 1970's and today protects almost 27 percent of the country (Vaughan 1994, Vaughan et al. 1998).

It is precisely this biodiversity that has been attracting ecotourists to the country, making this activity the primary source for foreign currency income; surpassing in the last ten years the three traditional major exports of coffee, bananas, and beef (Damon and Vaughan 1995). This is an important and swift change for the economic paradigm of a country, especially if we consider that coffee has been the primary economic engine of Costa Rica since the mid 19th century (Hall et al. 2000).

Costa Rica is considered to have a moderate number of endemics (Obando 2002), with around 1.4% of the known species (plants and vertebrates) being endemic to the country. It is estimated that around 11% of the total plant species are endemics, whereas the different vertebrate groups vary from a minimum of 0.8% in birds to a maximum of 20% for the amphibians (Obando 2002). Using plants and vertebrates, four great areas of endemism have been identified for continental Costa Rica (Fig. 15): the Central Volcanic Cordillera, the Talamanca Cordillera, the Central Pacific Region, and the Golfo Dulce Region. A fifth area has been identified in Coco Island, in the Pacific Ocean. From the ecosystem point of view, cloud forests are the most endemic ecosystems (Obando 2002).

This study is a first attempt to define a biodiversity atlas indicating the areas of high species richness and endemism for Costa Rica using an insect taxon (Scarabaeinae), instead of plants and vertebrates as has been

done in the past. The analysis focuses on continental Costa Rica; Coco Island was not included because no Scarabaeinae are known from this island. A similar analysis was done by Lumaret (1978, 1990) and Lumaret and Lobo (1996) for France and the Western Palearctic region respectively. This atlas represents a first step towards helping to define those areas most in need of conservation and sustainable use in Costa Rica using insects, as well as identifying those areas that have been undersampled in order to target future collecting efforts to these poorly-known areas. Similar analyses using plants (Araceae, Arecaceae, and Bromeliaceae), fresh-water fishes, and beetles (Scarabaeidae: Dynastinae) are almost finished and will be published soon as a sequel and complement to this analysis.



FIGURE 1. Map of Costa Rica showing major geographical landmarks and cities, roads, types of vegetation, and protected areas (national parks, national wildlife refuges, and biological reserves; numbered 1–48) (taken from Kohlmann et al. 2002).

Materials and Methods

Taxon information

Information regarding scarab beetle distribution was taken from the collections and electronic database of the National Biodiversity Institute (INBio). This institution has been collecting plants and insects of Costa Rica for the last 15 years and the studied material represents approximately 90,000 specimens of Scarabaeinae. This group has also been particularly well studied in relation to its systematics as the following pub-

lished works that cover Costa Rica can testify: Howden and Young 1981; Howden and Gill 1987, 1993; Edmonds 1994, 2000, 2004a; Génier 1996; Kohlmann 1997, 2000; Kohlmann and Solís 1996, 1997, 2001a, 2001b; Génier and Howden 1999; Rivera-Cervantes and Halffter 1999; Arnaud 2002; Kohlmann et al. 2002; Solís and Kohlmann 2002, 2003, 2004; Génier and Kohlmann 2003; Kohlmann and Wilkinson 2003. So far, 175 taxa of Scarabaeinae have been reported from Costa Rica (Table 1 and Appendix). This number is similar to the known species richness of other well-studied countries in the region. Approximately 132 species of Scarabaeinae are known from Panama (Howden and Young 1981; Howden and Gill 1987; Kohlmann 1997; Kohlmann and Solís 1997; Génier and Howden 1999; Kohlmann and Solís 2001b; Ratcliffe 2002; Solís and Kohlmann 2003; Edmonds 2004b, 2006), whereas Mexico has approximately 245 known species (Arnaud 2002, Morón 2003, McCleve and Kohlmann 2005, Delgado et al. 2006, Kohlmann and Solís 2006).

In conclusion, dung beetles are a group that has been particularly well sampled in Costa Rica, as well as systematically studied in great taxonomic detail; their analyzed distributional areas are relatively smaller than the study area, therefore complying with Müller's (1981) three tenets for making this group particularly well-suited for the present biogeographic analysis.

Vegetation base map

One of the most popular systems used in Costa Rica and in twelve other countries (Meza 2001), for the classification of vegetation, is the Life Zone System developed by Holdridge (1967). This system divides Costa Rica into 12 Life Zones and 12 Transition Zones based on environmental factors such as humidity, rainfall, and temperature (Fig. 2). The interplay between these variables defines bioclimatic units called Life Zones (Holdridge 1967). This system is thus independent of floristic relationships and the same zones can then reappear in different regions of the world. According to Hall (1984), this system takes into account not only variations caused by latitude, but also by altitude, and is therefore especially useful for tropical mountainous countries.

According to this classification, the five most extensive Costa Rican vegetation types are: tropical wet forest (wf-T) (10.5% of the total country area), premontane wet forest (wf-P) (7.2%), lower montane wet forest (wf-LM) (5.9%), premontane rain forest (rf-P) (5.6%), and tropical moist forest (mf-T) (5.5%) (Obando 2002).

We have to acknowledge some limitations of this system. The Holdridge life zone system can potentially vary along other environmental axes, besides total precipitation and temperature, such as edaphic or geologic conditions and this could impact species abundance and endemism. Bioclimatic regions such as the Pacific dry forest comprise long belts along mountain/volcanic ranges, and by assuming that these long belts share the same biodiversity category a potential risk can be generated of losing resolution when assigning conservation priority zones. For example, this Pacific dry forest spans the entire region going from the Guanacaste mountain range to the Tilarán mountain range (Fig. 1), representing areas of very diverse geologic origin, ranging from the Plio-Pleistocene (Guanacaste) to the Miocene (Tilarán).

GIS Analysis

Savitsky (1998a, 1998b) presents a very convincing case why digital mapping techniques using Geographic Information Systems (GIS), are faster, more efficient, and more powerful and versatile than traditional analog cartography. We have followed a GIS-oriented process for the elaboration of our biogeography atlas.

For the GIS analysis the following processes were done using ArcGIS and Microsoft Excel:

1.—Establishment and standardization of the databases for each taxon in relation to taxon names, type of endemism, and location of collecting sites. Information layers were generated using the collecting sites for each species.

2.—Standardization of geographic information. The layers containing the National System of Coordinates were transformed to geographic coordinates. For distributional referencing (see Appendix), each Holdridge life zone was numbered (Fig. 2).

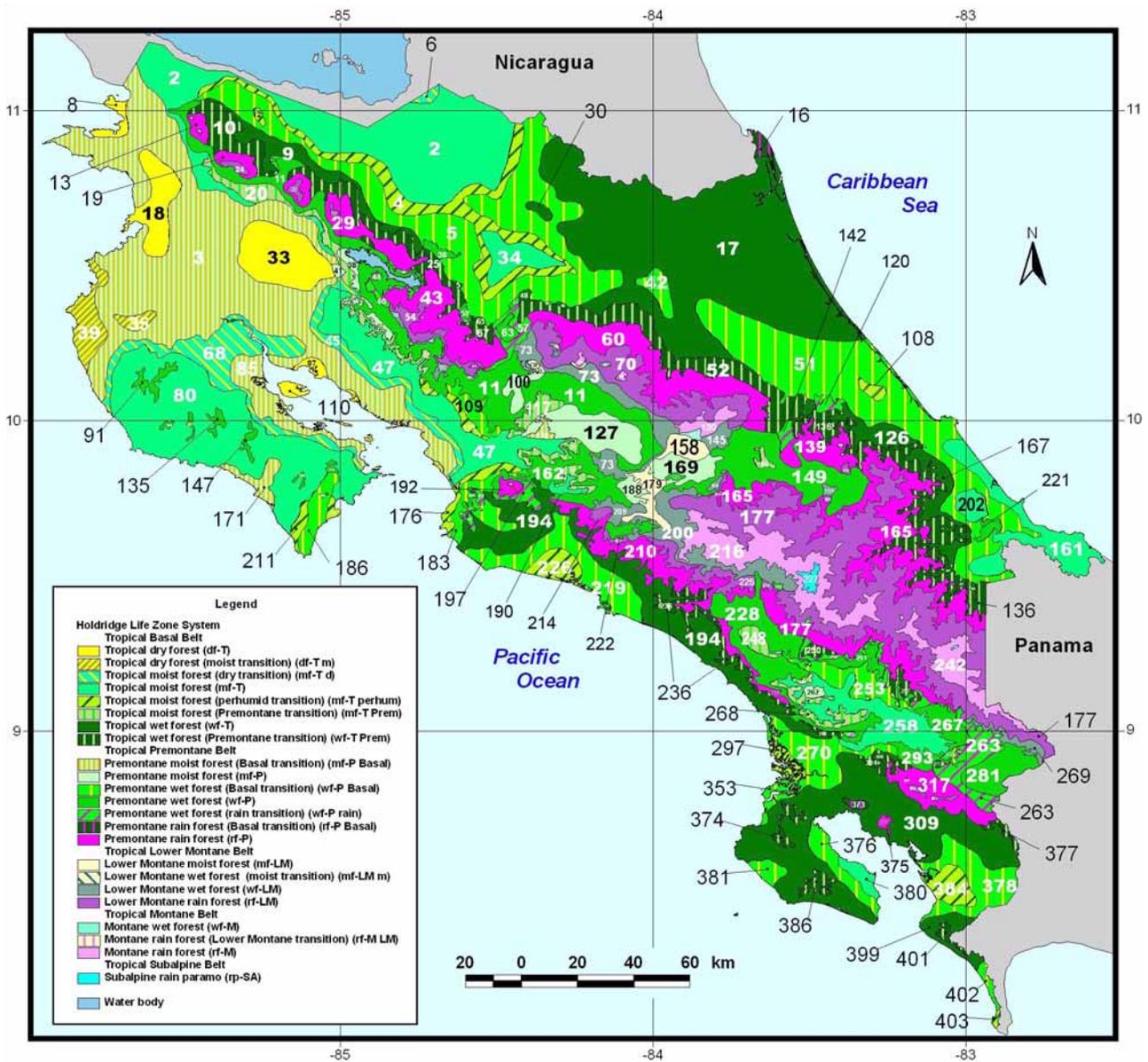


FIGURE 2. Map numbering the Holdridge life zones in Costa Rica.

3.—For each taxon, the occurrence points were superimposed on the Holdridge life zones and out of this product the number of collections and taxa, as well as the total species richness and endemics and type of endemism (endemics known to occur only in Costa Rica, endemics shared with Panama, endemics shared with Nicaragua, endemics shared with Nicaragua and Panama, total number of endemics for Costa Rica), were obtained for each life zone. Layers for the total species richness and each type of endemism were produced for Scarabaeinae. The base electronic map was derived from the one presented in Atlas Costa Rica 2000 (Instituto Tecnológico de Costa Rica, 2000).

4.—A gap analysis map was generated overlaying a map of protected areas separately over both species richness and endemism maps. These two maps contained each one of five different species ranks (1-5) (species richness: rank 1 [1-6], rank 2 [7-18], rank 3 [19-39], rank 4 [40-62], and rank 5 [63-89]; endemics: rank 1 [1-3], rank 2 [4-6], rank 3 [7-11], rank 4 [12-18], and rank 5 [19-25]), where rank 5 is the rank with the highest number of taxa. Later, four priority zones were defined by overlaying the protected areas map on top of the species richness and endemism map at the same time, producing a conservation priority gap analysis map. Priority zone 1 represents areas where the highest species richness (rank 5) coincides with the highest level of endemism (rank 5) (all rank 5 endemism areas also coincide in this case with rank 5 species richness areas);

priority zone 2 represents those areas of highest species richness (rank 5) that did not coincide with the highest level of endemism (rank 5). Priority zone 3 represents areas where the second highest rank (rank 4) of species richness and second highest rank of endemism (rank 4) coincide (in this case all rank 4 species richness areas also coincide with the rank 4 endemism areas), and priority zone 4 represents those areas with only the second highest rank of endemism (rank 4).

Results and Discussion

Distribution of collecting localities

Collections were made for the Scarabaeinae by INBio (Instituto Nacional de Biodiversidad, Costa Rica) in 409 different localities around the country (Fig. 3), representing a total effort of 2,869 collection days and approximately 90,000 specimens. The selection of collecting sites is often biased—in this case, INBio samples preferentially protected areas of the country more often than non-protected areas that have been modified by human activity.

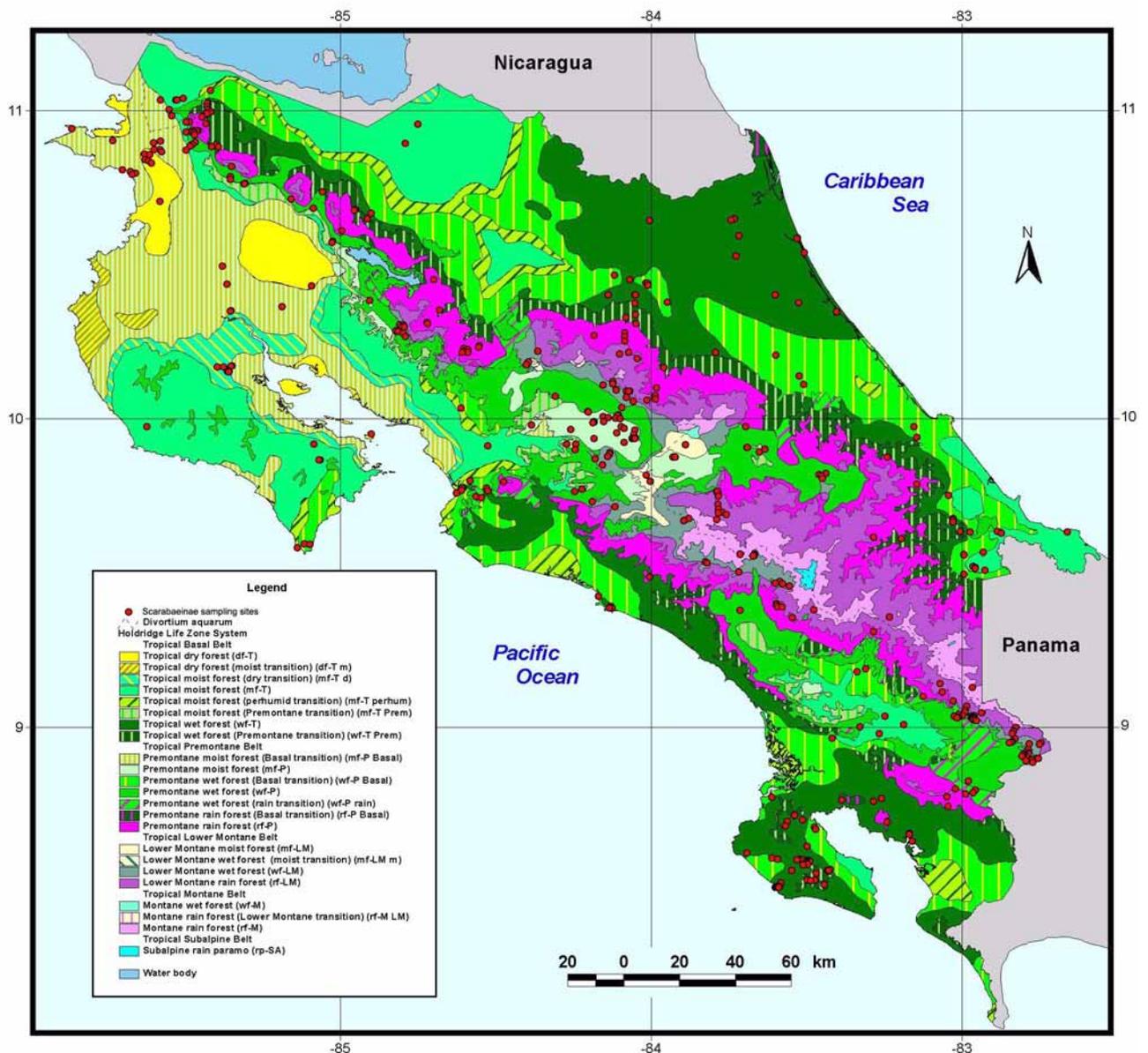


FIGURE 3. Map showing the collecting localities of the Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

A quick glance at the collecting localities map (Fig. 3) shows us that the northern part of Costa Rica, as well as the central Pacific, is under-collected; due mostly to the fact that these areas have been highly altered by agricultural activities. Other areas that also require more collecting effort are the Nicoya peninsula of northwestern Costa Rica and the higher parts of the Talamanca Cordillera to the southeast; the lack of roads in these regions is the main barrier to collecting these areas.

The appendix section of the paper presents a list of all the Scarabaeinae taxa used in this study and relates them to the number of life zones used for mapping their distribution (Fig. 2). Additional information is also provided in this section categorizing the endemism status for each taxon, as well as giving the complete list of the different life zones where each taxon has been collected.

Distribution of species richness by altitude levels and versants

As expected, the greatest species richness is found in the first altitude level (0-1000 m) along both coasts, as a result partly of altitude and partly of the greater total area of this altitude level in Costa Rica. Species richness (Table 1) ranges from 84 to 110 species. The Caribbean versant (Fig. 4) is the richest (110), and both the dry (97) and the wet (84) Pacific sections (Fig. 4) do not greatly differ in total numbers. The second altitudinal band (>1000 to 2000 m), despite its reduced total area, is still very rich in total numbers and even richer per square unit than the first altitude level. Total numbers tend to become very similar (65–71), and it is interesting to note that although the Pacific dry versant represents the smallest area of all three sections, it is the richest at this altitude band if we consider the estimated number of species per 100 km² (4.75) *versus* the values for the Caribbean (1.62) and the wet Pacific (2.77). The third altitude level (> 2000 m), being the highest and smallest in area, has reduced species numbers (5–10), the dry Pacific being the poorest (5) and the wet Pacific the richest (10).

TABLE 1. Number of species and endemics of Scarabaeinae* by altitude level in Costa Rica.

Versant	Altitude level	Area in km ² **	Percentage of total area	Number of species***	Mean number of species per 100 km ²	Number of endemic species****	Number of collections
Caribbean	0 to 1000 m	18,513	36.3	110	0.61	25	1003
	> 1000 to 2000 m	4,005	7.8	66	1.65	13(2)****	165
	> 2000 m	1,740	3.4	6	0.34	1	11
Subtotal Caribbean		24,258	47.5	130	0.53	32	1179
Wet Pacific	0 to 1000 m	9,767	19.1	84	0.86	13	519
	> 1000 to 2000 m	2,451	4.8	68	2.77	18	356
	> 2000 m	930	1.8	10	1.07	4	32
Subtotal Wet Pacific		13,148	25.8	118	0.90	23	907
Dry Pacific	0 to 1000 m	12,034	23.6	97	0.81	16	532
	> 1000 to 2000 m	1,495	2.9	71	4.75	22(6)****	245
	> 2000 m	103	0.2	5	4.85	1	6
Subtotal Dry Pacific		13,632	26.7	109	0.80	34	783
Total		51,038	100	174*	0.33	66	2869

(*) *Dichotomius costaricensis* is not considered in this analysis because only the country locality is known.

(**) Isla del Coco was not considered

(***) A same species can be found at different altitude levels or versants

(****) Numbers in parentheses indicate number of endemic species from the Dry Pacific or Caribbean versant that marginally penetrate into the other versant along mountain passes of the Guanacaste Cordillera, non-parenthesis number includes these ancillary species.

The Caribbean versant has the highest total species number (130) (Table 1) and the dry Pacific the lowest (109), most probably due to area and climate effects. However, if we consider the mean number of species per 100 km², the wet Pacific shows the highest number (0.90), followed by the dry Pacific (0.80), with the Caribbean distinctly in third place (0.53). These numbers would seemingly indicate a greater biodiversity on the Pacific versant.

Distribution of species richness by life zones

Lamentably, not all areas of Costa Rica have been collected with equal intensity. In order to define areas with a good collecting record and for comparative purposes, we have chosen 15 areas that have been collected for at least five years; they are indicated as a big number with an asterisk (89*) in Fig. 4 and parenthetically in the text below (89*).

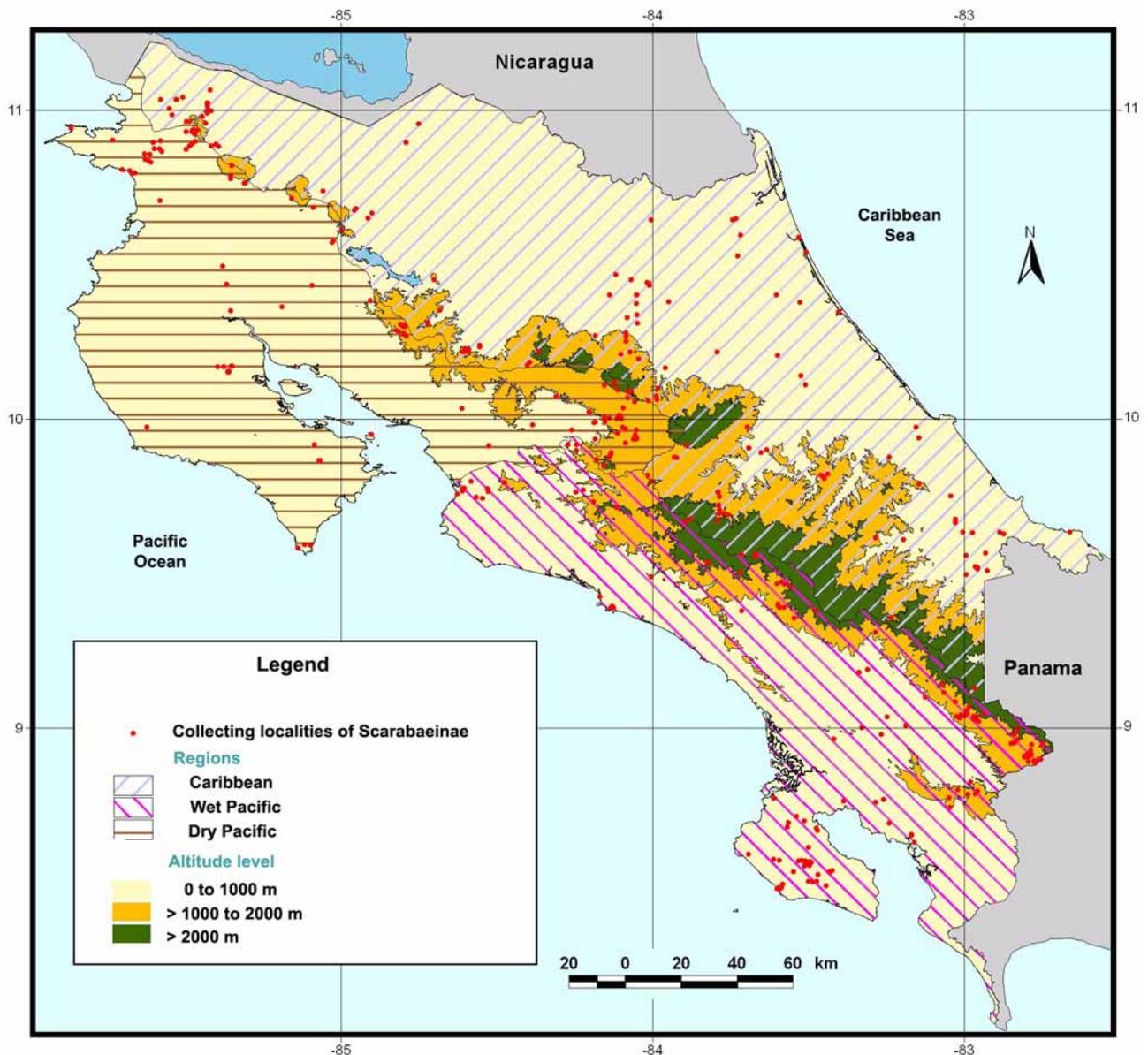


FIGURE 4. Map showing the distribution of Scarabaeinae collecting localities by altitude levels on the Caribbean and Pacific slopes.

The life zone that emerges with the largest recorded species richness (89*) corresponds to the premontane wet forest (wf-P) (approximately 750–1500 m) along the Pacific versant of the Guanacaste, Tilarán, and Central mountain range systems (Fig. 5). This same approximate area was named the Pacific mid-elevation region by DeVries (1987, 1997) and was considered by him to be a very complex area considering the multiplicity of habitats and microhabitats present. Using butterflies, DeVries (1987) considered this zone to be very species-rich and a major migrational corridor between the Atlantic and Pacific slopes, as well as a mixing-zone for species of both slopes. This last observation is also valid for the studied dung beetles, as the Caribbean slope species extend their distribution ranges in a limited way into the Pacific slope and contribute to the general species richness on the Pacific versant, as is the case with *Ateuchus candezei*, *Canthidium angusticeps*, *C. annagabrielae*, *C. ardens*, *C. haroldi*, *C. hespenheidei*, *C. pseudopuncticolle*, *C. vespertinum*, *Canthon aequinoctialis*, *C. angustatus*, *C. euryscelis*, *C. subhyalinus subhyalinus*, *Dichotomius satanas*, *Onthophagus coscineus*, *O. crinitus*, *O. nemorivagus*, *O. nyctopus*, *O. stockwelli*, *O. tapirus*, and *Scatimus erinnyos*.

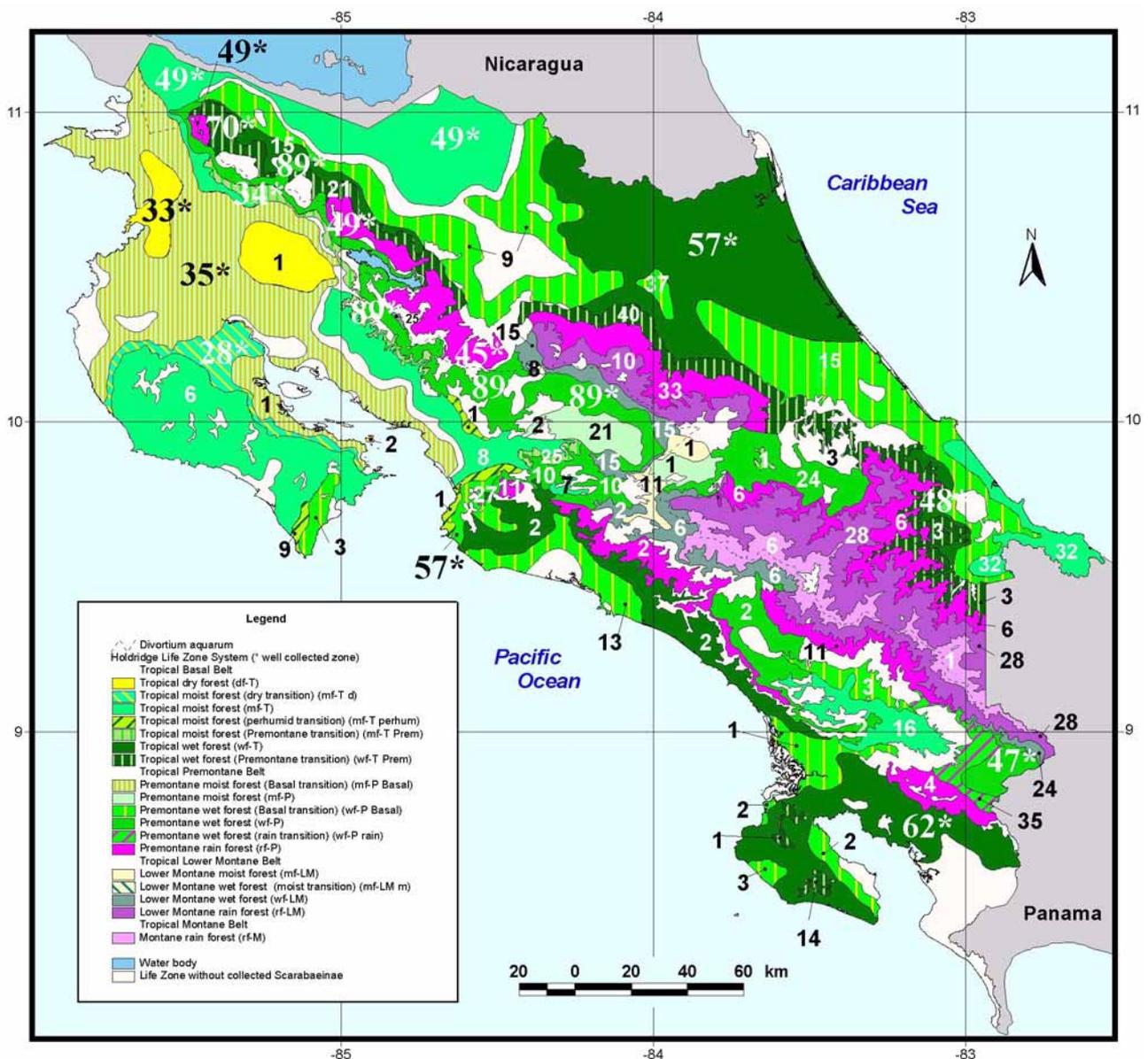


FIGURE 5. Map showing the recorded number of Scarabaeinae species per life zone. Numbers with an asterisk represent areas that have been collected for five years or more in Costa Rica. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

The opposite phenomenon, Pacific slope species invading the Atlantic slope, is not as common (for example: *Canthon morsei*, *C. deyrollei*, *Dichotomius centralis*, *D. yucatanus*, and *Onthophagus championi*) and this last occurrence can be seen in the second highest species richness (70*) recorded from the tropical wet forest (wf-T Prem) (premontane transition, approximately 800-1500 m), which lies on the Caribbean slope. This region was identified as one of the most species-diverse areas for butterflies by DeVries (1997). Fogden and Fogden (1997) also observed greater species richness in the foothills, rather than in the lowlands, and hypothesized that a greater variety of habitats in these regions resulted in greater species richness. Contrary to this study, Fogden and Fogden (1997) found greater species richness on the Caribbean foothills and not on the Pacific foothills. Savage (2002) arrived to a similar conclusion when he recorded the highest (195) and second highest (185) number of amphibian and reptile species along the Caribbean versant in premontane rain-forest and lowland moist forest, respectively; and not surprisingly he found that the amphibians peak in species number on the Talamanca mountain range. In any case, mid-elevational areas seem to be more species-rich than highlands or lowlands.

The third and fourth ranks were the tropical wet forests (wf-T) on the Pacific (62*) and Caribbean versants (57*) and the premontane wet forest (wf-P Basal) (basal transition) on the Pacific (57*) versant. It would appear that the high species richness of lowland forests tends to diminish inland, as is the case of the tropical moist forest (mf-T) (49*), and upwards, as is the case of the tropical wet forest (wf-T) (48*). Fogden and Fogden (1997) observed the same trend of a diversity decrease from the same life zone towards higher elevations in the Caribbean lowland rain forest, but they also mention an increase of rare and local species between 500 and 1000 meters above sea level. The same can be said here regarding scarab beetles; we can cite the cases of *Ateuchus solisi*, *Oxysternon silenus smaragdinum*, and *Uroxys platypyga* that can only be found at mid elevations. Fogden and Fogden (1997) and Savage (2002) also mention that the Pacific rain forest has become geographically isolated from its Caribbean counterpart having many endemic species. This same phenomenon has also been observed with the dung beetles, where many of the locally generated species follow a Caribbean-Pacific vicariant pattern like the cases of *Onthophagus cryptodicranius* - *Onthophagus dicranus*, *Phanaeus beltianus* - *Phanaeus changdiazi*, *Phanaeus pyrois pyrois* - *Phanaeus pyrois malyi*, and *Sulcophanaeus noctis cupricollis* - *Sulcophanaeus noctis noctis*.

Species richness generally diminishes with an increase in elevation, as in the case with the premontane rain forest (rf-P) (49*, 45*) and premontane wet forest (wf-P) (47*) (no Scarabaeinae were recorded in an insect inventory of the paramo undertaken by Kappelle [2005]). Species richness also generally diminishes with an increase in dryness, as in the case with the premontane moist forest (mf-P Basal) (basal transition) (35*), tropical moist forest (mf-T Prem) (premontane transition) (34*), tropical dry forest (df-T) (33*), and tropical moist forest (mf-T d) (dry transition) (28*). The apparent contradiction that the premontane wet forest of the Talamanca Cordillera is not as species rich (47*) as the equivalent forest (89*) along the Guana-caste, Tilarán, and Central mountain ranges seems to derive from the previously mentioned fact that in the second case Caribbean species manage to penetrate into the premontane wet forest, whereas in the first case, with the Talamanca mountain range being so high and cold, that it effectively blocks the penetration of Caribbean species into the Pacific versant.

Distribution of total endemic species

The map depicting the total number (strictly endemic plus shared with Nicaragua and/or Panama) of Costa Rican endemic species of Scarabaeinae by life zones (Fig. 6) shows clear areas of high endemism (arbitrarily chosen as having nine species or more): premontane wet forest (wf-P) (25), premontane rain forest (rf-P) (18, 13, 12, 9), tropical wet forest (wf-T) (15, 14, 12), lower montane rain forest (rf-LM) (14), tropical wet forest (wf-T Prem) (premontane transition) (14, 10), lower montane wet forest (wf-LM) (12), premontane wet forest (wf-P rain) (rain transition) (11), and premontane wet forest (rf-P Basal) (basal transition) (9). Mid-elevations with wet and rain forests tend to have more endemics, followed by wet tropical lowlands, higher ele-

vations come in third place and interestingly the tropical drier areas of the Pacific are the most endemic-poor areas.

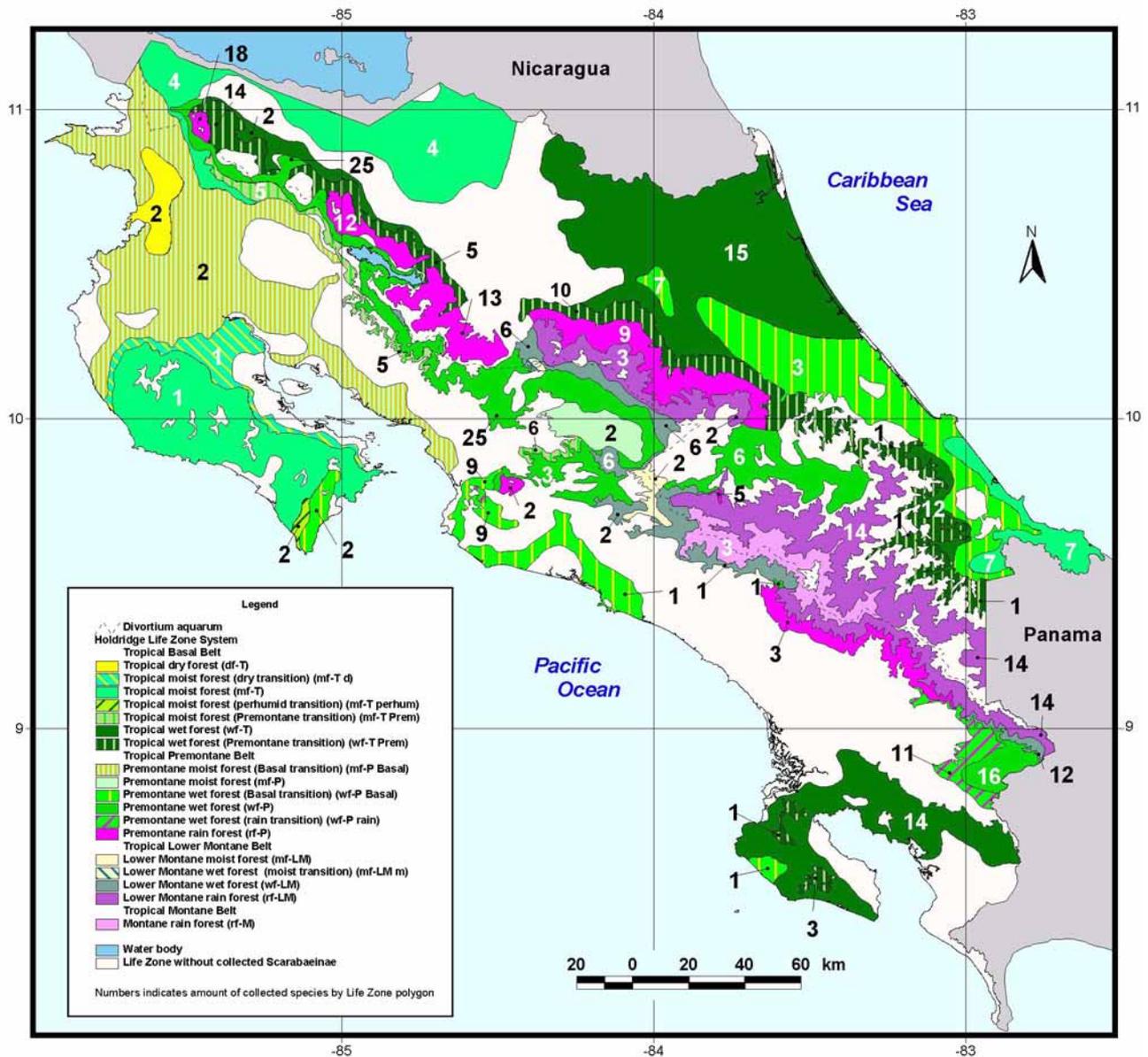


FIGURE 6. Map showing the total number of endemic (strictly endemic plus shared with Nicaragua and/or Panama) Scarabaeinae species in Costa Rica per life zone. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

Curiously, a very small and geologically young area like the Guanacaste mountain range (Pliocene-Pleistocene: Bergoing 1998, Valerio 1999, Alvarado 2000, Denyer and Kussmaul 2000) has a greater total number of endemics (18) than bigger and geologically older areas like the Talamanca mountain range (16, 14, 11) (Eocene-Pliocene: Coates 1997, Bergoing 1998, Denyer and Kussmaul 2000). This contradicts the theory of island biogeography (MacArthur and Wilson 1963, 1967) in its species-area relationship tenet and it also contradicts the modified species-area relationship put forward by Lomolino (2000a, b), where *in situ* speciation (island endemics) is assumed to occur in relatively large islands and not in smaller ones. It also contradicts the notion that older areas tend to have more endemics than younger ones (Müller 1981, Savage 2002).

Concluding, the majority of the endemics are associated with mountains and secondarily with humid low-

land tropical forests in the Golfo Dulce region and Northern Plains. To illustrate this point we can analyze the genus *Onthophagus* (reviewed by Kohlmann and Solís 2001a). The majority (9) of the endemic species of *Onthophagus* are found on the Talamanca mountain range. Five of them (*O. dorsipilulus*, *O. grataehelena*, *O. indediapterus*, *O. micropterus*, and *O. nubilus*) are exclusive in this mountain range. One species (*O. atrosericeus*) is shared with the Central mountain range, one (*O. propraecellens*) is shared with the Tilarán and Central mountain ranges, and finally two (*O. atriglabrus* and *O. orphnoides*) are shared with all mountain ranges.

The Central mountain range has only one endemic species (*O. singulariformis*); whereas the Tilarán and Guanacaste mountain ranges have a greater total of seven and six endemic species, respectively, where in addition to those already mentioned, four species are shared between these two mountain ranges (*O. andersoni*, *O. gazellinus*, *O. quetzalis*, and *O. solisi*). This analysis would seem to indicate that the poorest area in endemics is the Central mountain range, which seems to be under a heavy faunistic influence of the Talamanca mountain range. On the contrary, the Talamanca mountain range on one side, and the Guanacaste and Tilarán mountain ranges on the other, seem to represent important centers for the production of endemics. The last observation is important because it contradicts a previous study by Elizondo et al. (1989), based on vertebrates and plants, who found no reasons to support the hypothesis that the Tilarán and Guanacaste mountain ranges could represent areas for the production of endemics.

Eight more endemic species of *Onthophagus* can be found in the lowland tropical forests, six (*O. cryptod-icranius*, *O. genuinus*, *O. limonensis*, *O. nemorivagus*, *O. tapirus*, and *O. viridivinosus*) in the Caribbean versant, one (*O. coriaceoumbrosus*) in the Pacific versant, and one in both versants (*O. nyctopus*). The Caribbean lowlands have a relatively recent origin (Pliocene-Pleistocene, Bergoening 1998) yet are rich in endemics. Interestingly, no one has reported this fact before and the area is not considered to be of importance regarding endemics.

Distribution of Costa Rican endemic species

The majority of the Costa Rican endemic species (Fig. 7) are located along the Guanacaste, Tilarán, and Central mountain ranges in the premontane wet forest (wf-P) (9), tropical wet forest (wf-T Prem) (premontane transition) (9, 5), and premontane rain forest (rf-P) (9, 6, 4). Secondly, we can find Costa Rican endemics in the Pacific lowlands in tropical wet forest (wf-T) (8) and premontane wet forest (wf-P Basal) (basal transition) (3); and in the Caribbean versant in tropical wet forest (wf-T) (5, 4) and premontane wet forest (wf-P) (4). No Costa Rican endemic species have been recorded so far in the tropical dry forests of the Pacific. Interestingly, very few Costa Rican endemic species have been recorded in the Talamanca mountain range, where most of the endemic species are shared with Panama along the Talamanca-Chiriquí mountain range, which spans the border between both countries. This contradicts the findings by Savage (2002), where he reports that the number of Costa Rican endemic species of herpetofauna is highest in the Talamanca mountain range.

It is interesting to note that a number of these Costa Rican endemic species are exclusively concentrated along the Guanacaste mountain range. We can cite from this area: *Ateuchus fetteri*, *A. hendrichsi*, and *Canthidium priscillae*. Actually, *A. hendrichsi* is only known from Cacao volcano. DeVries (1987) had also defined this mountain range as a species pocket area, *i.e.* a place with rare or unusual species (not necessarily an area of endemism) and characterized by being small in area and having unusual climatic patterns.

Another area highly speciose in strict endemics is the Golfo Dulce region with its tropical wet forest (wf-T) (8). This area had already being identified as such by several authors (Elizondo et al. 1989; DeVries 1987, 1997; Fogden and Fogden 1997; Savage 2002; Obando 2002). This tropical wet forest was isolated from its Caribbean counterpart by the uplift of the Talamanca mountain range through the subduction of the Cocos Ridge beneath the Costa Rica – Panama Microplate (Coates 1997). This process seems to have started about three million years ago (Collins et al. 1995, Kolarsky et al. 1995, Meschede et al. 1999).

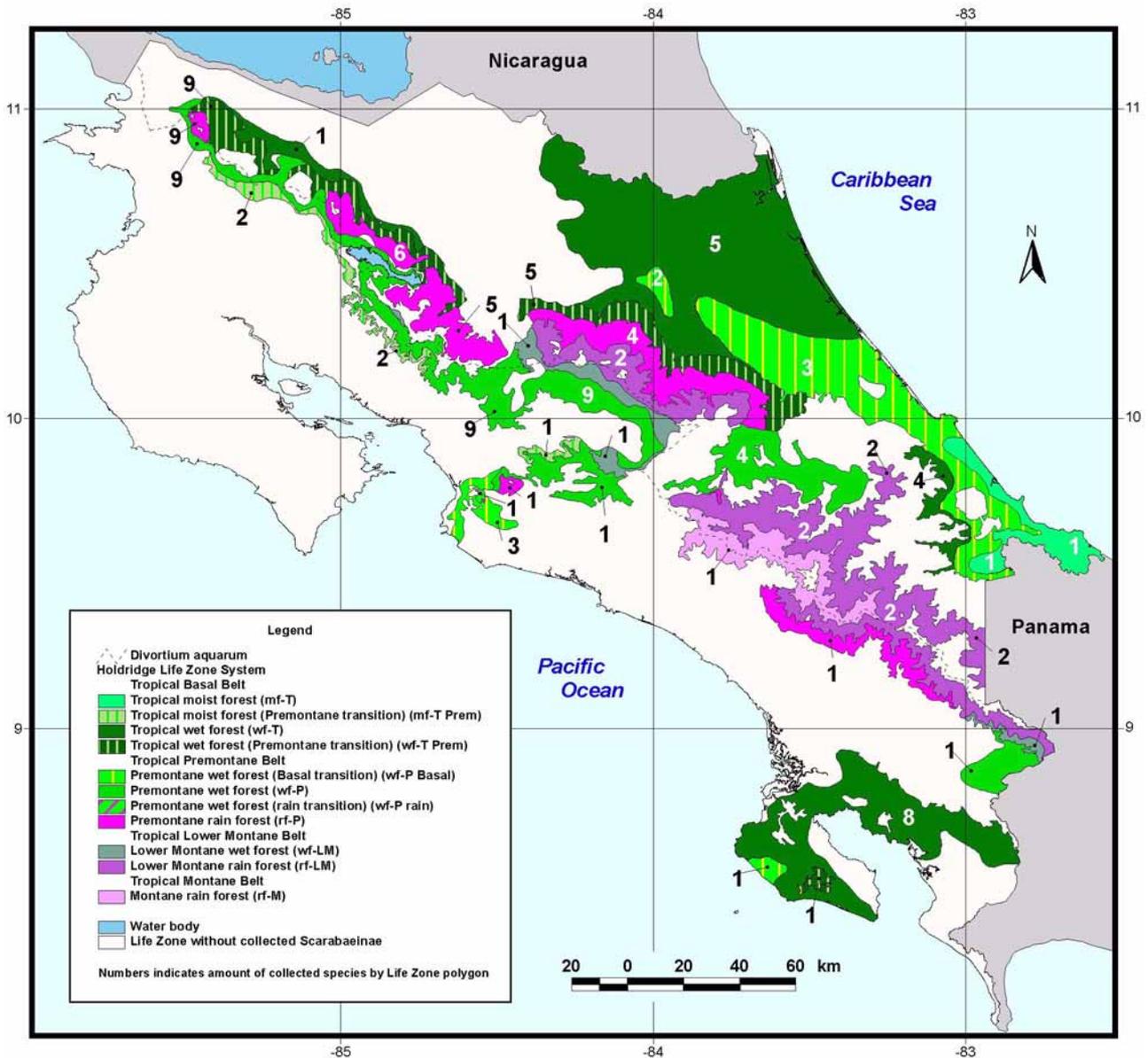


FIGURE 7. Map showing the collected number of strictly endemic Costa Rican Scarabaeinae species per life zone. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

Distribution of shared endemic species

The sharing of exclusive endemics with Nicaragua is not strong (Fig. 8), the highest number being reported for the premontane wet forest (wf-P) (4) and tropical moist forest (mf-T) (3). Secondly, shared endemics occur in the tropical wet forest (wf-T) (2), tropical dry forest (df-T) (2), and premontane moist forest (mf-P Basal) (basal transition) (2). It would appear that mid-elevation endemics from the Pacific mountain versant are the most important group of endemics exclusively shared with Nicaragua.

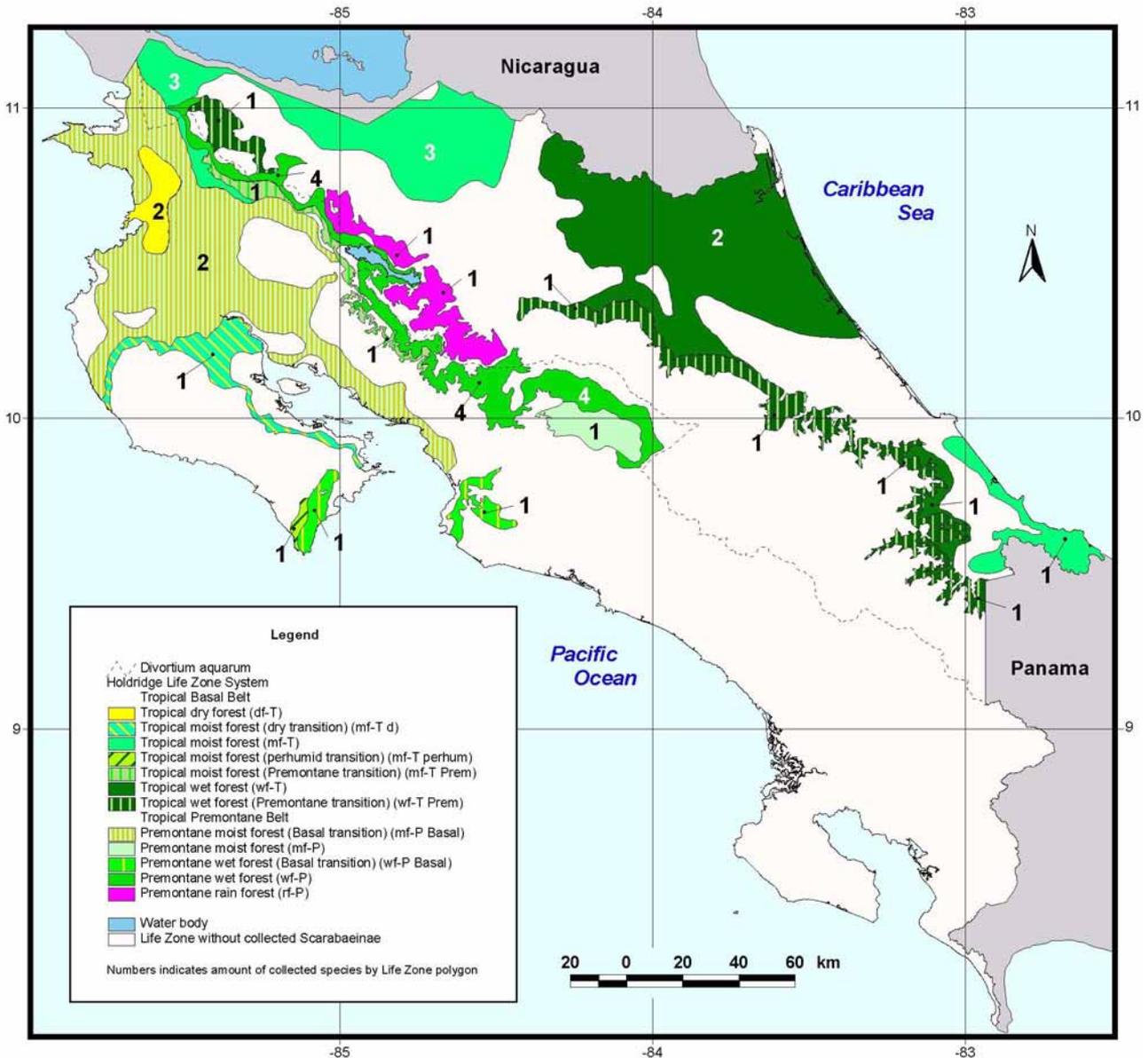


FIGURE 8. Map showing the collected number of endemic Scarabaeinae species per life zone in Costa Rica shared with Nicaragua. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

The most important group of exclusively shared endemics is the group shared with Panama (Fig. 9), especially mountain endemics along the whole length of the Guanacaste – Tamanca mountain axis, located in premontane wet forest (wf-P) (14, 10), premontane rain forest (rf-P Basal) (basal transition) (11), lower montane rain forest (rf-LM) (11, 6), premontane rain forest (rf-P) (7, 5), and premontane wet forest (wf-P Basal) (basal transition) (5). Secondly we have the lowland Pacific area with the tropical wet forest (wf-T) (6) and in a remote third place, the same type of forest on the Caribbean lowlands. Again, the relevance of the mountain ranges in the endemism process is evident.

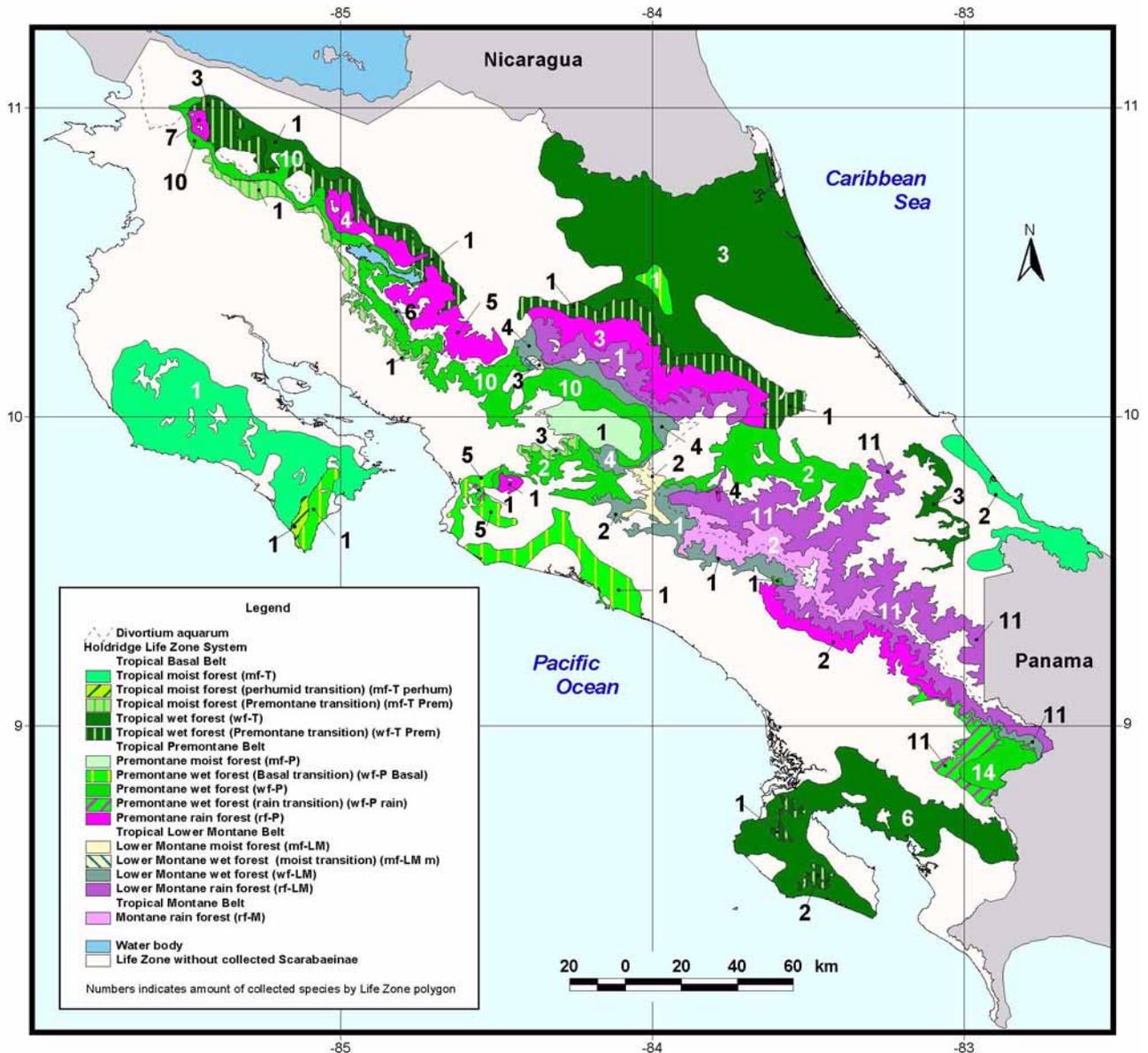


FIGURE 9. Map showing the collected number of endemic Scarabaeinae species per life zone in Costa Rica shared with Panama. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

Regarding the sharing of endemics with both countries (Fig. 10), this is a process clearly dominated by the Caribbean lowlands, where the tropical wet forest (5), the premontane wet forest (4), and the tropical moist forest (3) are this time clearly more important than the mountain endemics. This endemism pattern seems to follow a similar one described by Savage (2002) for the Costa Rican herpetofauna, going from the Bocas del Toro region in Panama, to the northwestern corner of Honduras.

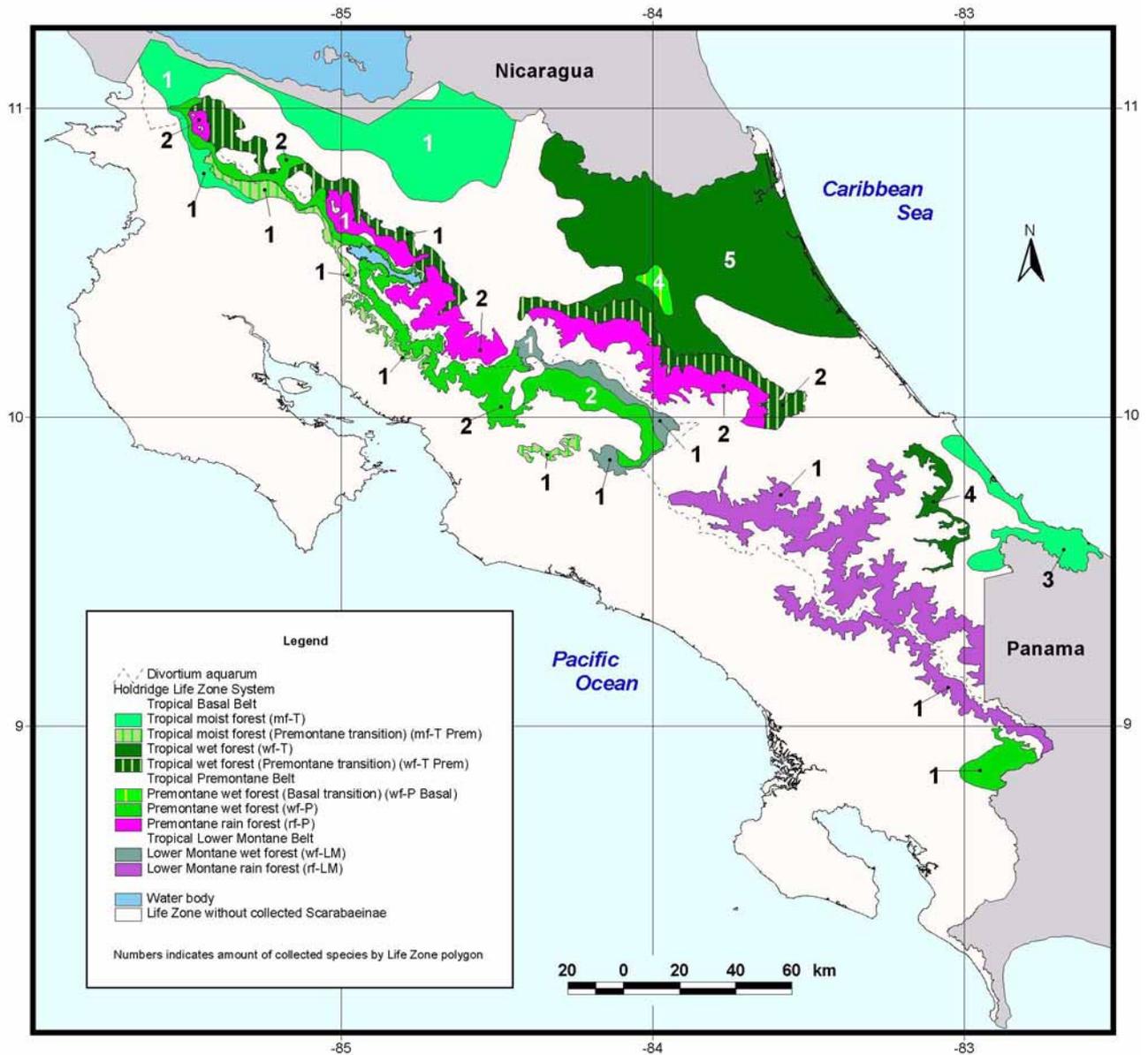


FIGURE 10. Map showing the collected number of endemic Scarabaeinae species per life zone in Costa Rica shared with Nicaragua and Panama. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

Priority zones for conservation

A species richness map is presented in Fig. 11, which demonstrates that many of the protected areas do not coincide with areas of high Scarabaeinae species richness. On the other hand, the two more numerous species richness categories have areas that are under protection, with the notable exception of the Central mountain range and many parts of the Tilarán mountain range.

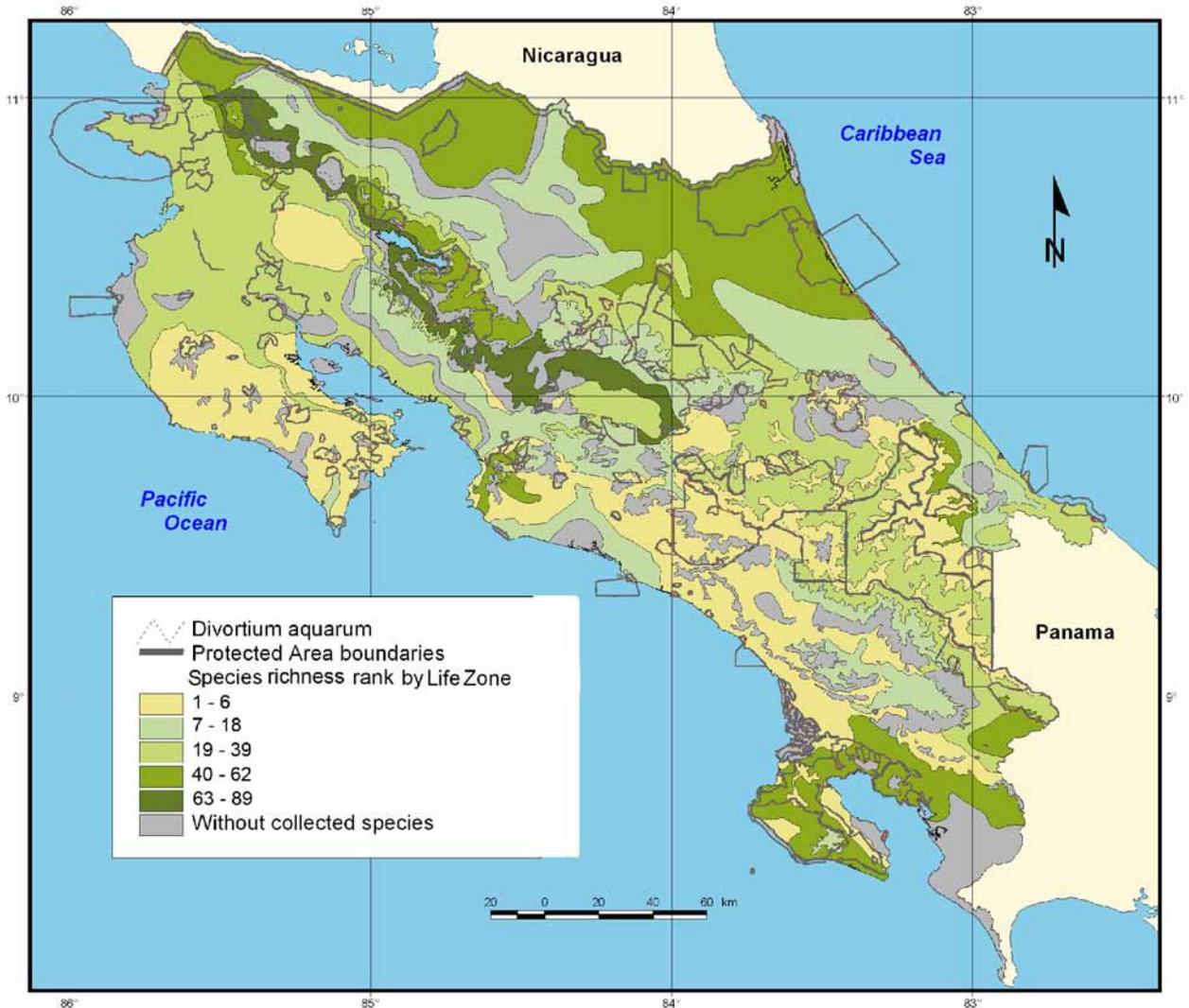


FIGURE 11. Map showing five different species richness rank levels for Scarabaeinae in Costa Rica and their overlap with the established protected areas. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

A map showing Scarabaeinae endemism by rank (Fig. 12) shows a somewhat similar result to the species richness map. However, endemism in the lower montane forest of Talamanca is one category up relative to the species richness map (Fig. 11). Finally, the gap analysis adds information from the two previous maps into one conservation priority-defining map (Fig. 13). Priority zone 1 indicates the areas where the highest species richness (rank 5) and the highest endemics number (rank 5) coincide. It is a very long area that stretches all the way from the Guanacaste to the Central Cordillera along the Pacific versant at mid-altitudes. Priority zone 2 depicts an area of only the highest species richness (rank 5), and is circumscribed to the mid-altitude Caribbean versant of the Guanacaste Cordillera. Priority zone 3 represents areas where the second highest rank (rank 4) of species richness and endemics number coincide, the areas in question being located along both versants and ranging from low to mid-altitudes. Finally, priority zone 4 represents an area of only the second highest rank (rank 4) of endemics numbers, and is located on both versants of the Talamanca Cordillera at mid-elevations.

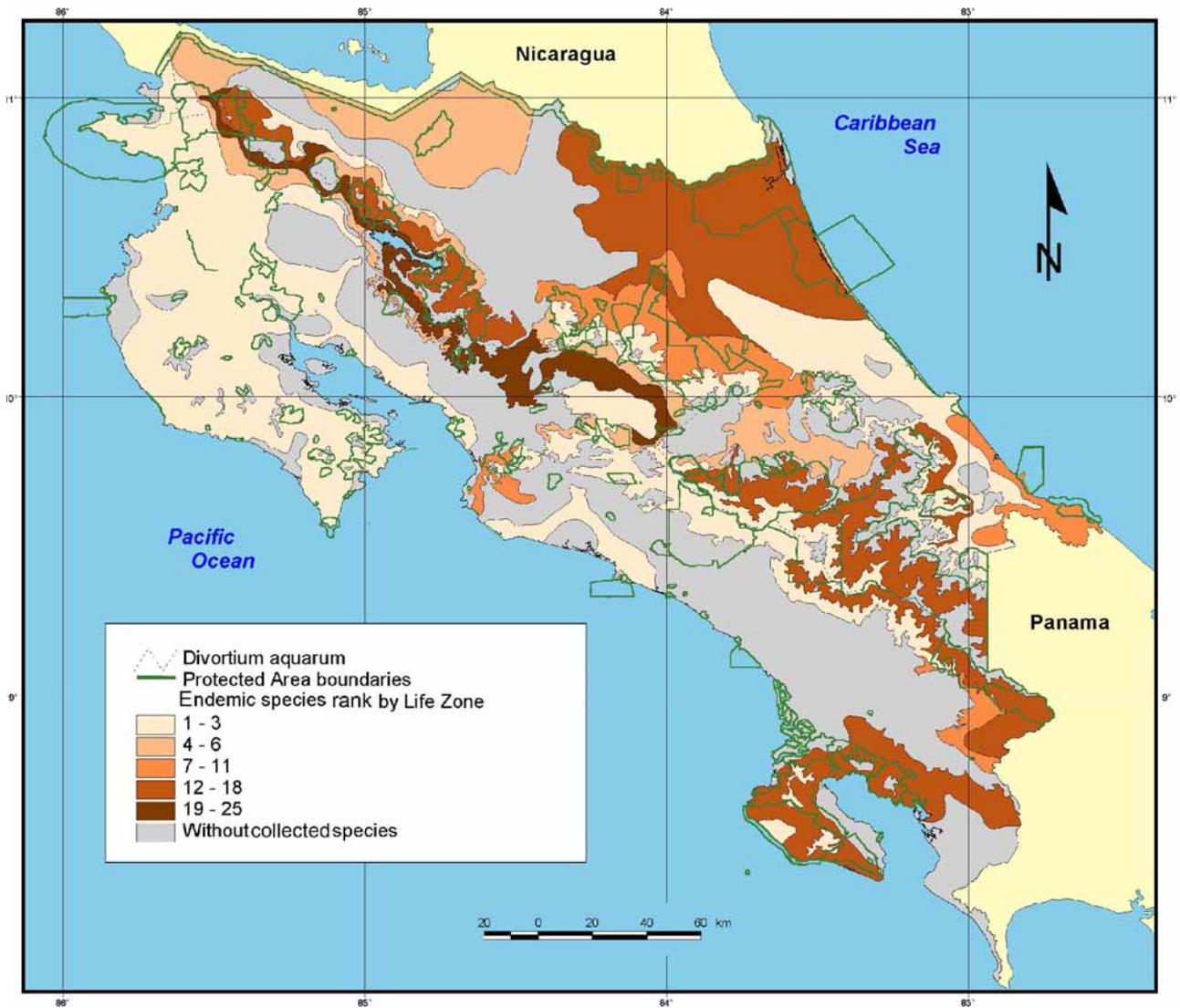


FIGURE 12. Map showing five different rank levels of Scarabaeinae endemism in Costa Rica and their overlap with the established protected areas. Areas in white represent zones where Scarabaeinae have not yet been recorded. Divortium aquarum = watershed divide.

Table 2 indicates the total areas of all four priority zones and the areas and percentages of each of them that are under some sort of protection category. Priority zone 1 has a total of 1539 km² and is the least protected category with only 12.83% of its area under protection. Priority zone 2 is represented by a total of 259 km², the smallest zone, but has 25.25% of its area under protection. Priority zone 3 has 7,426 km², the largest zone, with 39.05% of its area under protection. Finally, priority zone 4 has 2,360 km², and has the largest percentage under protection, with 81.16%.

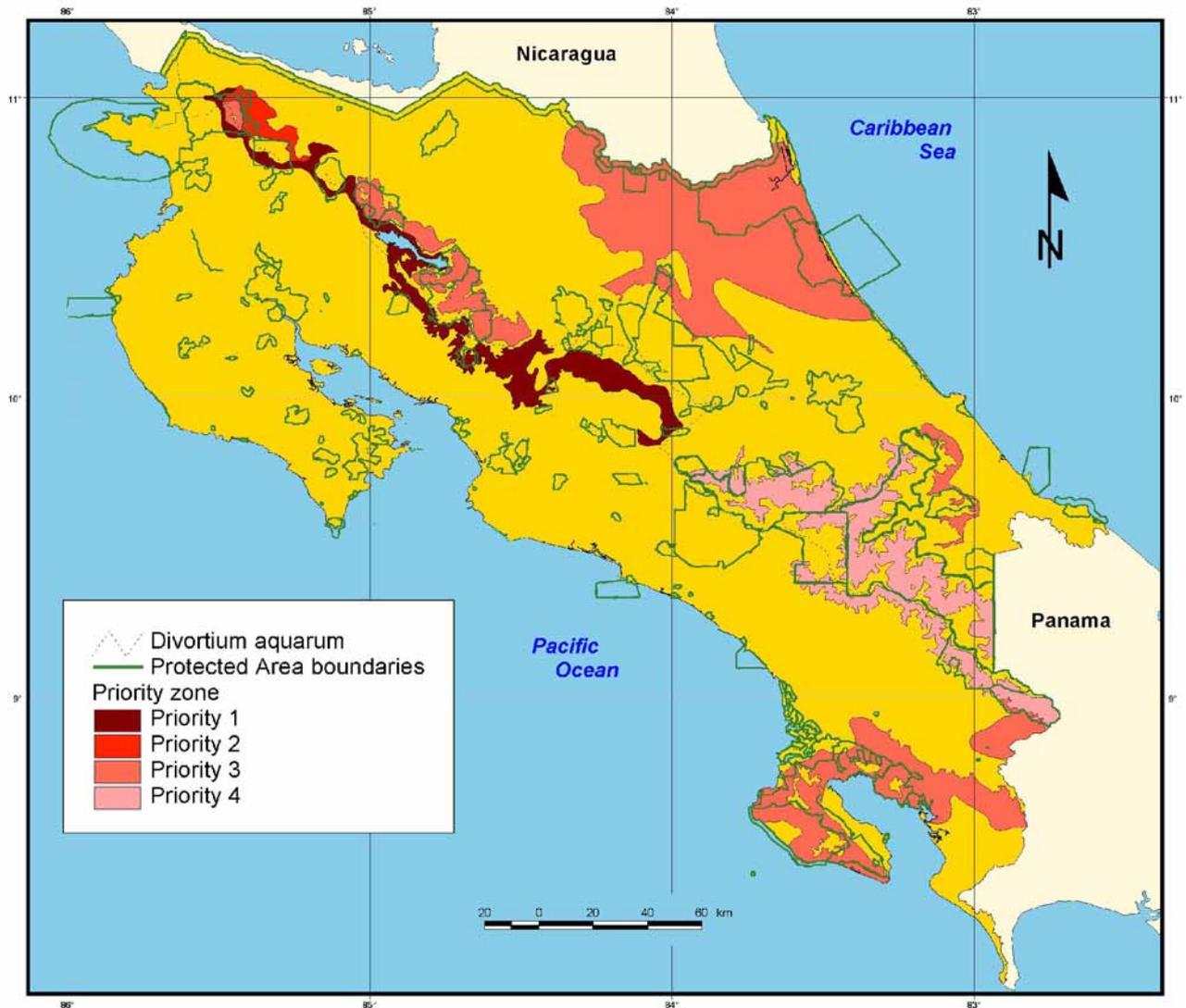


FIGURE 13. Map showing conservation priority zones in Costa Rica based on the analysis of the Scarabaeinae and their overlap with the established protected areas (see text of GIS Analysis in Materials and Methods for priority zone explanations). Divortium aquarum = watershed divide.

TABLE 2. Total area of priority zones and their areas and percentages* under protection according to management categories.

Areas of priority zones	Priority 1 1,593 km ² % (*)		Priority 2 259 km ² % (*)		Priority 3 7,426 km ² % (*)		Priority 4 2,360 km ² % (*)		TOTAL 11638 km ²	TOTAL % (*)
Area of protection categories in km ²										
State Farms	3.88	0.24	40.97	15.82	0.00	0.00	0.00	0.00	44.85	0.39
Wetlands	0.00	0.00	0.00	0.00	57.01	0.77	0.00	0.00	57.01	0.49
National Park	103.07	6.47	24.41	9.43	931.55	12.54	1,296.95	54.95	2,355.98	20.24
National Refuge	18.18	1.14	0.00	0.00	990.91	13.34	5.74	0.24	1,014.82	8.72
Biological Reserve	0.00	0.00	0.00	0.00	83.51	1.12	0.00	0.00	83.51	0.72
Forest Reserve	0.88	0.06	0.00	0.00	544.40	7.33	418.72	17.74	964.00	8.28
Protection Zone	78.37	4.92	0.00	0.00	292.33	3.94	194.23	8.23	564.00	4.85
Total area (in km ²) and percentage* under protection by priority category	204.38	12.83	65.38	25.25	2,899.71	39.05	1,915.64	81.16	5,085.12	43.69

(*) Percentages are calculated in relation to the total area of each priority category.

Ideally, more effort should be devoted to increase the area under protection for priority zone 1, although this might prove difficult. This region is now only 35% forested, due to urban and agricultural land usage (Fig. 14, Table 3). This area can be truly considered as a biodiversity hotspot for Costa Rica. Priority zone 2 is also heavily used for pastureland (approximately 34% of its area), although it could still accommodate new protected areas or an enlargement of already existing protected areas, because a considerable percentage is still forested (66% of the total area) (Fig. 14, Table 3). Priority zone 3 is under variable conditions (Fig. 14, Table 3). Neither the Tilarán nor the Southern Caribbean areas have been greatly altered by human activity; whereas the Golfo Dulce, Talamanca, and Northern Caribbean areas have. As a whole, the region still has the capacity for increasing the percentage of its area under protection, since approximately 66% of the total area is still forested land. Priority zone 4 is already under considerable protection, being located in relatively inaccessible mountain areas with low population densities and with only a tangential impact by agricultural activities, and showing the greatest percentage (96%) of forested lands (Fig. 14, Table 3).

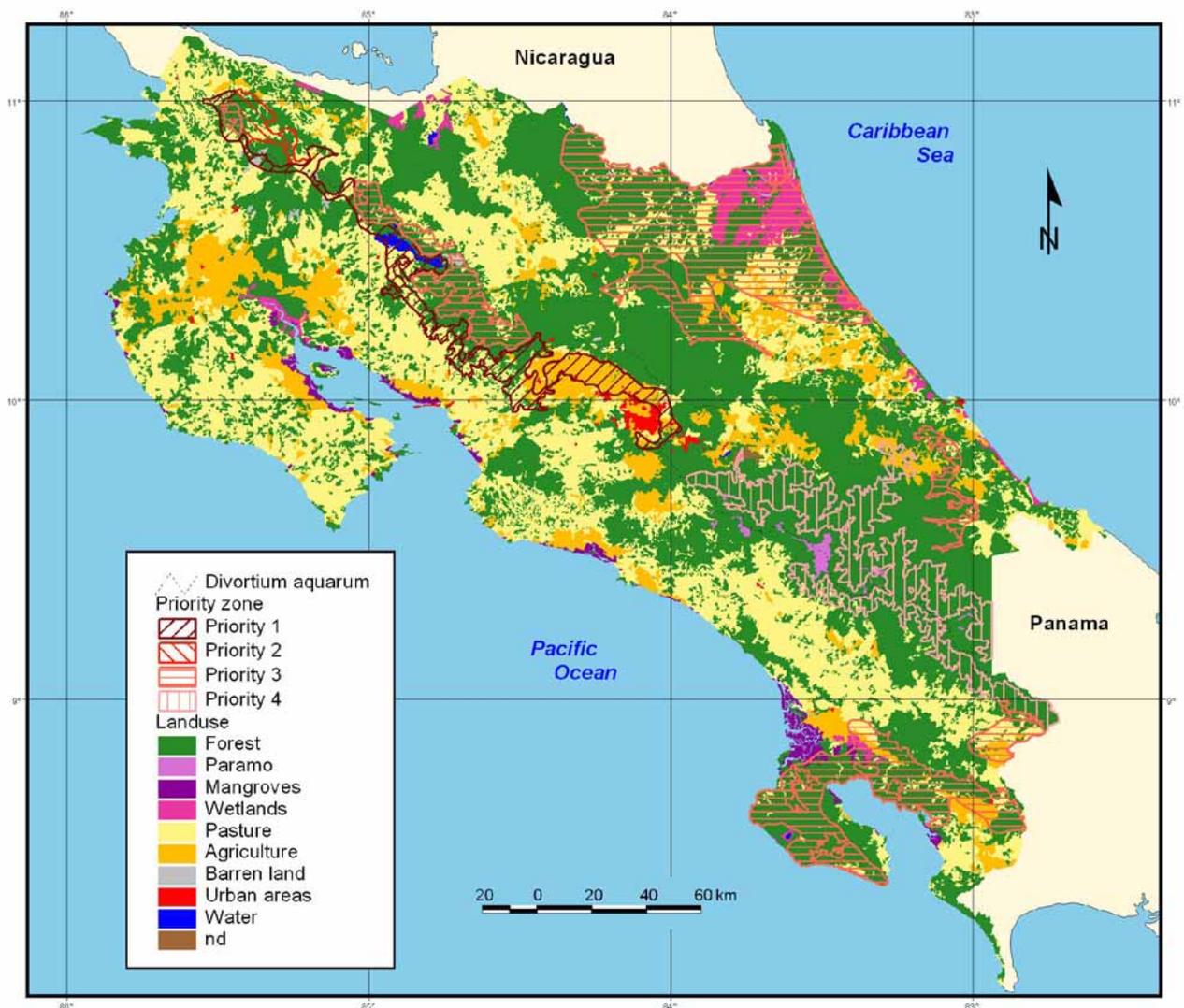


FIGURE 14. Map of land use (1992) with priority zone areas superimposed. See Fig. 13 for a detailed definition of each priority zone category. As can be deduced from this map, priority zone 1 represents a veritable hotspot for Costa Rica, because this zone is under heavy agricultural/pasture/urban threat. Divortium aquarum = watershed divide. Base map taken from Kohlmann et al. 2002).

TABLE 3. Total area of priority zones and their areas and percentages* under different land use conditions.

Areas of priority zones	Priority 1 1,593 km ² %(*)		Priority 2 259 km ² % (*)		Priority 3 7,426 km ² %(*)		Priority 4 2,360 km %(*)		TOTAL 11,638 km ²	TOTAL %(*)
Area of land use categories (1992) in km ²										
Forest	559	35.09	171	66.02	4,896	65.93	2,268	96.10	7,893	67.82
Paramo	0	0.00	0	0.00	0	0.00	8	0.34	8	0.07
Mangroves	0	0.00	0	0.00	35	0.47	0	0.00	35	0.30
Wetlands	0	0.00	0	0.00	731	9.84	0	0.00	731	6.28
Pasture	490	30.76	88	33.98	1,290	17.37	29	1.23	1,897	16.30
Agriculture	437	27.44	0	0.00	408	5.49	51	2.16	895	7.69
Barren land	15	0.94	0	0.00	15	0.20	0	0.00	31	0.27
Urban areas	23	1.44	0	0.00	4	0.05	0	0.00	27	0.23
Water	69	4.33	0	0.00	48	0.65	0	0.00	117	1.00
na**	0	0.00	0	0.00	0	0.00	4	0.17	4	0.04

(*) Percentages are calculated in relation to the total area of each priority category.

(**) Not available

Conclusions

In the past, the majority of the species richness and endemism studies of Costa Rica have relied principally on vertebrate distribution analyses and more recently on plants (Obando, 2002). Insects have not been prominent in these studies. This paper demonstrates that a different and perhaps a much more detailed picture can be gained by using invertebrates instead.

Costa Rica is perhaps the best-collected country in Central America. Not only through the work of many foreign scientists, but lately through the impressive work done by the National Institute of Biodiversity (INBio). Still, some areas have been undercollected, but the available information allows us to elucidate general patterns.

We observed that species richness is highest in the lower altitudes (Table 1). However, if we calculate a mean species density, it is then the medium altitudes that have the highest values (Table 1), with the dry Pacific region the area with the highest mean number. Following the same train of thought, the Caribbean versant has the highest total number of species (Table 1); however, the Pacific versant has the highest biodiversity per square unit.

In relation to life zones, this dung beetle analysis indicates that the premontane wet forest (approximately 750-1500 m) along the Pacific versant of the Guanacaste, Tilarán, and Central mountain range systems is the most species-rich area for this group in Costa Rica, thus supporting the previous altitude level analysis. This same area was also found to be very species rich for butterflies by DeVries (1987, 1997). The most likely explanation for this fact is that this area represents a transition-zone for species of both slopes. Vertebrate analyses by Fogden and Fogden (1997) and Savage (2002) also consider foothills of the Caribbean versant to be the most species-rich area for birds and herpetofauna, and hypothesize that here is a greater variety of habitats in these regions. The present analysis also shows that although scarab diversity is highest at mid-elevations it diminishes with an increase in mountain altitude and dryness in the North Pacific area.

Mid-elevations with moist and wet premontane and lower montane forests tend to have the greatest total number of endemics, followed by wet tropical lowlands. Higher elevations come in third place and the tropical drier areas of the Pacific are the most endemic-poor areas. Interestingly, a smaller and younger area like the Guanacaste mountain range has a greater number of endemics than a bigger and older area, like the Talamanca mountain range, thus apparently contradicting the tenets of island biogeography. The majority of the endemics are associated with mountains and in second place with humid lowland tropical forests in the Golfo

Dulce region and Northern Plains. The high endemism of the Northern Plains had not been reported for any organism before, an interesting fact because it is geologically very young (Pliocene-Pleistocene) (Bergoing 1998, Denyer and Kussmaul 2000).

The majority of the strictly endemic Costa Rican species are located along the Guanacaste, Tilarán, and Central mountain ranges, and in the rainforests of the Pacific, especially the Golfo Dulce region (Fig. 15) and Caribbean lowlands. Very few strictly endemic species are to be found in the Talamanca mountain range, thus contradicting Savage (2002), who reports the highest number of this class of endemics for the herpetofauna. Lastly, the most important group of shared endemics is the group shared with Panama, especially mountain endemics along the whole length of the Guanacaste-Talamanca mountain axis. The lowland Pacific area with the tropical wet forest and this same type of forest on the Caribbean lowlands represent areas of secondary importance in the sharing of species.



FIGURE 15. Map showing the different areas of Scarabaeinae endemism in Costa Rica: CC, Central Cordillera; CH, Herradura mountain; CT, Turrubares mountain; GD, Golfo Dulce region; G, Guanacaste mountain range; NP, northern plains; Ti, Tilarán mountain range; T, Talamanca mountain range. Base map taken from NASA.

The gap analysis of conservation priority areas shows that many protected areas do not coincide with regions of Scarabaeinae high species richness or endemism. It also shows that the zone with highest conservation priorities (priorities 1 and 2), the band stretching from the Guanacaste mountain range to the Tilarán mountain range to the Central mountain range (Fig. 13), is not greatly protected by conservation areas, especially along the Central mountain range and secondly at the Tilarán mountain range. The Central mountain range and Tilarán mountain range should be preferentially targeted by government planners and conservation agencies for new conservation areas.

Finally, Fig. 15 indicates the different regions in continental Costa Rica where high levels of Scarabaeinae endemism have been recorded. This study did not analyze the situation of Coco Island, because Scarabaeinae have not been recorded from there, but this island certainly represents an important center for endemics (Obando, 2002). This study corroborates other studies that have identified areas in Costa Rica as important centers for endemism based on vertebrate and plant information (Elizondo et al. 1989, Obando 2002, Savage 2002), like the Talamanca (Fig. 15, T) and Central (Fig. 15, CC) mountain ranges, the Golfo Dulce (Fig. 15, GD) region, and the Central Pacific, especially the Turrubares mountain (Fig. 15, CT) and the Herradura mountain range (Fig. 15, CH). However, new areas are proposed here, like the Guanacaste (Fig. 15, G) and Tilarán mountain ranges (Fig. 15, Ti), as well as the Caribbean Northern Plains (Fig. 14, NP).

Regarding the percentage of endemics, 37% of the known Scarabaeinae species in Costa Rica are regional endemics (Nicaragua-Costa Rica-Panama) (Table 4); whereas 18% are exclusively Costa Rican (Table 4). These figures are fairly similar to the levels of regional endemism (28%) and the strict endemism (12%) of the herpetofauna of Costa Rica (Savage 2002), which was considered to be the group with the highest endemism for the country (Obando 2002). These results seem to suggest that the use of insects in particular, and probably invertebrates in general, can give a much more detailed picture regarding areas of endemism than can be obtained using vertebrates or plants. We are proponents of using insects to study patterns of endemism more often than they have been in the past.

TABLE 4. Percentage of regional endemism for Costa Rican Scarabaeinae.

	Number	%
Total species	175	100
Non-endemic species	109	63
Endemic species	66	37
Exclusively Costa Rican	32	18
Shared with Panama	23	13
Shared with Nicaragua	5	3
Shared with Nicaragua and Panama	6	3

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APPENDIX 1. Species of Scarabaeinae by life zone area, life zones, and type of endemism in Costa Rica.

Species	Number of Life Zone Area	Life Zone	Endemism
<i>Agamopus lampros</i>	2, 3, 18, 29, 68, 160, 183	df-T, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-P Basal	Not endemic
<i>Anomiopus panamensis</i>	2, 10, 17, 183, 281, 309	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ateuchus aeneomicans</i>	183, 203, 281, 309, 372	wf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Ateuchus candezei</i>	10, 11, 13, 42, 51, 161, 167	mf-T, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ateuchus fetteri</i>	11, 13	rf-P, wf-P	Endemic to Costa Rica
<i>Ateuchus ginae</i>	160	mf-T Prem	Endemic shared with Nicaragua and Panama
<i>Ateuchus hendrichsi</i>	13	rf-P	Endemic to Costa Rica
<i>Ateuchus howdeni</i>	183, 309	wf-P Basal, wf-T	Not endemic
<i>Ateuchus rodriguezii</i>	2, 3, 10, 11, 13, 18, 20, 47, 68, 127, 160, 183, 211, 309	df-T, mf-P, mf-P Basal, mf-T, mf-T d, mf-T perhum, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ateuchus solisi</i>	10, 167	wf-T, wf-T Prem	Endemic to Costa Rica
<i>Ateuchus zoebischi</i>	10, 13, 25, 52, 167	rf-P, wf-T, wf-T Prem	Endemic to Costa Rica
<i>Bdelyrus seminudus</i>	10, 29, 43, 167, 177, 309	rf-LM, rf-P, wf-T, wf-T Prem	Not endemic
<i>Canthidium angusticeps</i>	2, 10, 13, 17, 29, 42, 167, 183, 203, 309, 386	mf-T, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthidium annagabrielae</i>	2, 10, 11, 13, 17, 37, 42, 43, 52, 60, 161, 167	mf-T, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Canthidium ardens</i>	2, 3, 5, 10, 11, 13, 17, 29, 37, 42, 43, 59, 60, 127, 161, 167, 177, 183, 203, 219, 263, 281, 309, 386, 381	mf-P, mf-P Basal, mf-T, rf-LM, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthidium aurifex</i>	11, 13, 60, 183, 211, 219, 309, 376	mf-T perhum, rf-P, wf-P, wf-P Basal, wf-T	Not endemic
<i>Canthidium centrale</i>	9, 10, 11, 17, 25, 29, 37, 42, 43, 52, 161, 167, 183, 203, 219, 281, 309, 372	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthidium discopygidiale</i>	11, 13, 43, 59, 60	rf-P, wf-LM, wf-P	Endemic shared with Panama
<i>Canthidium emoryi</i>	177, 204	rf-LM, rf-P	Endemic to Costa Rica
<i>Canthidium guanacaste</i>	2, 3, 11, 18, 68, 183, 186, 211	df-T, mf-P Basal, mf-T, mf-T d, mf-T perhum, wf-P, wf-P Basal	Endemic shared with Nicaragua
<i>Canthidium haroldi</i>	10, 11, 13, 17, 20, 29, 42, 43, 52, 60, 161, 167, 309, 386	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic

<i>Canthidium hespenheidei</i>	2, 5, 10, 11, 17, 29, 37, 42, 43, 52, 136, 161, 167, 183, 203, 309	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthidium laetum</i>	2, 3, 11, 18, 68, 127	df-T, mf-P, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
<i>Canthidium leucopterum</i>	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Canthidium macroculare</i>	281, 309	wf-P, wf-T	Not endemic
<i>Canthidium marianelae</i>	10, 11, 13, 29, 59, 70	rf-LM, rf-P, wf-LM, wf-P, wf-T Prem	Endemic to Costa Rica
<i>Canthidium marielae</i>	309	wf-T	Endemic to Costa Rica
<i>Canthidium pallidoalatum</i>	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Canthidium perceptibile</i>	11, 13, 29, 59, 263, 281	rf-P, wf-LM, wf-P, wf-P rain	Not endemic
<i>Canthidium planovultum</i>	73, 177, 209, 216, 269	rf-LM, rf-M, wf-LM	Endemic shared with Panama
<i>Canthidium priscillae</i>	29	rf-P	Endemic to Costa Rica
<i>Canthidium pseudopuncticolle</i>	2, 11	mf-T, wf-P	Not endemic
<i>Canthidium tenebrosus</i>	73, 177, 204, 209	rf-LM, rf-P, wf-LM	Endemic shared with Panama
<i>Canthidium tuberifrons</i>	10, 11, 13, 17, 29, 43, 160, 177, 240, 263, 269, 281	mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Canthidium variolosus</i>	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Canthidium vespertinum</i>	11, 13, 17, 29, 42, 43, 59, 167, 177, 204, 240, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Canthon aberrans</i>	11, 43, 59, 70, 177, 204	rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Canthon aequinoctialis</i>	2, 9, 10, 11, 17, 20, 25, 37, 42, 51, 52, 160, 161, 167, 183, 192, 203, 309, 386	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthon angustatus</i>	2, 10, 11, 17, 20, 25, 37, 52, 161, 167, 309	mf-T, mf-T Prem, wf-P, wf-T, wf-T Prem	Not endemic
<i>Canthon caelius</i>	80, 183, 186, 192, 211, 219, 309, 374, 386	mf-T, mf-T perhum, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
<i>Canthon cyanellus</i>	2, 3, 5, 10, 11, 17, 18, 20, 37, 42, 43, 68, 73, 161, 167, 179, 183, 186, 203, 211	df-T, mf-LM, mf-P Basal, mf-T, mf-T d, mf-T perhum, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthon deyrollei</i>	2, 3, 11, 18, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
<i>Canthon euryscelis</i>	2, 3, 10, 11, 18, 20, 68	df-T, mf-P Basal, mf-T, mf-T d, mf-T Prem, wf-P, wf-T Prem	Not endemic
<i>Canthon hartmanni</i>	11, 13, 177, 263, 281	rf-LM, rf-P, wf-P, wf-P rain	Endemic shared with Panama
<i>Canthon humboldti</i>	183, 192, 203, 309, 381	rf-P, wf-P Basal, wf-P rain, wf-T	Endemic to Costa Rica

<i>Canthon indigaceus chevrolati</i>	3, 11, 18, 20, 47, 68, 176, 179, 159, 190	df-T, mf-LM, mf-P Basal, mf-T, mf-T d, mf-T perhum, mf-T Prem, wf-P	Not endemic
<i>Canthon inusitatus</i>	70	rf-LM	Endemic to Costa Rica
<i>Canthon juvenicus</i>	253, 258, 309	mf-T, wf-P Basal, wf-T	Not endemic
<i>Canthon lituratus</i>	258	mf-T	Not endemic
<i>Canthon meridionalis</i>	2, 3, 10, 11, 17, 18, 60, 68, 80, 161, 183, 211, 258	df-T, mf-P Basal, mf-T, mf-T d, mf-T perhum, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Canthon moniliatus</i>	2, 10, 17, 37, 42, 52, 161, 167, 183, 192, 203, 219, 258, 281, 309, 317, 386	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Canthon morsei</i>	2, 3, 18, 183, 211	df-T, mf-P Basal, mf-T, mf-T perhum, wf-P Basal	Not endemic
<i>Canthon mutabilis</i>	10, 68, 179, 258, 309, 317, 376	mf-LM, mf-T, mf-T d, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Canthon septemmaculatum</i>	228, 258	mf-T, wf-P	Not endemic
<i>Canthon silvaticus</i>	17, 37, 42, 51, 161, 167	mf-T, wf-P Basal, wf-T	Endemic to Costa Rica
<i>Canthon subhyalinus subhyalinus</i>	2, 10, 11, 13, 20, 29, 43, 183, 309	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Canthon vazquezae</i>	3, 11, 13, 29, 43, 59, 127, 149, 165, 204, 240	mf-P, mf-P Basal, rf-P, wf-LM, wf-P	Not endemic
<i>Copris costaricensis costaricensis</i>	11, 13, 20, 29, 43, 59, 179, 204, 269, 281	mf-LM, mf-T Prem, rf-P, wf-LM, wf-P	Endemic shared with Panama
<i>Copris incertus</i>	10, 17, 25, 42, 43, 51, 52, 60, 167, 183, 210, 309	rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Copris laeviceps</i>	17, 167	wf-T	Not endemic
<i>Copris lugubris</i>	2, 3, 5, 9, 10, 11, 13, 17, 18, 20, 25, 29, 37, 42, 43, 51, 52, 59, 68, 80, 127, 160, 179, 183, 194, 203, 211, 219, 263, 281, 33, 119	df-T, mf-LM, mf-P, mf-P Basal, mf-T, mf-T d, mf-T perhum, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Copris subpunctatus</i>	70, 73, 89, 127, 179, 216,	mf-LM, mf-LM m, mf-P, rf-LM, rf-M, wf-LM	Endemic shared with Panama
<i>Copris tridentatus</i>	160	mf-T Prem	Endemic to Costa Rica
<i>Coprophanaeus boucardi</i>	2, 3, 11, 18, 29, 127	df-T, mf-P, mf-P Basal, mf-T, rf-P, wf-P	Endemic shared with Nicaragua
<i>Coprophanaeus chiriquensis</i>	177, 204, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic
<i>Coprophanaeus gilli</i>	10, 11, 13, 17, 20, 29, 43, 52, 59, 60	mf-T Prem, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Coprophanaeus kohlmanni</i>	10, 11, 13, 17, 20, 25, 29, 42, 43, 52, 60	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Coprophanaeus pecki</i>	11, 60, 161, 167, 183, 203, 263, 269, 281, 309, 386	mf-T, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama

<i>Coprophanæus solisi</i>	183, 309	wf-P Basal, wf-T	Endemic to Costa Rica
<i>Coprophanæus telamon corythus</i>	2, 3, 10, 11, 17, 18, 20, 29, 37, 42, 52, 68, 80, 149, 161, 167, 183, 203, 258, 263, 309, 190	df-T, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Cryptocanthon lindemanae</i>	309	wf-T	Endemic to Costa Rica
<i>Cryptocanthon osaensis</i>	309	wf-T	Endemic to Costa Rica
<i>Cryptocanthon solisi</i>	60	rf-P	Endemic to Costa Rica
<i>Deltochilum gibbosum panamensis</i>	9, 10, 17, 25, 42, 52, 165, 167, 183, 203, 309, 386	rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Deltochilum lobipes</i>	2, 3, 11, 18, 52, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P, wf-T Prem	Not endemic
<i>Deltochilum mexicanum</i>	10, 11, 13, 29, 43, 52, 59, 60, 70, 73, 165, 177, 179, 200, 204, 216, 240, 242, 263, 269, 281, 15	mf-LM, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Deltochilum parile</i>	2, 11, 29, 43, 59, 60, 70, 149, 177, 204, 240, 263, 269, 281	mf-T, rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic
<i>Deltochilum pseudoparile</i>	10, 11, 17, 20, 37, 42, 43, 52, 60, 161, 167, 183, 203, 263, 309, 386	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Deltochilum scabriusculum scabriusculum</i>	80	mf-T	Not endemic
<i>Deltochilum valgum acropyge</i>	17, 183, 203, 309	wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Dichotomius agenor</i>	183, 203, 190	mf-T, wf-P Basal, wf-P rain	Not endemic
<i>Dichotomius amicitiæ</i>	177, 200, 233, 263, 269, 281, 309	rf-LM, wf-LM, wf-P, wf-P rain, wf-T	Endemic shared with Panama
<i>Dichotomius annæ</i>	2, 3, 5, 9, 10, 11, 13, 17, 18, 20, 25, 29, 37, 42, 43, 59, 60, 68, 149, 160, 161, 167, 169, 183, 203, 89	df-T, mf-LM m, mf-P, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Dichotomius centralis</i>	2, 3, 11, 18, 20, 29, 47, 68, 127, 160, 190	df-T, mf-P, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-P	Not endemic
<i>Dichotomius costaricensis</i>	The type mentions only Costa Rica as the original locality	It seems possible that the species is a cave dweller.	Not endemic
<i>Dichotomius danieli</i>	9, 10, 11, 17, 25, 43, 52	rf-P, wf-P, wf-T, wf-T Prem	Endemic to Costa Rica
<i>Dichotomius favi</i>	17, 42, 161, 167	mf-T, wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
<i>Dichotomius rodrigo</i>	309, 386	wf-T, wf-T Prem	Endemic to Costa Rica

<i>Dichotomius satanas</i>	2, 5, 9, 10, 11, 13, 17, 20, 25, 29, 42, 43, 51, 52, 59, 60, 127, 149, 160, 161, 167, 183, 192, 203, 204, 263, 281, 309, 89	mf-LM m, mf-P, mf-T, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Dichotomius yucatanus</i>	2, 3, 10, 18, 20, 68, 127	df-T, mf-P, mf-P Basal, mf-T, mf-T d, mf-T Prem, wf-T Prem	Not endemic
<i>Eurysternus caribaeus</i>	2, 9, 10, 11, 13, 17, 20, 25, 29, 42, 43, 52, 60, 149, 160, 161, 165, 166, 167, 183, 203, 281, 309	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Eurysternus foedus</i>	17, 51, 57, 161, 183, 309	wf-T, wf-P Basal, mf-T	Not endemic
<i>Eurysternus hamaticollis</i>	183, 192, 203, 309	rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Eurysternus magnus</i>	10, 11, 13, 29, 59, 60, 127, 149, 165, 177, 204, 240, 263, 269, 281, 317	mf-P, rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Eurysternus mexicanus</i>	2, 10, 11, 13, 17, 20, 25, 29, 37, 43, 51, 52, 60, 68, 149, 160, 161, 167, 183, 192, 203, 258, 309	mf-T, mf-T d, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Eurysternus plebejus</i>	2, 10, 11, 17, 37, 42, 51, 52, 60, 160, 161, 167, 183, 203, 219, 258, 269, 309, 386, 381	mf-T, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Eurysternus streblus</i>	309, 386	wf-T, wf-T Prem	Not endemic
<i>Eurysternus velutinus</i>	10, 43, 52, 149, 309	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Malagoniella astyanax yucatanus</i>	2, 3, 18, 68, 85	df-T, mf-P Basal, mf-T, mf-T d	Not endemic
<i>Megathoposoma candezei</i>	9, 10, 11, 17, 42, 52, 167, 183, 192, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ontherus azteca</i>	10, 11, 13, 17, 160, 183	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ontherus brevipennis</i>	10, 219, 309	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Ontherus pseudodidymus</i>	9, 10, 11, 13, 17, 25, 29, 43, 52, 59, 60, 73, 127, 149, 162, 177, 200, 204, 263, 269, 281	mf-P, rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Ontherus sextuberculatus</i>	11, 17, 29, 51, 52, 60, 149, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic to Costa Rica
<i>Onthophagus acuminatus</i>	2, 3, 9, 10, 11, 17, 18, 25, 37, 42, 51, 52, 60, 68, 149, 160, 161, 167, 183, 258, 263, 309	df-T, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Onthophagus andersoni</i>	11, 13, 59, 281	rf-P, wf-LM, wf-P	Endemic to Costa Rica
<i>Onthophagus anthracinus</i>	11, 59, 73, 162, 179, 89	mf-LM, mf-LM m, wf-LM, wf-P	Not endemic
<i>Onthophagus atriglabratus</i>	11, 13, 29, 43, 60, 127, 263, 281, 317	mf-P, rf-P, wf-P, wf-P rain	Not endemic
<i>Onthophagus atrosericeus</i>	73, 177, 200, 216	rf-LM, rf-M, wf-LM	Not endemic
<i>Onthophagus batesi</i>	2, 3, 5, 9, 10, 11, 17, 18, 25, 37, 42, 47, 52, 68, 127, 161, 167, 183, 258, 281, 309	df-T, mf-P, mf-P Basal, mf-T, mf-T d, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic

<i>Onthophagus championi</i>	2, 3, 18, 47, 68, 183, 190	df-T, mf-P Basal, mf-T, mf-T d, wf-P Basal	Not endemic
<i>Onthophagus chryses</i>	10, 11, 13, 20, 29, 60, 263, 269, 281	mf-T Prem, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Onthophagus coriaceoumbrosus</i>	160, 183, 281, 309	mf-T Prem, wf-P, wf-P Basal, wf-T	Endemic shared with Panama
<i>Onthophagus coscineus</i>	2, 10, 11, 17, 20, 37, 42, 160, 167, 183, 194, 203, 219, 281, 309	mf-T, mf-T Prem, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Onthophagus crinitus</i>	2, 3, 10, 11, 160, 183, 192, 203	mf-P Basal, mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Onthophagus cryptodicranus</i>	17, 42, 167	wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
<i>Onthophagus cyanellus</i>	11, 73, 127, 162, 177, 179, 200, 216, 269, 281, 89, 158	mf-LM, mf-LM m, mf-P, rf-LM, rf-M, wf-LM, wf-P	Not endemic
<i>Onthophagus dicranus</i>	183, 219, 309	wf-P Basal, wf-T	Not endemic
<i>Onthophagus dorsipilulus</i>	177	rf-LM	endemic shared with Panama
<i>Onthophagus gazellinus</i>	10, 11, 43	rf-P, wf-P, wf-T Prem	Endemic shared with Nicaragua
<i>Onthophagus genuinus</i>	11, 17, 43, 52	rf-P, wf-P, wf-T, wf-T Prem	Endemic to Costa Rica
<i>Onthophagus grataehelenae</i>	73, 162, 177, 204, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Onthophagus hopfneri</i>	3, 18, 47, 68, 159	df-T, mf-P Basal, mf-T, mf-T d	Not endemic
<i>Onthophagus incensus</i>	10, 11, 13, 20, 29, 43, 59, 60, 70, 73, 127, 149, 162, 177, 179, 192, 200, 204, 240, 263, 269, 281, 89	mf-LM, mf-LM m, mf-P, mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Onthophagus inediapterus</i>	269	wf-LM	Endemic to Costa Rica
<i>Onthophagus landolti</i>	2, 3, 10, 11, 13, 18, 20, 25, 29, 68, 80, 127, 183, 258, 263, 269, 281, 309, 190	df-T, mf-P, mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Onthophagus limonensis</i>	10, 17, 37, 73, 161, 167, 177, 281	mf-T, rf-LM, wf-LM, wf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Onthophagus marginicollis</i>	2, 3, 5, 9, 17, 18, 42, 47, 51, 68, 161, 167, 183, 210, 258, 270, 309, 143, 190	df-T, mf-P, mf-P Basal, mf-T, mf-T d, rf-P, wf-P Basal, wf-T	Not endemic
<i>Onthophagus micropterus</i>	177, 216	rf-LM, rf-M	Endemic to Costa Rica
<i>Onthophagus nemorivagus</i>	10, 13, 17, 29, 43, 52, 60, 149, 167	rf-P, wf-P, wf-T, wf-T Prem	Endemic to Costa Rica
<i>Onthophagus notiodes</i>	60, 149	rf-P, wf-P	Endemic to Costa Rica
<i>Onthophagus nubilus</i>	240	rf-P	Endemic to Costa Rica

<i>Onthophagus nyctopus</i>	9, 10, 11, 13, 17, 20, 29, 37, 42, 43, 52, 161, 167, 183, 263, 281, 309	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Onthophagus orphnoides</i>	11, 13, 59, 177, 204, 263, 269, 281, 89	mf-LM m, rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Onthophagus praecellens</i>	2, 5, 10, 11, 17, 18, 20, 29, 42, 43, 51, 68, 127, 149, 160, 167, 183, 203, 211, 219, 228, 263, 281, 309	df-T, mf-P, mf-T, mf-T d, mf-T perhum, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Onthophagus propraecellens</i>	11, 59, 177, 240, 263, 269, 281, 89	mf-LM m, rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Onthophagus quetzalis</i>	13, 29	rf-P	Endemic to Costa Rica
<i>Onthophagus sharpi</i>	11, 29, 183, 192, 203, 219, 258, 263, 281, 309	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Onthophagus singulariformis</i>	52	Wf-TPrem	Endemic to Costa Rica
<i>Onthophagus solisi</i>	10, 13, 20, 29, 43	mf-T Prem, rf-P, wf-T Prem	Endemic to Costa Rica
<i>Onthophagus stockwelli</i>	10, 11, 161, 167	mf-T, wf-P, wf-T, wf-T Prem	Not endemic
<i>Onthophagus tapirus</i>	11, 17, 20, 37, 52, 136, 161, 167	mf-T, mf-T Prem, wf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Onthophagus viridivinosus</i>	2, 17, 37	mf-T, wf-T	Endemic shared with Nicaragua
<i>Oxysternon silenus smaragdinum</i>	136	wf-T Prem	Not endemic
<i>Pedaridium bottimeri</i>	161	mf-T	Endemic shared with Panama
<i>Pedaridium bradyporum</i>	51, 149, 183	wf-P, wf-P Basal	Endemic to Costa Rica
<i>Pedaridium pilosum</i>	2, 10, 11, 13, 17, 37, 43, 160, 162, 167, 183, 263, 309	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Phanaeus beltianus</i>	10, 11, 17, 20, 43, 51, 52	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Phanaeus changdiazii</i>	183	wf-P Basal	Endemic shared with Panama
<i>Phanaeus demon excelsus</i>	3, 18, 68, 127	df-T, mf-P, mf-P Basal, mf-T d	Not endemic
<i>Phanaeus eximius</i>	2, 3, 11, 18	df-T, mf-P Basal, mf-T, wf-P	Not endemic
<i>Phanaeus hermes</i>	240, 253, 258	mf-T, rf-P, wf-P Basal	Not endemic
<i>Phanaeus pyrois pyrois</i>	2, 3, 10, 11, 13, 17, 20, 25, 29, 37, 42, 43, 52, 60, 127, 149, 161, 167, 183, 203, 263, 281, 309, 386	mf-P, mf-P Basal, mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Phanaeus pyrois malyi</i>	160	mf-T Prem	Endemic to Costa Rica
<i>Phanaeus wagneri wagneri</i>	3, 11, 18, 47, 68, 127, 143	df-T, mf-P, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
<i>Pseudocanthon perplexus</i>	3, 18, 179	df-T, mf-LM, mf-P Basal	Not endemic

<i>Scatimus erinnyos</i>	9, 10, 11, 13, 17, 25, 29, 43, 52, 60, 149, 160, 167, 263, 281, 309	mf-T Prem, rf-P, wf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Scatimus ovatus</i>	2, 10, 13, 17, 25, 29, 42, 160, 167, 183, 253, 258, 309	mf-T, mf-T Prem, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Sisyphus mexicanus</i>	2, 3, 11, 18, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
<i>Sulcophanaeus noctis cupricollis</i>	2, 10, 11, 13, 17, 18, 20, 29, 43, 52, 160, 167	df-T, mf-T, mf-T Prem, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Sulcophanaeus noctis noctis</i>	183, 281, 309, 386	wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Sulcophanaeus velutinus</i>	10, 11, 13, 20, 29, 42, 59, 60, 70, 73, 149, 165, 177, 204, 240, 263, 269, 281	mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Trichillum arcus</i>	10, 11, 20, 25, 42	mf-T Prem, wf-P, wf-P Basal, wf-T Prem	Endemic to Costa Rica
<i>Uroxys boneti</i>	10, 11, 13, 17, 29, 42, 43, 59, 162, 167, 183, 281, 309	rf-P, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Uroxys deavilai</i>	2, 3, 11, 18	df-T, mf-P Basal, mf-T, wf-P	Not endemic
<i>Uroxys depressifrons</i>	11, 13, 29, 43, 52, 59, 60, 70, 73, 149, 204, 263, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Uroxys dybasi</i>	10, 11, 13, 43, 59, 73, 162	rf-P, wf-LM, wf-P, wf-T Prem	Endemic shared with Panama
<i>Uroxys gatunensis</i>	309	wf-T	Not endemic
<i>Uroxys gorgon</i>	10, 11, 17, 42, 52, 149, 161, 167, 183, 219, 309	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Uroxys metagorgon</i>	149	wf-P	Endemic shared with Panama
<i>Uroxys microcularis</i>	3	mf-P Basal	Not endemic
<i>Uroxys micros</i>	2, 10, 11, 18, 20, 29, 162	df-T, mf-T, mf-T Prem, rf-P, wf-P, wf-T Prem	Not endemic
<i>Uroxys nebulinus</i>	29, 70, 162, 177, 204	rf-LM, rf-P, wf-P	Not endemic
<i>Uroxys platypyga</i>	10, 11, 167	wf-T, wf-T Prem	Not endemic
<i>Uroxys transversifrons</i>	17, 43, 52, 60, 149	rf-P, wf-P, wf-T, wf-T Prem	Not endemic