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## Biodiversity conservation in Costa Rica: a correspondence analysis between identified biodiversity hotspots (Araceae, Arecaceae, Bromeliaceae, and Scarabaeinae) and conservation priority life zones

### Conservación de la biodiversidad en Costa Rica: análisis de la correspondencia entre áreas identificadas clave por su biodiversidad (Araceae, Arecaceae, Bromeliaceae y Scarabaeinae) y zonas de vida prioritarias para la conservación

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**Abstract.** This paper undertook an analysis of the distribution of high species richness and areas of endemism based on plants (Araceae, Arecaceae, and Bromeliaceae) and dung beetles (Scarabaeinae) inhabiting the different Holdridge Life Zones of Costa Rica. Using a geographic information system (GIS) we analyzed biogeographic provinces, in terms of their representativity in sampling areas, life zones, and protected areas. Species richness and endemism maps served as a base for conducting a gap analysis and defining 6 different levels of high priority conservation areas. What percentages of these priority areas are under some type of protection or conservation scheme and which of these areas should be enlarged were also investigated. The degree of feasibility that these areas under protection have for enlargement is indicated. A list is included of all the aforementioned registered species for Costa Rica, as well as their presence in the different Holdridge Life Zones and their endemism status. Four areas with the highest species richness were identified, and 3 new areas of endemism are proposed. The most important conservation priority areas are the tropical wet forests on the northeastern lowlands, the Osa Peninsula region, and the premontane wet forest along the Guanacaste, Tilarán and Central mountain ranges. This study clearly demonstrates the need to include and compare different groups of organisms in biodiversity-endemism studies, in order to obtain more robust and finer-grained studies.

Key words: high species richness areas, areas of endemism, life zones, representativity, Araceae, Arecaceae, Bromeliaceae, Scarabaeinae.

**Resumen.** El presente estudio analiza la distribución de áreas de alta riqueza específica y endemismos basado en plantas (Araceae, Arecaceae, y Bromeliaceae) y escarabajos del estiércol (Scarabaeinae), que habitan las diferentes Zonas de Vida de Holdridge en Costa Rica. Mediante el uso de un sistema de información geográfica (SIG) analizamos provincias biogeográficas, en relación a la representatividad de las áreas de muestreo, las zonas de vida y las áreas protegidas. Los mapas de alta riqueza específica y endemismo sirvieron de base para realizar un análisis de vacíos (gaps) y definir 6 niveles distintos de alta prioridad de áreas de conservación. También se investigó qué porcentaje de estas áreas prioritarias se encontraba bajo algún esquema de protección o conservación, y cuáles de estas áreas son susceptibles de ser ampliadas. Se indica igualmente el grado de factibilidad para que estas áreas crezcan. Incluimos una lista de todas las especies registradas para las familias antes mencionadas en Costa Rica, e indicamos su presencia en las diferentes Zonas de Vida de Holdridge, así como su condición de endemismo. Se identificaron 4 áreas de máxima riqueza específica y 3 áreas nuevas de alto endemismo. Las áreas prioritarias para la conservación identificadas fueron: (1), el bosque húmedo tropical de las tierras bajas del noreste; (2), la región de la península de Osa, y (3), el bosque húmedo premontano, a lo largo de las vertientes de las cordilleras de Guanacaste, Tilarán y Central. Este estudio demostró claramente la necesidad de incluir y comparar a diferentes grupos de organismos en estudios sobre patrones espaciales de biodiversidad-endemismo, con lo cual es posible obtener resultados más robustos y más detallados.

Palabras clave: áreas de alta riqueza específica, áreas de endemismo, zonas de vida, representatividad, Araceae, Arecaceae, Bromeliaceae, Scarabaeinae.

## Introduction

Biodiversity conservation has become one of the most urgent tasks facing humanity because of the accelerating rates of biodiversity loss (Pimm et al., 1995). It is precisely (and perhaps perversely) that the most biodiverse areas and those with the highest levels of biodiversity loss are the least protected and with the greatest need for data regarding their species richness and levels of endemism (Pimm, 2000). An appropriate action toward this goal would be the establishment of global inventories, although the time required for both surveying and documenting this plethora of taxa far outreaches our present capacity. Availability of adequate data is also a limiting factor (Prendergast et al., 1999). Therefore, development of biogeographic atlases can be proposed as a practical tool for biodiversity conservation (Prendergast et al., 1993; Morrone, 2000) and hotspot identification (areas that combine a high biodiversity with a high threat degree by humans; Myers, 1988; Kappelle, 2008). A very important task of biogeography atlases is the study of diversity and endemism patterns in order to protect rare and endangered species. As Lomolino et al. (2006) indicate, 2 major tasks of this process consist of documenting the intensities and

locations of hotspots for a particular taxonomic group and determining the degree to which different taxon-specific hotspots overlap spatially. Although levels of endemism and species richness are frequently positively correlated (Balmford and Long, 1995), unfortunately, many times such overlap does not exist (Bibby et al., 1992; Prendergast et al., 1993; Araujo, 2002; Cox and Moore, 2005; Lomolino et al., 2006). This fact compels the analysis of distribution patterns to be conducted region by region, in order to understand current scenarios and hence being able to identify biodiversity hotspots (Myers et al., 2000). As Gaston (2000) and Gaston and Spicer (2004) indicate, species are not uniformly distributed across the world and must therefore be mapped. Areas of high diversity usually elicit questions about their origins and possible conservation. However, other approaches such as the Method of Systematic Conservation Planning (Margules and Pressey 2000) is based on species rarity and complementarity rather than diversity hotspots.

The study and knowledge of the aforementioned situation in Costa Rica is of the utmost importance. Costa Rica belongs to one (Middle America) of the 36 world hotspots, as defined by Mittermeier et al. (2004). Costa Rica is a country with a small area (Fig. 1); it has 51 100 km<sup>2</sup>

of continental and insular land surface, representing 0.03% of the Earth's surface (Jiménez, 1995; Ministerio del Ambiente y Energía, 2000). In the world's diversity ranking, Costa Rica occupies the 20<sup>th</sup> place, approximately. As such, it is not considered a megadiverse country, since only 12 countries make up the list. However, what makes Costa Rica special is its species density (number of species per unit of area) (Valerio, 1999; Obando, 2002). Using this measure, Costa



**Figure 1.** Geographical areas in Costa Rica: C, Central Cordillera; F, Coastal mountain range; G, Guanacaste mountain range; H, Herradura mountain; I, Tilarán mountain range; L, northern plains; N, Nicoya peninsula (Pacific Northwest); O, Golfo Dulce/Osa Peninsula; P, Central Pacific; T, Talamanca mountain range; U, Turrubares mountain; V, Central Valley. (Map taken from Kohlmann et al., 2002).

Rica's place in the world is highly recognized (Valerio, 1999, 2006; Obando, 2002, 2007). This country contains approximately 3.6% of the total expected world's diversity, and if the total number of described species is considered, this number jumps then to 4.5%, with more than 90 000 known species (66 946 insect species, 11 451 plant species, and 5 253 other invertebrate species; Obando 2007). To give a comparative idea of species density, Costa Rica has 234.8 plant species per 1 000 km<sup>2</sup>, whereas Colombia, in second place, has only 43.8 plant species per 1 000 km<sup>2</sup> (Obando, 2007). Similarly, Costa Rica has 28.2 species of vertebrates (excluding fishes) per 1 000 km<sup>2</sup>, whereas Ecuador, the second most biodiverse vertebrate country per km<sup>2</sup> in the world, has 9.2 species per 1 000 km<sup>2</sup>, and the third most biodiverse vertebrate country, Malaysia, has only 4.4 vertebrate species per 1 000 km<sup>2</sup> (Valerio, 2006). This enormous biodiversity in Costa Rica is now under protection by a world-class national system of protected areas, which began in the 1970's and today protects almost 27% (governmental and private) of the national territory (Vaughan, 1994; Vaughan et al., 1998). Interestingly, Costa Rica is also the country with most ecotourists per km<sup>2</sup> worldwide, 22.47 international ecotourists/km<sup>2</sup> in the year 2007, with the African sub-Saharan countries as the next places with most ecotourists per km<sup>2</sup> (Kohlmann et al., 2008).

Costa Rica is considered to have a moderate proportion of endemics (Obando, 2007); approximately 1.3% of the known species are endemics. It is estimated that around 10% of the total plant species are endemics (1 102 species), whereas the different vertebrate groups vary from a minimum of 0.7% in birds to a maximum of 25% for the amphibians (Obando, 2007). Using these 2 groups (plants and vertebrates), 4 great areas of endemism have been identified for continental Costa Rica: the Central Volcanic Cordillera, the Talamanca Cordillera, the Central Pacific Region and the Osa Peninsula Region (Fig. 1); a fifth area has been identified on Cocos Island, in the Pacific Ocean (Elizondo et al., 1989). From the ecosystem point of view, the cloud forests are the most endemic ecosystems in the country (Obando, 2002), as the present study concludes too.

Adequate representation of biodiversity is ideally achieved by the use of multiple taxonomic groups (Stork and Samways, 1995; Halffter and Moreno, 2005; Pawar et al., 2007). However, due to time, funding, collection and taxonomic constraints for the majority of the groups, especially in tropical regions, many area-prioritization studies assume some similarity levels in species geographical distributions and consequently available groups are used as surrogates for others (Garson et al., 2002; Rondinini and Boitani, 2006; Pawar et al., 2007).

Despite the popularity of the surrogacy approach, its efficacy remains unclear (Moore et al., 2003; Graham and Hijmans, 2006; Lamoreux et al., 2006).

This paper is an attempt at analyzing the distributional congruence of 4 different tropical taxonomic groups (Araceae, Arecaceae, Bromeliaceae and Scarabaeinae) and describing their overlap at a fine scale. A recurrent question is whether plant and vertebrate distribution patterns are reflected by those of invertebrates as well (Howard et al. 1988). Moritz et al. (2001) found high levels of congruence with data on tropical insects, snails, plants, and vertebrates only in areas with a clear history of geographical vicariance. In some other cases, like in tiger beetles, there seems to be congruence; in other cases the relationships are not clear (Mittermeier et al., 2004). The present study identifies biodiversity provinces indicating and analyzing the spatial correspondence of areas of high species richness and endemism for Costa Rica, using dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) and plants (Araceae, Arecaceae and Bromeliaceae).

Our analysis focused on continental Costa Rica; Cocos Island was not included because no Scarabaeinae material has been collected from that locality and only 1 species of Aphodiinae has been found to date. This analysis represents an effort to help define those areas most in need of conservation and sustainable use in Costa Rica. The study will also help define those areas that have been under sampled and therefore future collecting efforts can be directed. This study is also an expansion and continuation of a previous study which used dung beetles for a gap analysis (Kohlmann et al., 2007), considered a pioneer study in Costa Rica (Arias et al., 2008), because it represents the first attempt to use the actual distribution of all species belonging to a specific taxonomic group.

## Materials and methods

*Taxon information.* Regarding the 3 plant families, Araceae, Arecaceae and Bromeliaceae, data on their distribution (geographic coordinates) were taken from the collections of the National Biodiversity Institute (INBio, [www.inbio.ac.cr](http://www.inbio.ac.cr)) and from the Missouri Botanical Garden electronic database ([www.mobot.org](http://www.mobot.org)), additional information was incorporated from Hammel et al. (2003). This information was further revised and updated by Drs. N. Zamora (Araceae and Arecaceae) and J. F. Morales (Bromeliaceae). The total number of plant species considered for this study is as follows (Appendices 1-3): Araceae, 229 species; Arecaceae, 107 species; Bromeliaceae, 187 species. No introduced species were considered for this study.

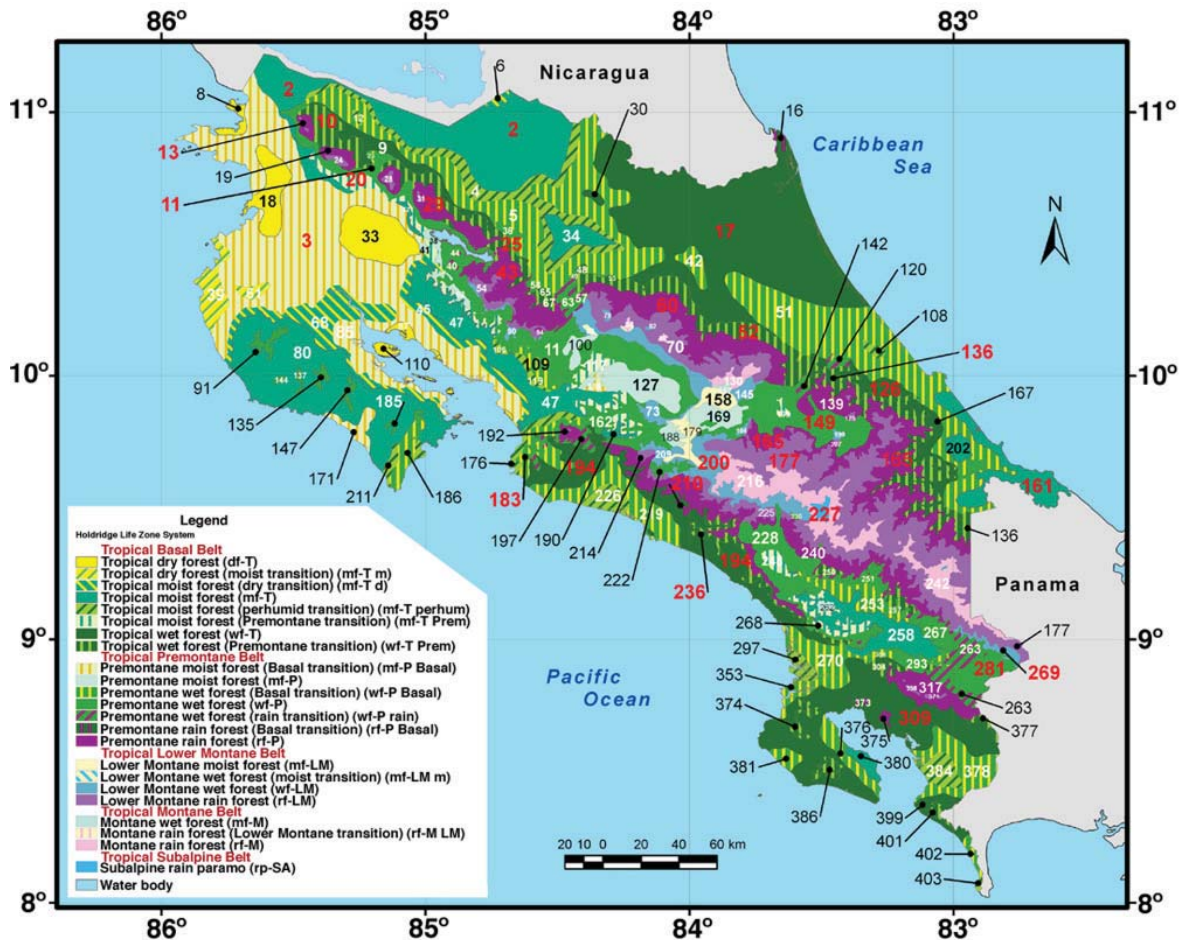
Information regarding Scarabaeidae beetle

distribution was also taken from the collections of the National Biodiversity Institute. The Scarabaeinae (Coleoptera: Scarabaeidae) have been particularly well studied (Kohlmann et al., 2007). So far, 174 native taxa of Scarabaeinae have been reported from Costa Rica (Appendix 4).

Concluding, the 4 chosen groups have 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, in accordance with Müller's (1981) 3 tenets for making these groups particularly well suited for the present biogeographic analysis. We are aware that the Araceae and Bromeliaceae tend to be hygrophilic by nature in Costa Rica, thus introducing some bias into the analysis, especially when discussing the drier northwest

Pacific areas. However, this situation is balanced by the fact that the Arecaceae and the Scarabaeinae have radiated in humid, as well as in dry areas, and are therefore good representatives of the northwest Pacific.

*Base vegetation map.* One of the most popular systems used in Costa Rica and in 12 other countries in the region (Meza, 2001) for vegetation classification is the Life Zone System developed by Holdridge (1967). This system divides Costa Rica into 12 Life Zones and 11 Transition Zones (Fig. 2) based on environmental factors such as humidity, rainfall, and temperature. This system is thus independent of floristic relationships and the same zones can then appear 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 (Meza, 2001).



**Figure 2.** Numbering the Holdridge Life Zone polygons in Costa Rica. Numbers in red represent life zones with 5 or more years of collecting, which are considered as well represented.

The Life Zone System maps were directly taken from the Atlas Costa Rica 2000 (Instituto Tecnológico de Costa Rica, 2000) and were not modified for the present study. Sampling effort in this study is not proportional to polygon size, due to the fact that most of the sampling was done by INBio and this institution samples in national parks and other conservation areas with original vegetation cover and not in modified areas; therefore, one can argue that polygon size did not bias neither the collecting effort, nor the collecting site inclusion, which might have incorporated possible changes in original vegetation or ground cover.

According to this classification, the 5 most extensive vegetation types are: tropical wet forest (10.5% of the total country area), premontane wet forest (7.2%), lower montane wet forest (5.9%), premontane rain forest (5.6%) and tropical moist forest (5.5%) (Obando, 2002).

There are some limitations to this system. Besides total precipitation and temperature, the Holdridge Life Zone system can potentially vary along other environmental axes, such as the edaphic conditions, which could impact species abundance and endemism. For example, bioclimatic regions such as the Pacific dry forest consist of long belts along mountain/volcanic ranges, and by assuming that these long belts all share the same biodiversity category, there would be a risk of losing resolution when assigning conservation priority zones.

No standardized functional ecological classification exists for Costa Rica (Obando, 2007). Some incomplete attempts have been tried at establishing an ecoregion system, without success. Very recently (Sistema Nacional de Áreas de Conservación (SINAC), 2007 a) a new system based on phytogeographic units has started to be implemented in Costa Rica.

*GIS Analysis.* Some of the many advantages of using GIS techniques are the storage of large amounts of spatial information, the ease for mapping many map layers, and their use in modeling and predicting species distributions. For these reasons we have followed a GIS-oriented process for the elaboration of our biogeographic analysis.

GIS and data analyses were carried out by using ArcView ®3.1 (ESRI, 2002), ArcGIS®9.2 (ESRI, 2006) and Microsoft Excel® (2002) following the process outlined below:

1.- Assembling and cleaning of the database for each taxon (taxon names, type of endemism and location of collection sites). The great majority of the data came from the National Institute of Biodiversity (INBio), and as such is less than 20 years old and derives from protected conservation areas. The Missouri Botanical Garden data have similar characteristics. Data layers were generated using the collection sites for each species.

2.- Refinement and geo-referencing of geographic

location data consisted of transformation to coverage format, correction of errors and inconsistencies such as redundant polygons, homogenization of geographic data bases, association of tables with the base map, addition of new collection points to original collection data bases, and elimination of redundant duplicate collection points. The layers containing the National System of Coordinates (Costa Rica Lambert North) were transformed to geographic coordinates (the same datum was always used: Fundamental de Ocotepeque, which is not compatible with generic geographical coordinate systems and requires specific parameters for its conversion). For distributional referencing (Appendices 1-4), each Holdridge Life Zone polygon was numbered (Fig. 2).

3.- For each taxon, the collection sites were superimposed on the Holdridge Life Zones obtaining the number of collection sites by taxa, as well as the total number of taxa, endemics and endemism type (endemics known to occur only in Costa Rica, shared with Panama, shared with Nicaragua, shared with Nicaragua and Panama, and total number for Costa Rica) for each life zone polygon.

For this study we found the use of the Holdridge system more amenable than distribution modeling for several reasons. First, the life zones of the Holdridge system have been well mapped, have been much used, and are very popular in Costa Rica, besides being considered very appropriate to the complexities of tropical vegetation (Gentry, 1978). It has also been widely used by the National Aeronautic and Space Administration (NASA) ([http://gcmd.nasa.gov/records/GCMD\\_GNV00005.html](http://gcmd.nasa.gov/records/GCMD_GNV00005.html)). The system has been compared to more sophisticated, mechanistic simulation models, and the Holdridge implementations generally showed similar or greater climate sensitivity with respect to spatial distribution of vegetation (Yates et al., 2000).

We did some preliminary comparisons with Maxent (Phillips et al., 2004, 2006), a species habitat-modeling program, using climate as a predicting variable. We found that the program consistently predicted areas where studied species do not occur. A Holdridge vs. Maxent comparison would be interesting, but at present we believe that under our circumstances of well-sampled taxa, computation resources, and model expertise, simple correlational models, such as Holdridge, may be of greater advantage.

4.- When overlaying collection sites on the Holdridge Life Zones, we followed Morrone's suggestions (2000) regarding the formal preparation of a biogeographic atlas, the elaboration of a distribution database and detailed locality and endemism maps. The base electronic map was derived from the one presented in Atlas Costa Rica 2000 (Instituto Tecnológico de Costa Rica, 2000).

5.- To create comparable maps for the different taxonomic groups of this study, the ranking levels of species richness and endemism by life zone were calculated in accordance with the classification used for the dung beetles of Costa Rica (Coleoptera: Scarabaeinae), as defined by Kohlmann et al. (2007) in a previous study. Accordingly, 5 species richness levels were established arbitrarily: up to 7% of the maximum species richness in a single life zone (class 1), up to 20% (class 2), up to 44% (class 3), up to 70% (class 4) and more than 70% (class 5). For the sake of this analysis and comparative purposes, only the 2 highest ranks (ranks 4 and 5) were shown and discussed, allowing us to focus the analysis on the richer and therefore more representative areas.

Concerning endemism, the limits for the 5 classes were set up arbitrarily as: up to 12% of maximum number of endemic species in a single life zone for class 1, with 24%, 46%, 72%, and  $\geq 72\%$  for classes 2 through 5, respectively. For each taxonomic group these relative values were converted into absolute values of species richness and endemism. Again, only the 2 most numerous ranks were used, following the logic outlined in the previous section.

6.- A conservation priority map was elaborated by overlaying maps of species numbers and endemics over a protected areas map to calculate percentages of areas under protection. Each of these 2 maps (number of species and endemics derived from step 5) indicated 5 different taxa classes with values 1-5, as defined by Kohlmann et al. (2007) in a previous study, where class 5 is the class with the highest number of taxa. Subsequently, the combination of species richness and endemism ranks by life zones was used to define 6 conservation priority areas in a gap analysis map according to Table 1. This differs from our previous approach (Kohlmann et al., 2007), where only 4 levels could be generated. The highest level (Priority 1) is assigned to life zones with top ranks both in species richness and endemism. The lowest priority level (Priority 6), results from a combination "rank 4 in species richness" and "rank <4 in endemism". Intermediate combinations define the priority levels 2 to 5 (Table 1).

**Table 1.** Definition of priority zones

Priority level	Species richness rank	Endemicity rank
1	5	5
2	<5	5
3	5	<5
4	4	4
5	<4	4
6	4	<4

This method of priority definition using complementarity (degree to which an area contributes otherwise unrepresented species to a set of areas), picturing the combination of areas of greatest species and endemism richness, was chosen following the suggestion made by Williams et al. (1996). They found that the areas chosen by using complementarity represented all the species many times over rather than by either choosing species or areas of endemism separately. They also found that it is also a well-suited method for supplementing an existing conservation network, in their case British birds. Equally, the decision to prioritize endemism over species richness in the definition process follows well-established recommendations expressed by Mittermeier et al. (2004), which are based on considering endemics as irreplaceable.

7.- Finally, a map showing the distribution of potential conflict areas was elaborated, overlaying the previous conservation priority areas map on a land use map. The land use map is derived from a 1992 map that was taken from the Terra Commission land ordination study for Costa Rica (Cotera et al., 1998).

## Results

*Distribution of collection localities:* The collection localities indicate that the northern part of Costa Rica, as well as the Central Pacific, are under sampled, due mostly to the fact that these areas have been highly transformed 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 one of the main barriers to collecting in these areas.

Unfortunately, not all areas of Costa Rica have been collected with equal intensity. In order to deal with under sampled areas, as well as to identify the areas with a good collecting effort, and for comparative purposes, regions with a collecting effort of 5 or more years were arbitrarily chosen for this study. The subsequent analyses will be based on these regions. Figure 2 shows the Holdridge Life Zone polygons associated with these collection records.

Appendices 1-4 contain a list of all the taxa used in this study and relate them to the number of life zones used for mapping their distribution (Fig. 2). Additional information is also provided (Appendices 1-4) for 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. Life zones areas depicted in grey (Figs. 3, 4), represent zones where no collecting efforts have been undertaken, thus indicating regions where collecting should be directed in the future.





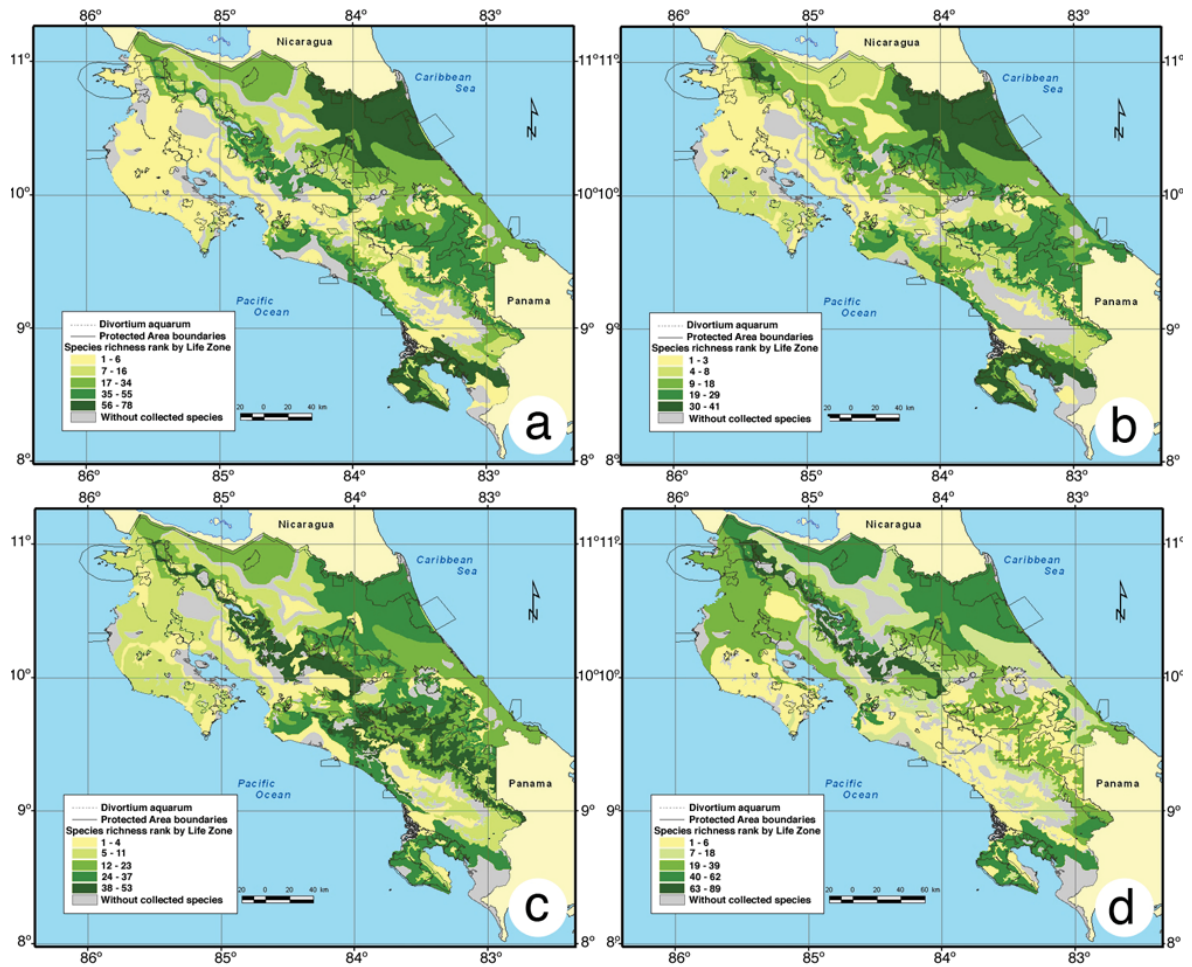
**c) Bromeliaceae**

Areas of priority zones	Priority 1 3177 km <sup>2</sup>	% (*)	Priority 2 0 km <sup>2</sup>	% (*)	Priority 3 2504 km <sup>2</sup>	% (*)	Priority 4 902 km <sup>2</sup>	% (*)	Priority 5 661 km <sup>2</sup>	% (*)	Priority 6 8854 km <sup>2</sup>	% (*)	Total 16098 km <sup>2</sup>	Total % (*)
State Farms	0.00	0.00	0.00	0.00	3.89	0.16	0.02	0.00	0.00	0.00	0.00	0.00	3.91	0.02
Wetlands	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	56.53	0.64	56.53	0.35
National Park	1 397.32	43.98	0.00	0.00	109.88	4.39	303.78	33.69	268.27	40.59	827.17	9.34	2 906.42	18.05
National Refuge	5.95	0.19	0.00	0.00	23.88	0.95	7.72	0.86	1.70	0.26	1 006.97	11.37	1 046.22	6.50
Biological Reserve	68.02	2.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	70.47	0.80	138.49	0.86
Forest Reserve	590.10	18.57	0.00	0.00	196.44	7.84	225.46	25.00	252.92	38.27	649.93	7.34	1 914.86	11.89
Protection Zone	325.02	10.23	0.00	0.00	146.68	5.86	37.23	4.13	40.36	6.11	135.23	1.53	684.52	4.25
National Monument	0.00	0.00	0.00	0.00	0.00	0.00	1.38	0.15	0.00	0.00	0.94	0.01	2.32	0.01
Total area (in km <sup>2</sup> ) and percentage* under protection by priority category	2 386.41	75.11	0.00	0.00	480.77	19.20	575.60	63.83	563.24	85.23	2 747.25	31.03	6 753.27	41.93

**d) Scarabaeinae**

Areas of priority zones	Priority 1 1593 km <sup>2</sup>	% (*)	Priority 2 0 km <sup>2</sup>	% (*)	Priority 3 259 km <sup>2</sup>	% (*)	Priority 4 7425 km <sup>2</sup>	% (*)	Priority 5 2360 km <sup>2</sup>	% (*)	Priority 6 6 2591 km <sup>2</sup>	% (*)	Total 14228 km <sup>2</sup>	Total % (*)
State Farms	3.89	0.24	0.00	0.00	40.96	15.82	0.00	0.00	0.00	0.00	6.70	0.26	51.55	0.36
Wetlands	0.00	0.00	0.00	0.00	0.00	0.00	56.98	0.77	0.00	0.00	0.00	0.00	56.98	0.40
National Park	103.08	6.47	0.00	0.00	24.37	9.41	931.88	12.55	1 296.85	54.94	75.58	2.92	2 431.76	17.09
National Refuge	18.17	1.14	0.00	0.00	0.00	0.00	990.87	13.34	5.74	0.24	372.48	14.38	1 387.26	9.75
Biological Reserve	0.00	0.00	0.00	0.00	0.00	0.00	83.52	1.12	0.00	0.00	0.00	0.00	83.52	0.59
Forest Reserve	0.87	0.05	0.00	0.00	0.00	0.00	544.09	7.33	418.86	17.74	0.00	0.00	963.82	6.77
Protection Zone	78.41	4.92	0.00	0.00	0.00	0.00	292.24	3.94	194.21	8.23	5.41	0.21	570.26	4.01
National Monument	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Total area (in km <sup>2</sup> ) and percentage* under protection by priority category	204.41	12.83	0.00	0.00	65.33	25.23	2 899.57	39.05	1 915.66	81.15	460.18	17.76	5 545.15	38.97

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



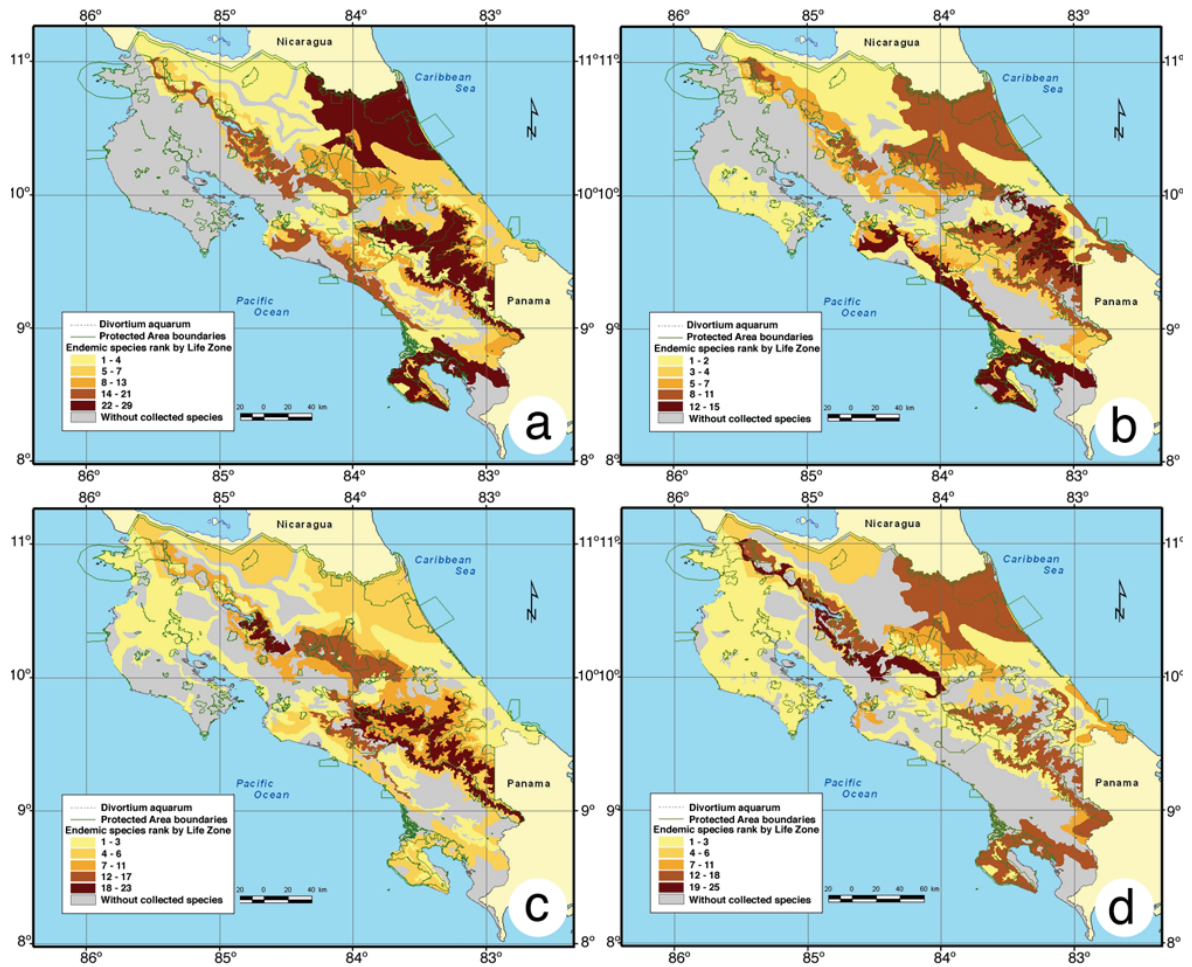
**Figure 3.** Distributions of species richness ranks for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

*Protection of life zone areas:* Costa Rica has a total mainland area of 51 042.8 km<sup>2</sup>. Out of these, 12 422.4 km<sup>2</sup> (24.3%), are under some sort of official governmental protection. Noteworthy is that 100% of the total area of the montane rain forest (lower montane transition) (rf-M LM) and the subalpine rain paramo (rp-SA) are protected. Other life zones with a high percentage of its area under protection include the premontane rain forest (basal transition) (rf-P Basal) (99.9%), montane rain forest (rf-M) (89.8%), and lower montane rain forest (rf-LM) (78.6%). All other life zones have less than 50% of their area under protection (Table 2).

*Distribution of species richness by life zone:* It should be noted that the highest species richness zones do not present spatial correspondence for the 4 taxa at the same time.

Araceae and Arecaceae (Fig. 3a-b) show the same zones of highest species richness in the tropical wet forest (wf-T) along the border with Nicaragua and the Osa Peninsula. On the contrary, Bromeliaceae and Scarabaeinae (Fig. 3c-d) show highest species richness in the premontane wet forest (wf-P), along the slopes of the Guanacaste, Tilarán and Central mountain ranges.

In relation to second rank zones, all 4 taxonomic groups correspond spatially with the tropical wet forest (wf-T) (Fig. 3a-d); all 3 plant families do so in the premontane rain forest; Araceae and Arecaceae in the lower montane rain forest (rf-LM); Araceae and Bromeliaceae in the premontane wet forest (wf-P); Araceae and Scarabaeinae in the tropical moist forest (mf-T); and finally the Arecaceae also show a second rank zone in the tropical



**Figure 4.** Distributions of endemism ranks for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae. Divortium aquarum = watershed divide.

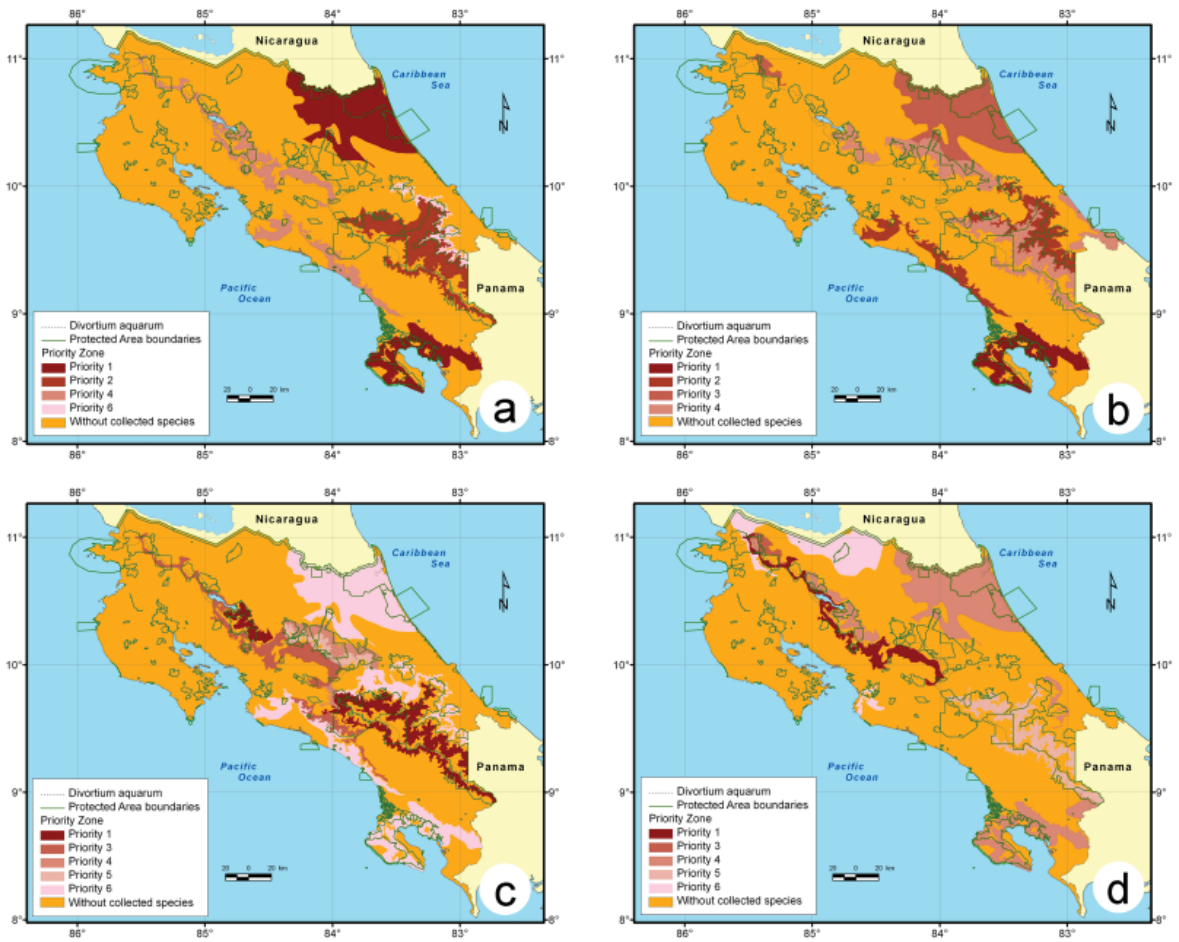
wet forest (premontane transition) (mf-T Prem). The Pacific Northwest shows the lowest species richness ranks for all 4 taxa, as expected for a drier region.

*Distribution of endemism by life zone:* We mapped the total number of endemic species (strictly endemic plus shared with Nicaragua and/or Panama) by life zone.

As was the case with the previous analysis, no spatial correspondences of the highest endemism zones exist for all 4 taxa (Fig. 4a-d). The only common zones are the tropical wet forest (wf-T) of Osa Peninsula between the Araceae and Arecaceae, the lower montane rain forest (rf-LM) between Araceae and Bromeliaceae, and the premontane rain forest (rf-P) between the Araceae and the Arecaceae. Interestingly, no spatial correspondence exists between the insect and the plant groups.

Several spatial correspondences occur for the second rank (Fig. 4a-d). Arecaceae, Bromeliaceae and Scarabaeinae in the premontane rain forest (rf-P); Araceae, Arecaceae and Scarabaeinae in the tropical wet forest (wf-T); Arecaceae and Scarabaeinae in the tropical wet forest (premontane transition) (wf-T Prem); Araceae and Scarabaeinae in the premontane wet forest (wf-P); Bromeliaceae and Scarabaeinae in the lower montane rain forest (rf-LM) and the lower montane wet forest (wf-LM); and finally the Arecaceae shows a second rank area in the tropical moist forest (mf-T).

*Representativity of the protected areas:* An analysis of the totality of the species for each of the 4 studied groups (Araceae, 29; Arecaceae, 107; Bromeliaceae, 187, and Scarabaeinae, 174) indicates that 205, 95, 156, and 165



**Figure 5.** Distributions of conservation priority zones for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

species, respectively, are present in protected areas. Likewise, an analysis for the total number of endemics for each of the 4 groups under study (Araceae, 113; Arecaceae, 50; Bromeliaceae, 80, and Scarabaeinae, 66) indicates that 97, 40, 64, and 64 species, respectively, are present in protected areas.

*Distribution of priority conservation areas:* Six priority conservation categories were previously defined; however, not all priority levels necessarily exist for every taxon under study (Fig. 5a-d).

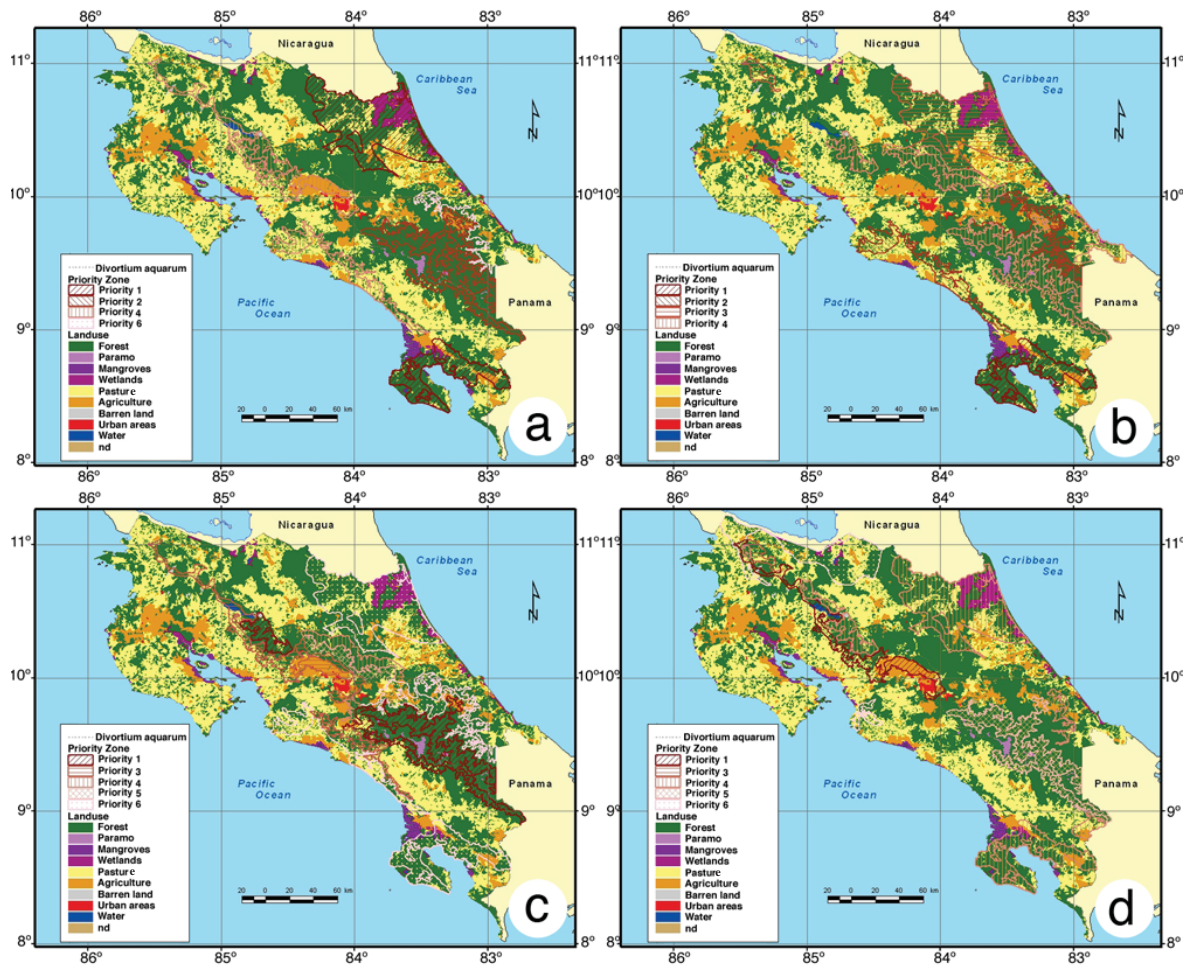
Araceae (Fig. 5a) and Arecaceae (Fig. 5b) have priority conservation areas 1 and 2 under official protection in 38% and 73% and 52% and 31,4% of their total areas, respectively; Bromeliaceae (Fig. 5c) and Scarabaeinae

(Fig. 5d) have only priority conservation areas 1 (no priority areas 2 are present) under official protection in 75% and 13% of their total areas, respectively.

*Distribution patterns within transformed areas:* Different priority conservation areas were superimposed on a land use map (1992) in order to correlate these areas with possible land use threats (Fig. 6a-d).

The Araceae analysis (Fig. 6a) shows that priority conservation area 1 has approximately 64% of its area as forest; approximately 17% is now converted to pasture, the main threat to this area. Priority conservation area 2 is approximately 93% forested and is under no apparent threat.

For the Arecaceae (Fig. 6b), approximately 77.5% of



**Figure 6.** Land use within identified priority areas for (a) Araceae, (b) Arecaeae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

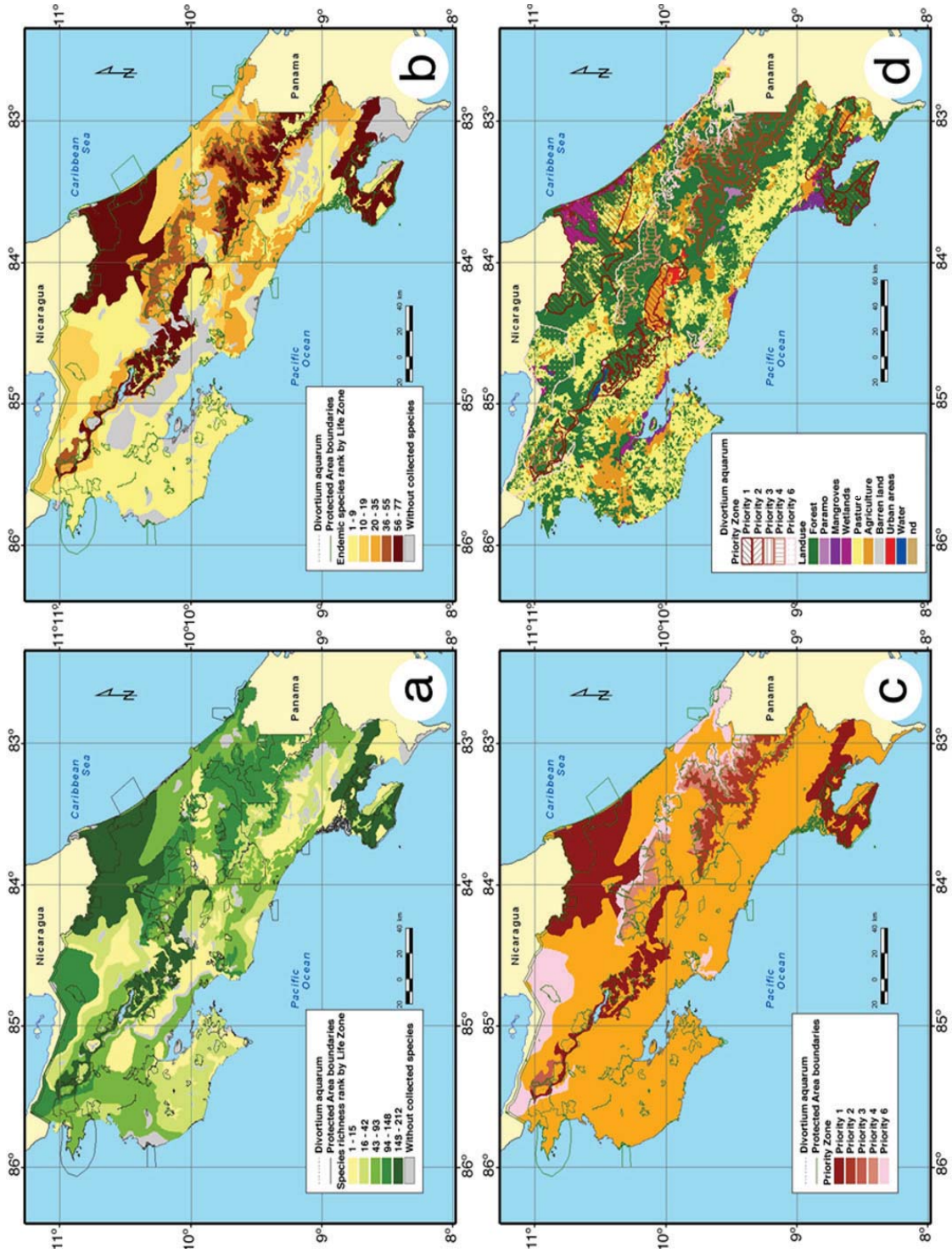
priority conservation area 1 is forested and approximately 11% is under pasture use. Priority conservation area 2 is approximately 70% forested, whereas the biggest possible threat seems to derive from pasture, 23% of this zone being under this type of use.

In the case of the Bromeliaceae (Fig. 6c), approximately 91% of the priority conservation area 1 is forested and only 6% is under pasture use. Priority conservation area 2 is not present for this taxon.

Finally, for the Scarabaeinae (Fig. 6d), only 35% of the priority conservation area 1 is forested, whereas pasture (approximately 31%) and agriculture (approximately 27.5%) have made strong inroads into this category. Priority conservation area 2 is not present for this taxon.

*Zones of highest species richness per life zone:* There

were 4 zones with highest species richness (Fig. 7a) according to the species richness overlay (Fig. 3a-d): the first 2 are the tropical wet forests (wf-T) in the northeastern corner, bordering Nicaragua (although most probably the central and southern Caribbean coast might also have high numbers that will become evident after a more intense collection program is applied), and the Osa Peninsula region. It would appear that the high species richness of these lowland forests tends to diminish inland, as is the case for the tropical moist forest (mf-T) in the northern Caribbean plains, and the tropical wet forest (wf-T) along the piedmont of the Caribbean versant. Both versants share naturally a very high number of common elements to the south with Panama. The third area of highest species richness is the premontane wet forest



**Figure 7.** Overall species (a) and endemic (b) species richness ranks, priority zones (c) and current land use/ land cover mosaic (d) based on the totality of the studied taxa and their overlap with the established protected areas. Areas in grey represent zones where no taxa have yet been recorded. Note that priority zone 5 was not generated in (c). As can be deduced from (d), priority zone 1 represents a veritable hotspot for Costa Rica, rich in species and endemics and also threatened by neighboring agricultural/pasture/urban activities. Divortium aquarum = watershed divide.

(wf-P) (approximately 750-1 500 masl) along the Pacific versant of the Guanacaste, Tilarán and Central mountain ranges. 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 because of its multiplicity of habitats and microhabitats. The same author 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 area has more species than the Talamanca mountain range to the South, which has a greater extension and is much older (Eocene) than the mountain ranges to the North (Eocene-Pleistocene) (Coates, 1997; Bergoeing, 1998; Valerio, 1999; Alvarado, 2000; Denyer and Kusmaul, 2000), thus contradicting all the tenets (time, species-area and modified species-area relationship) of the island biogeography theory. The last and fourth area is very small and is represented by the tropical wet forest (Premontane transition) (wf-T Prem) on the Caribbean versant of the Guanacaste mountain range.

The northwestern dry Pacific area of Costa Rica has been well sampled by many institutions throughout the years. However, it is evident that this area does not have a species richness level (rank 3) comparable with the Caribbean and South Pacific coasts or with the mid-elevation areas of the mountain ranges. Clearly, a dry climate with less precipitation can reduce the number of species (Townsend et al., 2008).

*Areas of highest endemism per life zone:* The areas of highest endemism (Fig. 7b) according to the overlay analysis (Fig. 4a-d), show great spatial correspondence with the previous analysis, containing the same aforementioned 3 areas. A similar situation had already been reported by Campbell (1999), who found that the majority of amphibians' species are endemic to Middle America and therefore there is a tendency of areas of high species diversity to overlap with areas of high endemism.

However, for this analysis there is also a fourth area, the lower montane rain forest (rf-LM) (approximately between 1 000 masl to 2 000 masl) on the Talamanca mountain range. The northwestern Pacific with a dry tropical forest, although well sampled, is not an area of high endemism at least for dung beetles, contrary to the high dung beetle endemism levels found in dry tropical forests along the Mexican Pacific coast (Kohlmann and Solís, 2006).

Obando (2002) reports in her study the existence of 5 major areas of endemism in Costa Rica. These areas are represented by Cocos Island, which was not considered in this study; the Golfo Dulce region (Fig. 1, O), the Cordillera Central (Fig. 1, C), the Talamanca mountain range (Fig. 1, T), and the Central Pacific region (Fig. 1, P), especially the coastal mountain ranges (Fig. 1, H and

U, Herradura and Turrubares hills, respectively). The Central Valley and Talamanca mountain range represent the most important areas of endemism, containing around an 80% of the endemic species, mostly conformed by the herpetofauna, birds and flora, as well as the majority of mammals threatened with extinction (Obando, 2002). The Osa Peninsula had also already been identified as an important endemism area by several authors (DeVries, 1987, 1997; Elizondo et al., 1989; Fogden and Fogden, 1997; Savage 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, a process that seems to have started about 3 million years ago (Coates, 1997). This vicariant process has produced a great number of vertebrate and insect sister species on the Caribbean and Pacific sides (Kohlmann and Wilkinson, 2007).

This study supports previously proposed areas of endemism, with the exception of the Central Pacific region, which this study assigned a rank level of only 3 (Fig. 7b). However, 3 new important areas of endemism are proposed here: the premontane wet forests (wf-P) of the Tilarán and Guanacaste mountain ranges and the tropical wet forest (wf-T) of the northeastern Caribbean (Fig. 7b). These last results are important because they contradict a previous study by Elizondo et al. (1989), based on vertebrates and plants, in which the authors found no reasons to support the hypothesis that the Tilarán and Guanacaste mountain ranges could represent areas for the generation of endemics. DeVries (1987) had already defined the Guanacaste 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. At the same time, the Caribbean lowlands have a relatively recent origin (Pliocene-Pleistocene; Bergoeing, 1998), yet are rich in endemics. The Tilarán and Guanacaste mountain ranges, as well as the Caribbean lowlands, were reported for the first time to be of importance in the generation of endemics by using dung beetles (Kohlmann et al., 2007), which is confirmed by this study's results.

*Life zones with highest overall species richness:* Table 3 indicates the overall species and endemics richness per group per life zone in Costa Rica. Only the life zones highlighted with a star in Table 3 have been well sampled (*i.e.* more than 5 years of collecting), therefore, they can be adequately compared. Table 3 also clearly shows those life zones where no members of the taxa under study have been found so far.

According to these results, the premontane rain forest (rf-P) life zone showing the highest total species

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

<b>a) Araceae</b>													
Areas of priority zones	Priority 1	% (*)	Priority 2	% (*)	Priority 3	% (*)	Priority 4	% (*)	Priority 5	% (*)	Priority 6	Total	
Total area	6111 km <sup>2</sup>		3344 km <sup>2</sup>		0 km <sup>2</sup>		3326 km <sup>2</sup>		0 km <sup>2</sup>		733 km <sup>2</sup>	13514 km <sup>2</sup>	
												% (*)	
Forest	3915	64.40	3119	93.38	0	1534	46.21	0	0.00	0.00	655	9223	68.46
Paramo	0	0.00	8	0.23	0	0	0.00	0	0.00	0.00	0	8	0.06
Mangroves	35	0.57	0	0.00	0	5	0.15	0	0.00	0.00	0	40	0.29
Wetlands	728	11.98	0	0.00	0	0	0.00	0	0.00	0.00	0	728	5.40
Pasture	1032	16.98	35	1.05	0	1194	35.97	0	0.00	0.00	20	2282	16.94
Agriculture	330	5.43	169	5.05	0	464	13.99	0	0.00	0.00	57	1020	7.57
Barren land	0	0.00	0	0.00	0	30	0.92	0	0.00	0.00	0	30	0.23
Urban areas	4	0.07	0	0.00	0	23	0.70	0	0.00	0.00	0	27	0.20
Water	34	0.57	0	0.00	0	69	2.07	0	0.00	0.00	0	103	0.76
na**	0	0.00	10	0.30	0	0	0.00	0	0.00	0.00	0	10	0.08
<b>b) Areaceae</b>													
Areas of priority zones	Priority 1	% (*)	Priority 2	% (*)	Priority 3	% (*)	Priority 4	% (*)	Priority 5	% (*)	Priority 6	Total	
Total area	1851 km <sup>2</sup>		3036 km <sup>2</sup>		4519 km <sup>2</sup>		4744 km <sup>2</sup>		0 km <sup>2</sup>		0 km <sup>2</sup>	14150 km <sup>2</sup>	
												% (*)	
Forest	1423	77.45	2118	69.94	2662	3968	83.83	0	0.00	0.00	0	10172	72.51
Paramo	0	0.00	0	0.00	0	8	0.16	0	0.00	0.00	0	8	0.05
Mangroves	35	1.88	5	0.17	0	0	0.00	0	0.00	0.00	0	40	0.28
Wetlands	36	1.95	0	0.00	692	33	0.70	0	0.00	0.00	0	761	5.43
Pasture	200	10.90	698	23.03	920	467	9.87	0	0.00	0.00	0	2285	16.29
Agriculture	141	7.66	202	6.67	190	167	3.52	0	0.00	0.00	0	699	4.98
Barren land	0	0.00	0	0.00	0	15	0.33	0	0.00	0.00	0	15	0.11
Urban areas	3	0.16	0	0.00	1	0	0.00	0	0.00	0.00	0	4	0.03
Water	0	0.00	0	0.00	34	0	0.00	0	0.00	0.00	0	34	0.25
na**	0	0.00	6	0.19	0	4	0.09	0	0.00	0.00	0	10	0.07

Area of land use categories (1992) in km<sup>2</sup>



<b>c) Bromeliaceae</b>												
Areas of priority zones												
Total area	Priority 1 3177 km <sup>2</sup>	% (*)	Priority 2 0 km <sup>2</sup>	% (*)	Priority 3 2504 km <sup>2</sup>	% (*)	Priority 4 902 km <sup>2</sup>	% (*)	Priority 5 661 km <sup>2</sup>	% (*)	Priority 6 8854 km <sup>2</sup>	Total 16098 km <sup>2</sup>
Area of land use categories (1992) in km <sup>2</sup>												
Forest	2884	90.88	0	0.00	1192	47.59	793	87.46	617	93.41	5548	11035
Paramo	10	0.33	0	0.00	0	0.00	0	0.00	0	0.00	0	10
Mangroves	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	40	40
Wetlands	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	728	728
Pasture	182	5.74	0	0.00	720	28.76	83	9.11	40	6.10	1815	2841
Agriculture	77	2.43	0	0.00	482	19.24	31	3.42	0	0.00	626	1216
Barren land	15	0.49	0	0.00	15	0.60	0	0.00	3	0.49	0	34
Urban areas	0	0.00	0	0.00	27	1.07	0	0.00	0	0.00	6	33
Water	0	0.00	0	0.00	69	2.74	0	0.00	0	0.00	35	104
na**	4	0.14	0	0.00	0	0.00	0	0.00	0	0.00	17	21
<b>d) Scarabaeinae</b>												
Areas of priority zones												
Total area	Priority 1 1593 km <sup>2</sup>	% (*)	Priority 2 0 km <sup>2</sup>	% (*)	Priority 3 259 km <sup>2</sup>	% (*)	Priority 4 7426 km <sup>2</sup>	% (*)	Priority 5 2360 km <sup>2</sup>	% (*)	Priority 6 2591 km <sup>2</sup>	Total 14229 km <sup>2</sup>
Area of land use categories (1992) in km <sup>2</sup>												
Forest	559	35.08	0	0.00	171	65.84	4896	65.93	2266	96.13	1279	9170
Paramo	0	0.00	0	0.00	0	0.00	0	0.00	8	0.32	0	8
Mangroves	0	0.00	0	0.00	0	0.00	35	0.47	0	0.00	0	35
Wetlands	0	0.00	0	0.00	0	0.00	731	9.84	0	0.00	97	828
Pasture	490	30.79	0	0.00	88	34.08	1290	17.37	29	1.22	1065	2963
Agriculture	437	27.43	0	0.00	0	0.08	408	5.49	51	2.15	129	1025
Barren land	15	0.95	0	0.00	0	0.00	15	0.20	0	0.00	4	34
Urban areas	23	1.46	0	0.00	0	0.00	4	0.05	0	0.00	0	28
Water	69	4.31	0	0.00	0	0.00	48	0.65	0	0.00	9	126
na**	0	0.00	0	0.00	0	0.00	0	0.00	4	0.18	0	5

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

(\*\*) Not available

richness for all plant taxa (second for the Scarabaeinae) and premontane wet forest (wf-P) for the Scarabaeinae. These life zones cover one of the largest geographical areas in the country, at altitudes ranging from 500 masl to 1 700 masl, and temperatures varying between 17 °C and 24 °C (Valerio, 2006). The upper limit of this category corresponds spatially with the frost line or with the so-called “coffee line” (Valerio, 2006).

The second life zone with the highest number of species is the tropical wet forest (wf-T) for the Araceae and Arecaceae and the lower montane rain forest (rf-LM) for the Bromeliaceae (Table 3). Tropical wet forest (wf-T) is present on both slopes. Its altitude ranges from 0 masl to 500 masl, and it has an average temperature above 24 °C (Valerio, 2006). The tropical wet forest (wf-T) is

generally considered to be the most species rich ecosystem in Costa Rica (Fogden and Fogden, 1997; Valerio, 1999); however, this was not the case for the present study. These results also confirm that the dry Pacific Northwest is not a species-rich area for the studied groups, although some groups, such as legumes and cacti, which are more adapted to drier climates, are actually highly diversified in this environment (Valerio, 1999; Lomolino et al., 2006).

*Life zones with highest overall endemics richness:* Considering the overall number of endemics (Table 3), we arrived, not surprisingly, to an identical result as the previous analysis. The premontane rain forest (rf-P) is the life zone with the highest total endemics richness for all plant taxa (second for the Scarabaeinae) and premontane wet forest (wf-P) for the Scarabaeinae. The premontane rain forest (rf-P) is present on the Pacific, as well as on the Caribbean slopes, and although Valerio (2006) indicates that few endemic species are present in this forest type, the Araceae and Arecaceae on the Talamanca mountain range (Fig. 4a-b), and the Bromeliaceae on the Tilarán mountain range (Fig. 4c), show here their highest levels of endemism, thus supporting Obando's (2002) conclusion that the cloud forest is the most endemics-rich ecosystem of Costa Rica.

As before, the second life zone with the highest number of endemics is the tropical wet forest (wf-T) for the Araceae and Arecaceae and the lower montane rain forest (rf-LM) for the Bromeliaceae.

*Number of local and regional endemics:* Regarding the percentage of endemics (Table 4), local (Costa Rica) and regional (Nicaragua-Costa Rica-Panama) values are fairly high, as compared to the local (12%) and regional (28%) endemism that Savage (2002) reported for the herpetofauna of Costa Rica, which was considered to be the group with the highest endemism for the country (Obando, 2002). These figures also compare well with the estimates that Obando (2002) established for plant endemism (12%) in Costa Rica and plant (30%) and insect (18%) endemism on Cocos Island. Mammals and birds on the contrary present low values of endemism of 0.8% and 2.5%, respectively, according to Obando (2002), being this one reason for not developing a conservation analysis using only these groups.

The results also indicate that many endemic species are shared with Panama. These results seem to suggest that the use of insect and plants in particular, can give a much more detailed picture of areas of endemism than can be obtained by the sole use of vertebrates, as has been the case lately. These groups should be used as often as possible for conservation studies.

**Table 4.** Percentages of local and regional endemism

	Number	%
<b>Araceae</b>		
Total species	229	100
Non-endemic species	116	51
Endemic species	113	49
Exclusively Costa Rica	36	15
Shared with Panama	58	25
Shared with Nicaragua	5	3
Shared with Nicaragua and Panama	14	6
<b>Arecaceae</b>	Number	%
Total species	107	100
Non-endemic species	57	54
Endemic species	50	46
Exclusively Costa Rica	21	19
Shared with Panama	19	18
Shared with Nicaragua	2	2
Shared with Nicaragua and Panama	8	7
<b>Bromeliaceae</b>	Number	%
Total species	187	100
Non-endemic species	107	57
Endemic species	80	43
Exclusively Costa Rica	40	21
Shared with Panama	39	20
Shared with Nicaragua	2	0.5
Shared with Nicaragua and Panama	4	1.5
<b>Scarabaeinae</b>	Number	%
Total species	177	100
Non-endemic species	109	62
Endemic species	68	38
Exclusively Costa Rica	32	18
Shared with Panama	25	14
Shared with Nicaragua	5	3
Shared with Nicaragua and Panama	6	3

## Discussion

*Representativity of protected areas:* The representativity analysis indicates that a high number (Araceae 89%, Arecaceae 89%, Bromeliaceae 83%, and Scarabaeinae 95%) of the total species are already included by the established protected area system. A similar analysis concerning endemic species also shows the presence of high numbers (Araceae 86%, Arecaceae 80%, Bromeliaceae 80%, and Scarabaeinae 97%) in these protected areas. It is possible that the numbers for plants may be slightly underestimated, because the dung beetles have been more thoroughly collected (Araceae, 2 108 localities; Arecaceae, 1 410 localities; Bromeliaceae, 1 571 localities; Scarabaeinae, 2 869 localities). It can be argued that the representation of both species and endemics in protected areas is already high. However, this fact does not guarantee their safeguarding or viability in the long run, because a range collapse could still occur. The endemic population or the community, to which it pertains, could still be marginal or vulnerable to natural or human induced processes. At present we do not have the necessary information in order to establish the minimum required area to ensure species protection.

*Distribution of priority conservation areas:* Information taken from the maps, which relate species and endemic species richness with current conservation areas (Figs. 7a and 7b) represented a basis for a gap analysis, by means of a conservation priority map (Fig. 7c). Priority area 1 indicates congruence between the highest species richness (rank 5) and the highest endemics (rank 5) numbers. Three areas are defined in this category: the tropical wet forest (wf-T) along the northeastern border with Nicaragua and in the Osa Peninsula and the premontane wet forest (wf-P) along the Guanacaste, Tilarán and Central mountain ranges. Priority area 2 indicates the areas where the highest endemism level (rank 5) corresponds spatially with areas below the highest species richness level (rank <5). One area is defined in this category: the lower montane rain forest (rf-LM) on the Talamanca mountain range.

Priority area 1, the biggest zone of all, has 8 201 km<sup>2</sup> and has 35% of its area under protection. Even though these numbers could be interpreted as a false sense of security, actually, the tropical wet forest is reasonably protected as can be observed from Fig. 7b, especially the area of the Osa Peninsula; however, the premontane wet forest (1 593 km<sup>2</sup>), represented mainly by cloud forest, along the Guanacaste, Tilarán and Central mountain ranges, is protected, because only 13% of its area is under protection (Kohlmann et al., 2007). Priority area 2 is represented by a total of 2 278 km<sup>2</sup> and has the highest percentage under protection (81%). The best-protected area in terms of

surface area is represented by the Talamanca mountain range. Priority area 3 is the smallest area (259 km<sup>2</sup>) with 65% of its area under protection, while priority area 6 (4 519 km<sup>2</sup>) is the least protected category with 21%. All priority areas add up to 17 099 km<sup>2</sup>, of which 40% are under some kind of protection, which overall could be considered a number to be improved upon.

*Distribution of conflict areas:* The map showing the distribution of potential conservation conflicts (Fig. 7d) is an overlay of Figure 7c on a land-use map.

Ideally, most conservation effort should be devoted to increase the area under protection for priority area 1, although this might prove difficult. In principle, 60% of it is still forested and could therefore allow an increase in protected areas, whereas 19% is under pasture and 9% under agricultural use. However, most of the potential increase in protected areas is associated with the tropical wet forest of the Caribbean and Osa Peninsula lowlands (Fig. 7d). Again, the area located along the Guanacaste, Tilarán and Central mountain ranges faces a very different situation (Fig. 7d). This area has only 35% of its land forested whereas 31% and 27% are under pasture and agriculture use, respectively. Therefore, the area has very limited possibilities of increasing protection areas and great probabilities of being overrun by pastoral-agricultural activities (Kohlmann et al., 2007). It should be remembered that this area showed one of the highest rankings in species richness for Bromeliaceae (Fig. 3c) and Scarabaeinae (Fig. 3d) and endemism for the Scarabaeinae (Fig. 4d). This area can be considered as a true biodiversity hotspot for Costa Rica and should be paramount for the official conservation planners.

Priority area 2 still has 96% of its area as forest, so there is a great opportunity for taking effective protective action. This is actually the protected area with the highest amount of forested area and is mainly located in almost uninhabited areas on the higher reaches of the Talamanca mountain range, where already the biggest conservation area, the international La Amistad Park, is located. This area is also of great importance because it represents one of the highest rankings in species richness for Bromeliaceae (Fig. 3c) and in endemism for Araceae (Fig. 4a) and Bromeliaceae (Fig. 4c).

Overall, of the 17 099 km<sup>2</sup> identified as priority areas, 67.5% are still forested and therefore show a promise of an increase in protection. It is also clear from the data that pastureland activities emerge as probably the main threat to biodiversity conservation, because of their extension (18.5%) and proximity to the priority areas, whereas agriculture occupies the second place (7.2%), and urban areas represent only a very small threat (0.16%).

A forest cover analysis showed that during the 2000-

2005 period forest cover increased by 125 000 ha (2.4% of the national territory), especially in the Guanacaste Peninsula, while forest loss was in the order of 34 500 ha (Estado de la Nación, 2007). It is to be hoped that this trend may continue and contribute to the preservation of the Costa Rican biodiversity.

*Representativity and complementarity:* In the past, the majority of the species richness and endemism studies in Costa Rica have relied basically on vertebrate distribution analysis, especially birds and large vertebrates as indicators of human impacts on biodiversity, and more recently plants have also been employed for this purpose (Obando, 2002; SINAC, 2007a). Insects have not been prominent in these studies.

It is shown in this paper that a different and perhaps a much more refined picture can be gained by using 3 plant families and one dung beetle subfamily instead (Figs. 3-7). This analysis suggests the existence of 3 previously undetected areas of endemism (Fig. 7b) that had not been registered by the use of vertebrates. Although overlap between the different groups is nonrandom, it is not perfect, thus the need for analyzing as many taxonomic groups as possible. In this study, hotspots for species richness tended to overlap with hotspots of endemism (Fig. 7c), thus defining the different conservation priority zones generated by this study.

Costa Rica is perhaps the best-collected country in Central America, not only through the work of many foreign scientists, but lately through the important work done by the INBio (Obando, 2007). Still, some areas have been under collected, but the available information allows us to elucidate general patterns.

This analysis attempts to be a complementary representation and contribution to the excellent proposal presented by the National System of Conservation Areas of Costa Rica (Sistema Nacional de Áreas de Conservación (SINAC), 2007b). Such analysis, however, did follow a different conceptual and methodological approach by defining a conservation strategy oriented toward the necessity of representativity of selected species (plant and vertebrate species listed as endemic, red list and zero extinction), ecological systems and connectivity of core areas. The SINAC (2007b) thus proposed the undertaking of the project entitled "Propuesta de Ordenamiento Territorial para la Conservación de la Biodiversidad de Costa Rica" (Proposal of Territorial Ordination for the Conservation of Biodiversity in Costa Rica). The aim of the project is to maintain representative samples of the natural richness of the country, correlating them with productive activities of national or local importance that are conservation-compatible by supporting its conservation planning strategy mostly on a phytogeographic system

that would act as a biodiversity surrogate. In the specific case of the terrestrial environment the aim was to identify vegetation types that are not adequately represented by the present net of conservation areas.

However, a recent study by Rodrigues and Brooks (2007) suggests that the use of environmental data (forest types, vegetation systems, ecoregions, floristic regions, species assemblages, abiotic data) as biodiversity surrogates are substantially less effective than cross-taxon surrogates ("extent to which conservation planning based on complementary representation of species surrogates effectively represents target species", Rodrigues and Brooks, 2007: 719), where surrogacy is defined as the "extent to which conservation planning based on a particular set of biodiversity features (surrogates) effectively represents another set (targets)" (Rodrigues and Brooks, 2007:714).

Additionally, Pawar et al. (2007) carried out a very interesting conservation biogeography hierarchical analysis of cross-taxon distributional congruence in northeast India, using amphibians, reptiles, and birds from tropical rainforest sites. They found that life-history characteristics common to certain groups contribute to observed patterns of congruence. Pawar et al. (2007) also found that the analysis of biologically different subgroups can improve the resolution of congruence analysis by unveiling fine-scale differences between otherwise concordant groups, thus providing a better resolution even with single-group data. This congruence can then be used as a surrogate simplifying the processes of area prioritization and conservation. The present paper is thus a first attempt at aiming in this direction in Costa Rica and will hopefully shed some light on the urgent and necessary need for cross-taxon analyses and the prioritization of conservation areas.

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**Appendix 1.** Araceae species by Life Zone number, type, and endemism status in Costa Rica.

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Anthurium acutangulum</i>	10, 17, 19, 20, 25, 37, 43, 136, 161, 165, 210	mf-T, mf-T Prem, rf-P, wf-T, wf-T Prem	Not endemic
<i>Anthurium acutifolium</i>	160, 178, 183, 194, 210, 258, 270, 309, 317, 376, 386	mf-T, mf-T Prem, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
<i>Anthurium alatipedunculatum</i>	309, 374, 381, 386	wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Anthurium allicola</i>	136	wf-T Prem	Not endemic
<i>Anthurium angustispadix</i>	177, 192, 210, 225, 233, 240, 263, 269, 281, 358	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Anthurium antioceanum</i>	177	rf-LM	Endemic shared with Panama
<i>Anthurium austini-smithii</i>	17, 52, 54, 165	rf-LM, rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Anthurium bakeri</i>	2, 9, 10, 11, 13, 17, 24, 25, 37, 43, 51, 60, 136, 165, 194, 263, 269, 309, 374, 378, 381, 386	mf-T, rf-LM, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium bittneri</i>	177	rf-LM	Endemic of Costa Rica
<i>Anthurium bradeanum</i>	2, 17, 25, 42, 165	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Anthurium brenesii</i>	2, 11, 13, 20, 40, 43, 70	mf-T, mf-T Prem, rf-LM, rf-P, wf-P, wf-P rain	Endemic of Costa Rica
<i>Anthurium brownii</i>	9, 10, 11, 20, 25, 136, 194, 309	mf-T Prem, wf-P, wf-T, wf-T Prem	Not endemic
<i>Anthurium burgeri</i>	317	rf-P	Endemic of Costa Rica
<i>Anthurium caperatum</i>	43, 52, 165, 177, 204, 209, 210, 240	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
<i>Anthurium carnosum</i>	24, 177, 200, 209, 242, 269	rf-LM, rf-M, wf-LM	Endemic shared with Panama
<i>Anthurium clavatum</i>	177, 204	rf-LM, rf-P	Endemic of Costa Rica
<i>Anthurium clavigerum</i>	2, 9, 10, 17, 25, 43, 51, 136, 161, 165, 263, 309	mf-T, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium clidemioides</i>	17, 309	rf-LM, rf-M, wf-LM	Endemic shared with Panama
<i>Anthurium concinnatum</i>	70, 73, 99, 177, 200, 204, 216, 242	rf-LM, rf-M, rf-P, wf-LM	Endemic shared with Panama
<i>Anthurium consobrinum</i>	2, 9, 10, 11, 17, 25, 37, 52	mf-T, wf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Anthurium cotobrusii</i>	240, 281	rf-P, wf-P	Endemic shared with Panama
<i>Anthurium cubense</i>	2, 11, 80, 183, 186, 194	mf-T, wf-P, wf-P Basal, wf-T	Not endemic
<i>Anthurium cucullispatham</i>	11, 165	rf-P, wf-P	Endemic shared with Panama
<i>Anthurium cuspidatum</i>	10, 17, 25, 29, 42, 43, 51, 52, 136, 149, 165, 194, 204, 210, 240, 317	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Anthurium davidsoniae</i>	20, 165, 177, 204	mf-T Prem, rf-LM, rf-P	Endemic shared with Panama
<i>Anthurium durandii</i>	43, 165, 177, 194, 197, 203, 210, 240, 272, 309, 374, 386	rf-LM, rf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Anthurium dwyeri</i>	60	rf-P	Not endemic



<i>Anthurium erythrostachyum</i>	210	rf-P	Endemic shared with Panama
<i>Anthurium eximium</i>	183, 194, 210, 309, 317, 374, 386	rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Anthurium fatioense</i>	136, 149, 161, 165	mf-T, rf-P, wf-P, wf-T Prem	Endemic shared with Panama
<i>Anthurium flexile</i>	10, 11, 13, 17, 20, 40, 161, 176, 177, 183, 194, 309	mf-T, mf-T perhum, mf-T Prem, rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium formosum</i>	17, 51, 52, 60, 136, 149, 165, 177, 200, 204, 216	rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Anthurium friedrichsthali</i>	17, 37, 42, 54, 126, 136, 194, 203, 309	rf-LM, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium gracile</i>	2, 9, 17, 37, 51, 161, 167, 309, 380	mf-T, wf-P Basal, wf-T	Not endemic
<i>Anthurium hacumense</i>	183, 194, 210, 309, 375, 381	rf-P, wf-P Basal, wf-T	Not endemic
<i>Anthurium hoffmannii</i>	43, 54, 59, 165, 200, 210, 214, 225, 228, 237, 240, 251, 263, 269, 281, 374, 386	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Endemic shared with Panama
<i>Anthurium hornitense</i>	165	rf-P	Endemic shared with Panama
<i>Anthurium interruptum</i>	9, 10, 17, 19, 24, 25, 40, 43, 50, 136, 149, 309	mf-P, rf-LM, rf-P, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium kauthii</i>	51, 161	mf-T, wf-P Basal	Not endemic
<i>Anthurium lancifolium</i>	17, 136, 149, 161, 165, 169, 177, 204, 309, 317, 374, 386	mf-P, mf-T, rf-LM, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Anthurium lentii</i>	52, 60, 165, 177, 204, 216	rf-LM, rf-M, rf-P, wf-T Prem	Not endemic
<i>Anthurium limonense</i>	34	mf-T	Endemic of Costa Rica
<i>Anthurium llanense</i>	161, 165	mf-T, rf-P	Endemic shared with Panama
<i>Anthurium longispitatum</i>	177	rf-LM	Endemic shared with Panama
<i>Anthurium louisii</i>	165, 177	rf-LM, rf-P	Endemic of Costa Rica
<i>Anthurium michelii</i>	5, 11, 25, 29, 35, 40, 43, 54, 60, 165, 317, 386	rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Anthurium microspadix</i>	10, 11, 13, 19, 24, 29, 43, 54, 70, 73, 149, 162, 165, 177, 192, 200, 204, 209, 240, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Anthurium montevidense</i>	54	rf-LM	Endemic of Costa Rica
<i>Anthurium obtusilobum</i>	10, 11, 24, 25, 40, 43, 50, 60, 136, 139, 149, 165, 204	mf-P, rf-LM, rf-P, wf-P, wf-P rain, wf-T Prem	Not endemic
<i>Anthurium obtusum</i>	2, 10, 17, 34, 40, 42, 43, 67, 73, 136, 161, 183, 200, 263, 309, 386	mf-T, rf-P, wf-LM, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium ochranthum</i>	5, 9, 10, 13, 17, 20, 29, 43, 51, 120, 136, 183, 194, 263, 309, 374, 376	mf-T Prem, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium oerstedianum</i>	192, 194, 197, 203, 237, 240, 317, 386	rf-P, wf-P rain, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Anthurium ortegianum</i>	149	wf-P	Not endemic

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Anthurium pagazanum</i>	136, 165, 177	rf-LM, rf-P, wf-T Prem	Endemic shared with Panama
<i>Anthurium pallens</i>	70	rf-LM	Endemic shared with Panama
<i>Anthurium paludosum</i>	51, 161	mf-T, wf-P Basal	Not endemic
<i>Anthurium pandariforme</i>	11, 43, 54, 60, 149, 165	rf-LM, rf-P, wf-P	Not endemic
<i>Anthurium pentaphyllum</i>	17, 43, 51, 167, 210, 258, 309	mf-T, rf-P, wf-P Basal, wf-T	Not endemic
<i>Anthurium pittieri</i>	10, 11, 13, 19, 20, 24, 43, 54, 59, 70, 73, 194, 231, 240	mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Anthurium prolatum</i>	165, 177	rf-LM, rf-P	Endemic shared with Panama
<i>Anthurium propinquum</i>	60, 165	rf-P	Not endemic
<i>Anthurium protensum</i>	11, 54, 60, 70, 73, 75, 165, 177, 204	rf-LM, rf-P, wf-LM, wf-P	Endemic shared with Panama
<i>Anthurium ramonense</i>	2, 17, 19, 20, 25, 40, 43, 51, 54, 70, 149, 161, 165, 309	mf-T, mf-T Prem, rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Anthurium ranchoanum</i>	11, 54, 59, 70, 165, 177, 200, 216	rf-LM, rf-M, rf-P, wf-LM, wf-P	Endemic shared with Panama
<i>Anthurium ravenii</i>	17, 136, 167, 183, 194, 309, 381, 386	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Anthurium salvinii</i>	11, 13, 43, 52, 59, 60, 73, 186, 240	rf-P, wf-LM, wf-P, wf-P Basal, wf-T Prem	Not endemic
<i>Anthurium scandens</i>	2, 10, 11, 13, 17, 20, 43, 54, 59, 70, 73, 136, 149, 158, 165, 177, 192, 200, 209, 210, 242, 269, 309	mf-LM, mf-T, mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Anthurium scherzerianum</i>	5, 11, 25, 29, 60, 136, 165, 177, 204	rf-LM, rf-P, wf-P, wf-P Basal, wf-T Prem	Endemic of Costa Rica
<i>Anthurium schottianum</i>	43	rf-P	Endemic of Costa Rica
<i>Anthurium seibertii</i>	177, 200, 225, 269	rf-LM, wf-LM	Endemic shared with Panama
<i>Anthurium spathiphyllum</i>	17, 24, 42	rf-LM, wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
<i>Anthurium spectabile</i>	60, 136	rf-P, wf-T Prem	Endemic of Costa Rica
<i>Anthurium standleyi</i>	73, 127, 162	mf-P, wf-LM, wf-P	Endemic of Costa Rica
<i>Anthurium subsignatum</i>	17, 37, 51, 136	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Anthurium tenerum</i>	43	rf-P	Not endemic
<i>Anthurium tibense</i>	136, 165	rf-P, wf-T Prem	Endemic shared with Panama
<i>Anthurium testaceum</i>	9, 11, 13, 54, 70, 177, 240, 263, 269	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T	Not endemic
<i>Anthurium tilaranense</i>	10, 11, 13, 19, 20, 24, 40, 43, 52, 149	mf-T Prem, rf-LM, rf-P, wf-P, wf-P rain, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Anthurium tonduzii</i>	165, 210, 240	rf-P	Not endemic
<i>Anthurium trisectum</i>	17	wf-T	Not endemic
<i>Anthurium upalaense</i>	2, 17, 37, 126, 136, 161, 165, 167	mf-T, rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Anthurium utleyorum</i>	11, 40, 43, 54, 59, 70	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic of Costa Rica
<i>Anthurium validifolium</i>	263, 269, 281	wf-LM, wf-P, wf-P rain	Endemic shared with Panama

<i>Anthurium watermaliense</i>	51, 54, 60, 70, 136, 149, 165, 177	rf-LM, rf-P, wf-P, wf-P Basal, wf-T Prem	Endemic shared with Panama
<i>Anthurium wendlingeri</i>	52, 120, 136, 165, 177	rf-LM, rf-P, wf-P rain, wf-T Prem	Not endemic
<i>Caladium bicolor</i>	17, 42, 127, 194, 270	mf-P, wf-P Basal, wf-T	Not endemic
<i>Chlorospatha croatiana</i>	43, 136	rf-P, wf-T Prem	Not endemic
<i>Dieffenbachia aurantiaca</i>	272, 309	wf-T, wf-T Prem	Endemic shared with Panama
<i>Dieffenbachia bechiana</i>	17	wf-T	Endemic shared with Panama
<i>Dieffenbachia concinna</i>	17, 42, 309, 376	wf-P Basal, wf-T	Endemic of Costa Rica
<i>Dieffenbachia grayumiana</i>	17, 42	wf-P Basal, wf-T	Endemic of Costa Rica
<i>Dieffenbachia hammelii</i>	17, 42, 60	rf-P, wf-P Basal, wf-T	Endemic shared with Nicaragua
<i>Dieffenbachia longispatha</i>	17, 60, 136	rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Dieffenbachia oerstedii</i>	5, 10, 11, 13, 20, 29, 40, 43, 60, 80, 139, 183, 186, 197, 210, 240, 317	mf-T, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Dieffenbachia tonduzii</i>	5	wf-P Basal	Not endemic
<i>Dracontium gigas</i>	17, 42	wf-P Basal, wf-T	Endemic shared with Nicaragua
<i>Dracontium pittieri</i>	176, 194, 203, 309	mf-T perhum, wf-P rain, wf-T	Endemic of Costa Rica
<i>Dracontium soconuscum</i>	183	wf-P Basal	Not endemic
<i>Dracontium spruceanum</i>	51, 136, 309	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Heteropsis oblongifolia</i>	9, 10, 17, 37, 42, 136, 161, 210, 272, 309	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Homalomena erythropus</i>	309	wf-T	Not endemic
<i>Homalomena hammelii</i>	17, 52	wf-T, wf-T Prem	Endemic of Costa Rica
<i>Homalomena picturata</i>	309	wf-T	Not endemic
<i>Homalomena wendlandii</i>	17, 126, 149, 165, 270, 309	rf-P, wf-P, wf-P Basal, wf-T	Not endemic
<i>Monstera adansonii</i>	2, 11, 20, 68, 162, 171, 186, 210, 248, 309	mf-P Basal, mf-T, mf-T d, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T	Not endemic
<i>Monstera buseyi</i>	11, 19, 43, 60, 183, 197, 203, 309	rf-P, wf-P, wf-P Basal, wf-P rain, wf-T	Endemic shared with Panama
<i>Monstera costaricensis</i>	17, 161, 309	mf-T, wf-T	Endemic of Costa Rica
<i>Monstera deliciosa</i>	43, 52, 60, 149, 165, 177, 210, 242, 269, 281	rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-T Prem	Not endemic
<i>Monstera dissecta</i>	11, 17, 37, 40, 54, 73, 309	rf-LM, wf-LM, wf-P, wf-P rain, wf-T	Not endemic
<i>Monstera dubia</i>	309	wf-T	Not endemic
<i>Monstera epipremnoides</i>	13, 192, 200, 209	rf-P, wf-LM	Endemic of Costa Rica
<i>Monstera filamentosa</i>	17, 136, 309	wf-T, wf-T Prem	Not endemic
<i>Monstera glaucescens</i>	17, 42, 165	rf-P, wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
<i>Monstera lentii</i>	165, 177	rf-LM, rf-P	Endemic shared with Panama

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Monstera luteymlii</i>	25	wf-T Prem	Endemic of Costa Rica
<i>Monstera membranacea</i>	183, 194, 309	wf-P Basal, wf-T	Endemic shared with Panama
<i>Monstera molinae</i>	10	wf-T Prem	Endemic shared with Panama
<i>Monstera obliqua</i>	161	mf-T	Not endemic
<i>Monstera oreophila</i>	11, 13, 54, 59, 73, 165, 177, 216, 225, 263	rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Monstera pinnatipartita</i>	186, 194, 197, 309, 317	rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Monstera pittieri</i>	17, 165, 183, 203, 309, 386	rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Monstera punctulata</i>	263, 281, 309	wf-P, wf-P rain, wf-T	Not endemic
<i>Monstera spruceana</i>	11, 17, 51	wf-P, wf-P Basal, wf-T	Not endemic
<i>Monstera standleyana</i>	17, 43, 149	rf-P, wf-P, wf-T	Endemic shared with Nicaragua and Panama
<i>Monstera tenuis</i>	13, 17, 20, 43, 177, 194	mf-T Prem, rf-LM, rf-P, wf-T	Endemic shared with Nicaragua and Panama
<i>Monstera tuberculata</i>	2, 5, 10, 11, 17, 161	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Montrichardia arborescens</i>	37, 42	wf-P Basal, wf-T	Not endemic
<i>Philodendron alliodorum</i>	17, 42, 309, 381	wf-P Basal, wf-T	Not endemic
<i>Philodendron alticola</i>	177	rf-LM	Endemic shared with Panama
<i>Philodendron angustilobum</i>	42, 183	wf-P Basal	Not endemic
<i>Philodendron anisotomum</i>	40, 43, 54, 60, 73, 179, 200, 210, 240, 269	mf-LM, rf-LM, rf-P, wf-LM, wf-P rain	Not endemic
<i>Philodendron aromaticum</i>	17	wf-T	Endemic of Costa Rica
<i>Philodendron aurantiifolium</i>	17, 42, 120, 136, 183, 281, 309	wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron auriculatum</i>	194, 210, 309	rf-P, wf-T	Endemic of Costa Rica
<i>Philodendron bakeri</i>	19, 43	rf-P	Endemic shared with Nicaragua and Panama
<i>Philodendron brenesii</i>	11, 24, 40, 54, 73, 165, 177, 209	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Philodendron brevispathum</i>	17, 37, 161	mf-T, wf-T	Not endemic
<i>Philodendron brunneicaule</i>	43	rf-P	Endemic shared with Panama
<i>Philodendron burgeri</i>	162, 309, 376	wf-P, wf-P Basal, wf-T	Endemic shared with Panama
<i>Philodendron chirripoense</i>	240	rf-P	Endemic of Costa Rica
<i>Philodendron cotobrusense</i>	281	wf-P	Endemic of Costa Rica
<i>Philodendron cotonense</i>	263, 269, 281, 317	rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Philodendron crassispatum</i>	177, 204, 242	rf-LM, rf-M, rf-P	Endemic shared with Panama
<i>Philodendron cretosum</i>	10, 17, 25, 42	wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama

<i>Philodendron davidsonii</i>	17		wf-T	Endemic shared with Panama
<i>Philodendron dodsonii</i>	120, 210, 263		rf-P, wf-P rain	Not endemic
<i>Philodendron dominicalense</i>	200		wf-LM	Endemic of Costa Rica
<i>Philodendron ensifolium</i>	10, 17, 136		wf-T, wf-T Prem	Not endemic
<i>Philodendron findens</i>	10, 43, 60, 149		rf-P, wf-P, wf-T Prem	Endemic shared with Panama
<i>Philodendron fragrantissimum</i>	161, 309		mf-T, wf-T	Not endemic
<i>Philodendron grandipes</i>	17, 136, 194, 309, 317, 386		rf-P, wf-T, wf-T Prem	Not endemic
<i>Philodendron grayumii</i>	51, 161		mf-T, wf-P Basal	Endemic shared with Panama
<i>Philodendron hederaceum</i>	183, 251, 309		wf-P, wf-P Basal, wf-T	Not endemic
<i>Philodendron herbaceum</i>	17, 42, 52, 161		mf-T, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Philodendron inaequilaterum</i>	17, 42, 43, 149, 166, 186, 309, 376		mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T	Not endemic
<i>Philodendron jacquimii</i>	3, 11, 59, 68, 80, 160, 183, 186, 251		mf-P Basal, mf-T, mf-T d, mf-T Prem, wf-LM, wf-P, wf-P Basal	Not endemic
<i>Philodendron jodavisanianum</i>	25, 197, 309, 386		wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron kanappiae</i>	210		rf-P	Endemic shared with Panama
<i>Philodendron lentii</i>	34, 149		mf-T, wf-P	Endemic shared with Nicaragua and Panama
<i>Philodendron ligulatum</i>	17		wf-T	Not endemic
<i>Philodendron microstictum</i>	194, 210, 309, 376		rf-P, wf-P Basal, wf-T	Endemic of Costa Rica
<i>Philodendron opacum</i>	29, 42, 203, 309		rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Philodendron platypetiolatum</i>	9, 17, 52, 60		rf-P, wf-T, wf-T Prem	Not endemic
<i>Philodendron popenoei</i>	194, 270, 309, 317		rf-P, wf-P Basal, wf-T	Not endemic
<i>Philodendron pterotum</i>	194, 197, 309		wf-P rain, wf-T	Endemic shared with Nicaragua and Panama
<i>Philodendron purpureoviride</i>	10, 269, 272, 281, 309, 317, 386		rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Philodendron radiatum</i>	17, 37		wf-T	Not endemic
<i>Philodendron rayanum</i>	11, 17, 60, 309		rf-P, wf-P, wf-T	Endemic shared with Panama
<i>Philodendron rhodoaxis</i>	17, 42, 43, 60, 136, 194, 203, 228, 309		rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron rigidifolium</i>	17, 42, 60, 136, 167, 309		rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Philodendron rojasianum</i>	237		rf-P	Not endemic
<i>Philodendron rothschuhianum</i>	10, 11, 37, 42, 43, 60, 161, 165, 281		mf-T, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Philodendron sagittifolium</i>	2, 37, 86, 149, 194, 210, 263, 281, 309, 374, 376		mf-T, rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron scalarinerve</i>	17		wf-T	Not endemic

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Philodendron schottianum</i>	200, 269	wf-LM	Endemic shared with Panama
<i>Philodendron schottii</i>	9, 10, 51	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Philodendron squamicaule</i>	52	wf-T Prem	Not endemic
<i>Philodendron standleyi</i>	43, 59, 60, 149, 204, 225, 317	rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Philodendron stramicicaule</i>	11, 13	rf-P, wf-P	Not endemic
<i>Philodendron strictum</i>	149, 197, 204, 210	rf-P, wf-P, wf-P rain	Not endemic
<i>Philodendron sulcatum</i>	17, 42, 43, 60, 166, 194, 228, 309	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T	Not endemic
<i>Philodendron sulcicaule</i>	51	wf-P Basal	Endemic shared with Panama
<i>Philodendron tenne</i>	5, 10, 17, 19, 40, 309, 374	rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron thalassicum</i>	43, 54, 70, 165, 177, 200, 204	rf-LM, rf-P, wf-LM	Endemic shared with Panama
<i>Philodendron tripartitum</i>	10, 11, 17, 25, 29, 43, 60, 186, 197, 210, 225, 263, 309, 374	rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron tuerckheimii</i>	52, 60, 120, 309	rf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Philodendron verrucosum</i>	29, 43, 165, 177, 210, 240	rf-LM, rf-P	Not endemic
<i>Philodendron wendlandii</i>	17, 51, 136	wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Philodendron wilburii</i>	17, 29, 43, 75, 177, 194, 210, 270, 309	rf-LM, rf-P, wf-LM, wf-P Basal, wf-T	Endemic shared with Panama
<i>Pistia stratiotes</i>	2, 3, 11, 17, 64, 183, 226, 309	mf-P Basal, mf-T, mf-T d, mf-T perthum, wf-P, wf-P Basal, wf-T	Not endemic
<i>Rhodospatha moritziana</i>	51, 120, 136, 149	wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Rhodospatha pellucida</i>	17, 42, 52, 126	wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Rhodospatha wendlandii</i>	11, 177, 183, 216, 269, 309, 374	rf-LM, rf-M, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Spathiphyllum atrovirens</i>	11, 20, 43, 86, 269, 281	mf-T Prem, rf-LM, rf-P, wf-LM, wf-P	Endemic shared with Panama
<i>Spathiphyllum friedrichsthali</i>	2, 17, 51, 161	mf-T, wf-P Basal, wf-T	Not endemic
<i>Spathiphyllum fulvovirens</i>	17, 43, 60	rf-P, wf-T	Not endemic
<i>Spathiphyllum laeve</i>	17, 25, 29, 42, 43, 51, 139, 165	rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Spathiphyllum montanum</i>	13, 20, 70, 165, 177, 192, 240, 281	mf-T Prem, rf-LM, rf-P, wf-P	Endemic shared with Panama
<i>Spathiphyllum phrynifolium</i>	11, 13, 51, 52, 194, 197, 203, 237, 309	rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Spathiphyllum silvicola</i>	194, 205, 309, 374, 381, 386	wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Spathiphyllum wendlandii</i>	51, 136, 167, 183, 194, 210, 309	rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
<i>Stenospermation angustifolium</i>	9, 10, 17, 19, 43, 51, 52, 136, 161, 162, 183, 194, 240, 309, 374, 386	mf-T, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Stenospermation majus</i>	25	wf-T Prem	Endemic of Costa Rica

<i>Stenospermatum marantifolium</i>	5, 10, 11, 25, 43, 52, 60, 120, 166, 231, 269, 309	mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Stenospermatum robustum</i>	43, 60, 136, 309	rf-P, wf-T, wf-T Prem	Not endemic
<i>Stenospermatum sessile</i>	11, 40, 43, 59, 70, 165, 177, 179	mf-LM, rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
<i>Stenospermatum spruceanum</i>	25, 43, 165, 177	rf-LM, rf-P, wf-T Prem	Not endemic
<i>Syngonium angustatum</i>	2, 3	mf-P Basal, mf-T	Not endemic
<i>Syngonium armigerum</i>	136	wf-T Prem	Endemic of Costa Rica
<i>Syngonium castroi</i>	309	wf-T	Endemic of Costa Rica
<i>Syngonium hastiferum</i>	309	wf-T	Endemic of Costa Rica
<i>Syngonium hoffmannii</i>	11, 13, 40, 43, 73, 136, 177, 240, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T Prem	Endemic shared with Panama
<i>Syngonium laterinervium</i>	309, 386	wf-T, wf-T Prem	Endemic shared with Panama
<i>Syngonium macrophyllum</i>	9, 17, 60, 309	rf-P, wf-T	Not endemic
<i>Syngonium mauroanum</i>	251	wf-P	Endemic shared with Panama
<i>Syngonium oduberi</i>	309, 317, 376	rf-P, wf-P Basal, wf-T	Endemic of Costa Rica
<i>Syngonium peliocladum</i>	17, 51	wf-P Basal, wf-T	Endemic shared with Panama
<i>Syngonium podophyllum</i>	10, 11, 17, 136, 186, 194, 203, 309	wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Syngonium rayi</i>	17, 210	rf-P, wf-T	Endemic shared with Panama
<i>Syngonium schottianum</i>	9, 17, 42, 43	rf-P, wf-P Basal, wf-T	Not endemic
<i>Syngonium standleyanum</i>	43	rf-P	Endemic shared with Nicaragua
<i>Syngonium triphyllum</i>	2, 37, 43, 51, 161, 183, 194, 197, 309, 376	mf-T, rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Syngonium wendlandii</i>	162, 183, 203, 212	wf-P, wf-P Basal, wf-P rain	Endemic of Costa Rica
<i>Urospatha grandis</i>	17, 42, 161	mf-T, wf-P Basal, wf-T	Not endemic
<i>Xanthosoma dealbatum</i>	183, 194, 263, 309	wf-P Basal, wf-P rain, wf-T	Endemic of Costa Rica
<i>Xanthosoma mexicanum</i>	11, 47, 68, 80, 91, 119, 127, 171, 183, 258	mf-P, mf-P Basal, mf-T, mf-T d, mf-T perthum, wf-P, wf-P Basal	Not endemic
<i>Xanthosoma robustum</i>	374	wf-T Prem	Not endemic
<i>Xanthosoma undipes</i>	11, 60, 149, 165, 177, 263, 309	rf-LM, rf-P, wf-P, wf-P rain, wf-T	Not endemic
<i>Xanthosoma wendlandii</i>	3, 11, 20, 47, 80, 183, 197, 203	mf-P Basal, mf-T, mf-T Prem, wf-P Basal, wf-P rain	Not endemic

**Appendix 2.** Arecaceae species by Life Zone number, type, and endemism status in Costa Rica

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Acoelorrhaphe wrightii</i>	2	mf-T	Not endemic
<i>Acrocomia aculeata</i>	18, 68, 190, 376	df-T, mf-T, wf-P Basal	Not endemic
<i>Aiphanes aculeata</i>	309	wf-T	Not endemic
<i>Aiphanes hirsuta</i>	317	rf-P	Not endemic
<i>Asterogyne maritima</i>	9, 10, 17, 34, 37, 42, 52, 60, 161, 194, 309, 373, 374, 386	mf-T, rf-P, wf-P Basal, wf-T Prem	Not endemic
<i>Astrocaryum alatum</i>	4, 10, 161, 167, 183	mf-T, mf-T perhum, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Astrocaryum confertum</i>	42	wf-P Basal	Endemic shared with Panama
<i>Astrocaryum standleyanum</i>	161, 219, 376	mf-T, wf-P Basal	Not endemic
<i>Attalea butyracea</i>	3, 80, 183, 203, 253	mf-P Basal, mf-T, wf-P Basal, wf-P rain	Not endemic
<i>Bactris ana-juliae</i>	210	rf-P	Endemic of Costa Rica
<i>Bactris baileyana</i>	171, 183, 194, 309, 376	mf-P Basal, wf-P Basal, wf-T	Endemic shared with Panama
<i>Bactris caudata</i>	165, 166	mf-T Prem, rf-P	Endemic shared with Nicaragua and Panama
<i>Bactris coloradensis</i>	17, 52, 136	wf-T, wf-T Prem	Not endemic
<i>Bactris dianaura</i>	10, 11, 13, 20, 59, 177, 204, 210, 240	mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-T Prem	Endemic shared with Panama
<i>Bactris gasipaes</i>	161, 309	mf-T, wf-T	Not endemic
<i>Bactris glandulosa</i>	166, 183, 194, 197, 210, 263, 272, 309, 317	mf-T Prem, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Bactris gracilior</i>	9, 10, 17, 42, 52, 136, 161, 165	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Bactris grayumii</i>	10, 17, 21, 37	wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Bactris guineensis</i>	3, 171	mf-P Basal	Not endemic
<i>Bactris herreraana</i>	194, 309, 386	wf-T, wf-T Prem	Endemic of Costa Rica
<i>Bactris hondurensis</i>	2, 5, 10, 17, 21, 29, 37, 40, 42, 43, 51, 52, 60, 136, 161, 167, 183, 194, 203, 309	mf-T, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Bactris longiseta</i>	4, 9, 17	mf-T perhum, wf-T	Endemic of Costa Rica
<i>Bactris major</i>	2, 3, 17, 80, 183, 309, 376, 384	mf-P Basal, mf-T, mf-T perhum, wf-P Basal, wf-T	Not endemic
<i>Bactris maraja</i>	161, 309	mf-T, wf-T	Not endemic
<i>Bactris militaris</i>	17, 161, 270	mf-T, wf-P Basal, wf-T	Endemic shared with Panama
<i>Bactris polystachya</i>	161	mf-T	Endemic of Costa Rica
<i>Calyptrogyne condensata</i>	161	mf-T	Endemic shared with Panama



<i>Calyptrogyne ghiesbreghtiana</i>	10, 11, 13, 17, 20, 21, 25, 37, 43, 52, 59, 60, 161, 177, 309, 317, 374, 375	mf-T, mf-T Prem, rf-LM, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Calyptrogyne herrerae</i>	165	rf-P	Endemic of Costa Rica
<i>Calyptrogyne trichostachys</i>	5, 9, 10, 11, 19, 29, 43, 165	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Chamaedorea amabilis</i>	43, 52, 136, 149	rf-P, wf-P, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea anemophila</i>	10, 165	rf-P, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea binderi</i>	194, 263	wf-P rain, wf-T	Endemic of Costa Rica
<i>Chamaedorea brachyclada</i>	194, 237, 240, 263, 309, 317, 374	rf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea costaricana</i>	11, 13, 54, 70, 73, 149, 160, 177, 204, 216, 225, 269, 281, 358	mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P	Not endemic
<i>Chamaedorea crucensis</i>	177, 225, 269, 281	rf-LM, wf-LM, wf-P	Endemic of Costa Rica
<i>Chamaedorea dammeriana</i>	9, 10, 11, 13, 17, 19, 24, 25, 29, 35, 40, 43, 51, 60, 136, 161, 165, 167, 183, 192, 194, 197, 203, 219, 309, 386	mf-T, rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Chamaedorea deckeriana</i>	10, 11, 17, 25, 42, 43, 52, 136, 161, 177, 194, 309, 374	mf-T, rf-LM, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Chamaedorea geonomiformis</i>	60, 149, 165, 225, 309, 374	rf-LM, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Chamaedorea graminifolia</i>	177	rf-LM	Endemic shared with Nicaragua
<i>Chamaedorea hodellii</i>	60, 70, 165, 177, 204	rf-LM, rf-P	Endemic of Costa Rica
<i>Chamaedorea incurvata</i>	225	rf-LM	Endemic of Costa Rica
<i>Chamaedorea lucidifrons</i>	17, 25, 42, 43, 52, 136, 161, 167	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Chamaedorea macrospadix</i>	11, 20, 43, 54, 59, 99, 120, 127, 136, 161, 162, 165, 166, 177, 183, 194, 197, 203, 204, 210, 236, 263, 272, 281, 309, 374	mf-P, mf-T, mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea matae</i>	183, 194, 203, 309, 374, 386	wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea palmeriana</i>	60, 70, 136, 165, 177	rf-LM, rf-P, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea parvifolia</i>	54, 59, 70, 200, 209, 216, 269	rf-LM, rf-M, wf-LM	Endemic of Costa Rica
<i>Chamaedorea pinnatifrons</i>	2, 5, 10, 11, 13, 17, 25, 42, 43, 47, 51, 52, 54, 59, 60, 70, 73, 75, 120, 126, 136, 149, 161, 162, 177, 192, 194, 200, 204, 210, 216, 225, 240, 263, 269, 281, 317	mf-T, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Chamaedorea piscifolia</i>	210	rf-P	Endemic of Costa Rica
<i>Chamaedorea pittieri</i>	200, 216	rf-M, wf-LM	Endemic shared with Panama
<i>Chamaedorea pumila</i>	10, 19, 25, 26, 29, 40, 43, 52, 60, 149, 177, 237, 309, 317, 374	rf-LM, rf-P, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Chamaedorea pygmaea</i>	177, 225, 269	rf-LM, wf-LM	Not endemic
<i>Chamaedorea robertii</i>	43, 60	rf-P	Endemic shared with Panama

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Chamaedorea rosbeltiae</i>	165	rf-P	Endemic of Costa Rica
<i>Chamaedorea rossteniorum</i>	210	rf-P	Endemic shared with Panama
<i>Chamaedorea scheryi</i>	43, 52, 60, 70, 74, 164, 177	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea stenocarpa</i>	317	rf-P	Not endemic
<i>Chamaedorea tepelilote</i>	9, 10, 11, 17, 42, 43, 51, 52, 54, 60, 80, 120, 127, 136, 161, 162, 166, 167, 177, 183, 186, 204, 309	mf-P, mf-T, mf-T Prem, rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Chamaedorea undulatifolia</i>	10, 25, 29, 54, 70, 177	rf-LM, rf-P, wf-T Prem	Endemic of Costa Rica
<i>Chamaedorea warscewiczii</i>	10, 11, 29, 43, 60, 136, 200, 240	rf-P, wf-LM, wf-P, wf-T Prem	Endemic shared with Panama
<i>Chamaedorea zamorae</i>	183, 194, 197, 203, 225, 309, 374	rf-LM, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Colpothrinax aphanope</i>	165	rf-P	Endemic shared with Nicaragua and Panama
<i>Colpothrinax cookii</i>	136, 165	rf-P, wf-T Prem	Not endemic
<i>Cryosophila grayumii</i>	20, 176, 183, 210, 270, 309	mf-T perhum, mf-T Prem, rf-P, wf-P Basal, wf-T	Endemic of Costa Rica
<i>Cryosophila guagara</i>	167, 194, 309, 372	wf-P Basal, wf-T	Endemic shared with Panama
<i>Cryosophila warscewiczii</i>	2, 10, 17, 42, 52, 127, 136, 167	mf-P, mf-T, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Desmoncus costaricensis</i>	80, 136, 161, 194, 309	mf-T, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Desmoncus schippii</i>	10, 17, 37, 42, 161, 375	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Desmoncus stans</i>	263, 309, 386	wf-P rain, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Elaeis oleifera</i>	10, 161, 171, 194	mf-P Basal, mf-T, wf-T, wf-T Prem	Not endemic
<i>Euterpe precatoria</i>	5, 17, 25, 52, 60, 309, 373	rf-P, rf-P Basal, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Geonoma brenesii</i>	109	wf-T Prem	Not endemic
<i>Geonoma congesta</i>	9, 10, 17, 25, 37, 42, 51, 52, 161, 165, 194, 309, 375	wf-P Basal	Endemic of Costa Rica
<i>Geonoma cuneata</i>	5, 10, 17, 19, 25, 43, 51, 52, 54, 59, 127, 136, 161, 165, 176, 183, 194, 203, 210, 225, 269, 309, 386	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Geonoma deversa</i>	2, 9, 10, 13, 17, 60, 80, 194, 309, 374, 376, 386	wf-T Prem	Not endemic
<i>Geonoma edulis</i>	10, 11, 13, 24, 54, 70, 177, 200, 216, 269	rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-T Prem	Not endemic
<i>Geonoma epetiolata</i>	52, 60	rf-P, wf-T Prem	Endemic shared with Panama
<i>Geonoma ferruginea</i>	5, 10, 11, 13, 25, 40, 43, 52, 60, 70, 149, 162, 165	rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T Prem	Not endemic
<i>Geonoma hoffmanniana</i>	11, 54, 62, 70, 149, 177, 200, 216, 225, 269	mf-P, rf-LM, rf-M, wf-LM, wf-P	Not endemic
<i>Geonoma interrupta</i>	5, 10, 11, 17, 24, 37, 51, 52, 70, 161, 183, 194, 200, 309, 386	mf-T, rf-LM, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic

<i>Geonoma longevaginata</i>	17, 37, 42, 136, 161, 309, 373, 375	mf-T, rf-P, rf-P Basal, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Geonoma monospatha</i>	188, 192	mf-P, rf-P	Endemic shared with Panama
<i>Geonoma oxycarpa</i>	5, 11, 13, 17, 25, 43, 52, 60, 165, 166, 197, 309	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Geonoma procumbens</i>	10, 17, 19	rf-P Basal, wf-T	Not endemic
<i>Geonoma scoparia</i>	309, 373	rf-LM, rf-P	Endemic of Costa Rica
<i>Geonoma talamancana</i>	165, 177	rf-P, wf-P rain	Endemic of Costa Rica
<i>Hyospatha elegans</i>	60, 120, 165	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Iriartea deltoidea</i>	10, 43, 52, 60, 161, 309, 376, 386	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Manicaria saccifera</i>	37	wf-T	Not endemic
<i>Neonicholsonia watsonii</i>	10, 19, 24, 25, 43, 60, 176, 183, 194, 197, 270, 309, 373, 374	mf-T perhum, rf-LM, rf-P, rf-P Basal, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Oenocarpus mapora</i>	194, 309	wf-T	Not endemic
<i>Pholidostachys pulchra</i>	17, 52, 60, 127, 381	mf-P, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Prestoea acuminata</i>	60, 67, 70, 165, 177, 200, 269, 358	rf-LM, rf-P, wf-LM, wf-T Prem	Not endemic
<i>Prestoea decurrens</i>	10, 17, 19, 25, 42, 43, 52, 70, 161, 203, 309, 374	mf-T, rf-LM, rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Prestoea ensiformis</i>	109, 194	wf-P Basal, wf-T	Not endemic
<i>Prestoea longepetiolata</i>	11, 20, 43, 60, 165, 169, 177, 225, 242, 269	mf-P, mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P	Not endemic
<i>Prestoea schultzeana</i>	309, 317	rf-P, wf-T	Not endemic
<i>Raphia taedigera</i>	37, 309, 373	rf-P Basal, wf-T	Not endemic
<i>Reinhardtia gracilis</i>	9, 10, 11, 17, 24, 25, 43, 51, 52, 136, 139, 165	rf-LM, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Reinhardtia koschnyan</i>	4, 34	mf-T, mf-T perhum	Not endemic
<i>Reinhardtia latisecta</i>	9, 10, 17, 309	wf-T, wf-T Prem	Not endemic
<i>Reinhardtia simplex</i>	5, 10, 11, 17, 19, 34, 43, 51, 67, 136, 161, 194, 197, 309	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Sabal mauritiformis</i>	219	wf-P Basal	Not endemic
<i>Socratea exorrhiza</i>	17, 52, 60, 161, 167	mf-T, rf-P, wf-T, wf-T Prem	Not endemic
<i>Syechanthus fibrosus</i>	17, 51, 60, 126, 165, 263	rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Syechanthus warszewiczianus</i>	9, 10, 17, 19, 25, 43, 52, 60, 135, 136, 165, 210, 219, 309, 317, 374, 386	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Welfia georgii</i>	17, 52, 60, 167, 309	rf-P, wf-T, wf-T Prem	Not endemic

**Appendix 3.** Bromeliaceae species by Life Zone number, type, and endemism status in Costa Rica.

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Aechmea angustifolia</i>	10, 17, 34, 51, 52, 136, 161, 194, 231, 309, 376	mf-T, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Aechmea aquilega</i>	166	mf-T Prem	Not endemic
<i>Aechmea bracteata</i>	2, 17, 161	mf-T, wf-T	Not endemic
<i>Aechmea castelnavii</i>	183, 194, 270	wf-P Basal, wf-T	Not endemic
<i>Aechmea dactylina</i>	2, 203, 216, 309, 219	mf-T, rf-M, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Aechmea lueddemianiana</i>	2, 10, 13	mf-T, rf-P, wf-T Prem	Not endemic
<i>Aechmea magdalenae</i>	2, 11, 37, 80, 136, 161, 183, 272, 309	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Aechmea mariae-reginae</i>	17, 43, 52, 136, 167, 177	rf-LM, rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Aechmea mexicana</i>	43, 136, 149, 162, 194, 204, 216, 269	rf-M, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
<i>Aechmea nudicaulis</i>	17, 19, 37, 42, 136, 161, 38	mf-P, mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Aechmea penduliflora</i>	13	rf-P	Not endemic
<i>Aechmea pittieri</i>	3, 160, 161, 197, 210, 240, 269, 293	mf-P Basal, mf-T, mf-T Prem, rf-P, wf-LM, wf-P, wf-P rain	Endemic of Costa Rica
<i>Aechmea pubescens</i>	2, 9, 10, 11, 17, 25, 37, 43, 51, 52, 136, 149, 161, 167, 183, 194, 210, 269, 281, 309, 374, 376, 386	mf-T, rf-P, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Aechmea tillandsioides</i>	2, 17, 43, 149, 161, 194, 216, 309, 374, 386	mf-T, rf-M, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Aechmea tonduzii</i>	210, 240, 263, 317, 386	rf-P, wf-P rain, wf-T Prem	Endemic shared with Panama
<i>Aechmea veitchii</i>	165, 177, 200, 204	rf-LM, rf-P, wf-LM	Not endemic
<i>Ananas ananassoides</i>	258	mf-T	Not endemic
<i>Androlepis skimmeri</i>	17, 19, 40, 177	rf-LM, rf-P, wf-P rain, wf-T	Not endemic
<i>Araeococcus pectinatus</i>	194, 203, 210, 309, 374, 376	rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Billbergia macrolepis</i>	250	wf-T Prem	Not endemic
<i>Bromelia hemispherica</i>	11, 194	wf-P, wf-T	Not endemic
<i>Bromelia pinguin</i>	3, 20, 68, 171, 18, 8, 174, 211	df-T, mf-P Basal, mf-T d, mf-T perthum, mf-T Prem	Not endemic
<i>Bromelia plumieri</i>	3, 11, 80, 258	mf-P Basal, mf-T, wf-P	Not endemic
<i>Catopsis berteroniana</i>	2, 52	mf-T, wf-T Prem	Not endemic
<i>Catopsis hahnii</i>	188	mf-P	Not endemic
<i>Catopsis juncifolia</i>	17, 51, 60, 136	rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Catopsis morreniana</i>	24, 51, 136, 149, 183, 194, 203, 210, 376	rf-LM, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic

<i>Catopsis nitida</i>	11, 54, 59, 60, 73, 162, 179, 200, 204, 145	mf-LM, rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Catopsis nutans</i>	2, 11, 20, 43, 59, 73, 162, 177, 179, 194, 203, 209, 210, 216	mf-LM, mf-T, mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P rain, wf-T	Not endemic
<i>Catopsis paniculata</i>	59, 73, 127, 136, 177, 179, 209	mf-LM, mf-P, rf-LM, wf-LM, wf-T Prem	Not endemic
<i>Catopsis pedicellata</i>	2	mf-T	Not endemic
<i>Catopsis sessiliflora</i>	11, 17, 50, 51, 136, 161, 162, 194, 204, 210, 228, 269, 309, 374, 219	mf-P, mf-T, rf-P, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Catopsis wangerinii</i>	11, 70, 73, 177, 179, 186, 200, 204, 209, 269	mf-LM, rf-LM, rf-P, wf-LM, wf-P, wf-P Basal	Not endemic
<i>Greigia columbiana</i>	216, 242	rf-M	Not endemic
<i>Greigia sylvicola</i>	11, 70, 165, 177, 216, 242, 252	p-SA, rf-LM, rf-M, rf-P, wf-P	Endemic shared with Panama
<i>Guzmania angustifolia</i>	43, 52, 54, 136, 200, 240, 269	rf-LM, rf-P, wf-LM, wf-T Prem	Not endemic
<i>Guzmania blassii</i>	29, 43, 177, 200, 204, 210, 216, 227	p-SA, rf-LM, rf-M, rf-P, wf-LM	Endemic of Costa Rica
<i>Guzmania circinnata</i>	177	rf-LM	Not endemic
<i>Guzmania compacta</i>	2, 10, 19, 43, 59, 200	mf-T, rf-P, wf-LM, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Guzmania condensata</i>	60, 177, 200	rf-LM, rf-P, wf-LM	Not endemic
<i>Guzmania coriostachya</i>	11, 40, 43, 59, 60	rf-P, wf-LM, wf-P, wf-P rain	Not endemic
<i>Guzmania desautelsii</i>	2, 10, 11, 17, 43, 51, 210, 269	mf-T, rf-P, wf-LM, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
<i>Guzmania donnellsmithii</i>	2, 10, 19, 43, 52, 136, 269	mf-T, rf-P, wf-LM, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Guzmania glomerata</i>	10, 17, 43, 51, 165, 177, 200	rf-LM, rf-P, wf-LM, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Guzmania herrerae</i>	5, 11, 25, 43, 149	rf-P, wf-P, wf-P Basal, wf-T Prem	Endemic of Costa Rica
<i>Guzmania lingulata</i>	13, 17, 37, 43, 52, 136, 161, 194, 210, 231, 309, 375	mf-T, rf-P, wf-T, wf-T Prem	Not endemic
<i>Guzmania monostachia</i>	2, 17, 20, 51, 52, 73, 136, 161, 183, 194, 200, 204	mf-T, mf-T Prem, rf-P, wf-LM, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Guzmania musaica</i>	136, 165	rf-P, wf-T Prem	Not endemic
<i>Guzmania nicaraguensis</i>	11, 40, 43, 177	rf-LM, rf-P, wf-P, wf-P rain	Not endemic
<i>Guzmania obtusiloba</i>	43, 70, 165, 204	rf-LM, rf-P	Not endemic
<i>Guzmania patula</i>	177, 194, 210, 263, 374, 280	rf-LM, rf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Guzmania plicatifolia</i>	25, 43, 54, 59, 165, 177, 200, 204	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
<i>Guzmania polycephala</i>	43, 60, 177	rf-LM, rf-P	Endemic shared with Panama
<i>Guzmania sanguinea</i>	11, 13	rf-P, wf-P	Not endemic
<i>Guzmania scandens</i>	43, 54, 60, 177, 200, 204	rf-LM, rf-P, wf-LM	Endemic shared with Panama

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Guzmania scherzeriana</i>	11, 17, 43, 51, 52, 136, 204, 210, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Guzmania skotakii</i>	149, 204	rf-P, wf-P	Endemic of Costa Rica
<i>Guzmania spectabilis</i>	70, 165, 194	rf-LM, rf-P, wf-T	Endemic of Costa Rica
<i>Guzmania sprucei</i>	35, 43, 51, 60, 136	rf-P, wf-P Basal, wf-T Prem	Not endemic
<i>Guzmania stenostachya</i>	13, 25, 43, 165, 177, 200, 204	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
<i>Guzmania subcorymbosa</i>	10, 24, 29, 43	rf-LM, rf-P, wf-T Prem	Not endemic
<i>Guzmania zahni</i>	194, 210, 216, 263, 309, 374, 386	rf-M, rf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Mezobromelia pleiotricha</i>	149, 210	rf-P, wf-P	Not endemic
<i>Pitcairnia arcuata</i>	10, 11, 43, 136, 309, 317, 386	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Pitcairnia atrorubens</i>	10, 11, 25, 29, 43, 60, 161, 177, 240, 263, 269, 281, 309	mf-T, rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Pitcairnia brittoniana</i>	10, 11, 13, 60, 167, 177, 204, 210, 216, 240	rf-LM, rf-M, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Pitcairnia calcicola</i>	3, 64, 68, 91	mf-P Basal, mf-T d, wf-P	Endemic of Costa Rica
<i>Pitcairnia funkiae</i>	10, 25	wf-T Prem	Endemic of Costa Rica
<i>Pitcairnia guzmanoides</i>	177, 179	mf-LM, rf-LM	Not endemic
<i>Pitcairnia halophila</i>	171, 194, 309, 219	mf-P Basal, wf-P Basal, wf-T	Endemic of Costa Rica
<i>Pitcairnia heterophylla</i>	11, 13, 24, 73, 192, 209, 210, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic
<i>Pitcairnia kalbreyeri</i>	54, 165, 179, 204, 187	mf-LM, rf-LM, rf-P, wf-P	Not endemic
<i>Pitcairnia lyman-smithiana</i>	204	rf-P	Endemic shared with Panama
<i>Pitcairnia maidifolia</i>	11, 59, 162, 197, 210, 214, 309, 386	rf-LM, rf-P, wf-LM, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Pitcairnia megasepala</i>	258, 309, 253, 373	mf-T, rf-P Basal, wf-P Basal, wf-T	Not endemic
<i>Pitcairnia membranifolia</i>	73	wf-LM	Endemic of Costa Rica
<i>Pitcairnia quiescoides</i>	386	wf-T Prem	Not endemic
<i>Pitcairnia saxicola</i>	209	wf-LM	Not endemic
<i>Pitcairnia valerioi</i>	29, 43, 52, 60	rf-P, wf-T Prem	Endemic shared with Panama
<i>Pitcairnia wendlandii</i>	43, 136, 149, 165, 166, 200, 204	mf-T Prem, rf-P, wf-LM, wf-P, wf-T Prem	Not endemic
<i>Puya dasylirioides</i>	149, 216	rf-M, wf-P	Endemic of Costa Rica
<i>Puya floccosa</i>	177, 240	rf-LM, rf-P	Not endemic
<i>Racinaea adpressa</i>	11, 40, 54, 73, 149, 177, 179, 200, 204, 210, 79	mf-LM, rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic

<i>Racinaea contorta</i>	10, 42, 52, 60, 136	rf-P, wf-P Basal, wf-T Prem	Endemic shared with Nicaragua and Panama
<i>Racinaea rothschuhiana</i>	149, 169	mf-P, wf-P	Not endemic
<i>Racinaea schumanniana</i>	70, 73, 177, 200, 209, 92	rf-LM, wf-LM	Not endemic
<i>Racinaea spiculosa</i>	43, 73, 149, 177, 179, 200, 204, 79	mf-LM, rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Romnbergia hathewayi</i>	17, 42, 51, 52, 60, 136	rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
<i>Tillandsia abdita</i>	73, 162, 209	wf-LM, wf-P	Endemic of Costa Rica
<i>Tillandsia acostae</i>	17, 51, 52, 149, 194, 210, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Tillandsia anceps</i>	9, 10, 37, 43, 60, 136, 161, 162, 177, 194, 210, 309, 374, 376	mf-T, rf-LM, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Tillandsia balbisiana</i>	2, 17, 176, 183, 258, 309, 380	mf-T, mf-T perhum, wf-P Basal, wf-T	Not endemic
<i>Tillandsia biflora</i>	177, 200, 216, 242, 269	rf-LM, rf-M, wf-LM	Not endemic
<i>Tillandsia brachycaulos</i>	3, 11, 20, 68, 80, 127, 183, 194, 197, 210, 272, 309	mf-P, 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>Tillandsia bulbosa</i>	2, 9, 11, 17, 25, 40, 136, 161, 165, 169, 183, 194, 210, 231, 63	mf-P, mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Tillandsia butzii</i>	11, 59, 73, 179, 209, 269, 145	mf-LM, wf-LM, wf-P	Not endemic
<i>Tillandsia caput-medusae</i>	20, 47, 160, 171, 178, 183, 194, 197, 203, 210, 18	df-T, mf-P Basal, mf-T, mf-T Prem, rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Tillandsia cauliflora</i>	210	rf-P	Endemic of Costa Rica
<i>Tillandsia complanata</i>	60, 73, 177, 200	rf-LM, rf-P, wf-LM	Not endemic
<i>Tillandsia excelsa</i>	11, 54, 59, 60, 70, 73, 165, 177, 179, 210, 309	mf-LM, rf-LM, rf-P, wf-LM, wf-P, wf-T	Not endemic
<i>Tillandsia fasciculata</i>	2, 11, 20, 73, 80, 183, 194, 197, 203, 210, 240	mf-T, mf-T Prem, rf-P, wf-LM, wf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
<i>Tillandsia festuoides</i>	2, 5, 17, 19, 25, 34, 43, 51, 73, 136, 161, 167	mf-T, rf-P, wf-LM, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Tillandsia filifolia</i>	51, 52, 149, 166	mf-T Prem, wf-P, wf-P Basal, wf-T Prem	Not endemic
<i>Tillandsia flexuosa</i>	376	wf-P Basal	Not endemic
<i>Tillandsia insignis</i>	11, 25, 43, 54, 60, 165, 177, 204	rf-LM, rf-P, wf-P, wf-T Prem	Endemic shared with Panama
<i>Tillandsia ionantha</i>	3	mf-P Basal	Not endemic
<i>Tillandsia juncea</i>	11, 20, 43, 59, 73, 162, 194, 240, 281	mf-T Prem, rf-P, wf-LM, wf-P, wf-T	Not endemic
<i>Tillandsia lampropoda</i>	73, 179	mf-LM, wf-LM	Not endemic
<i>Tillandsia leiboldiana</i>	11, 13, 17, 43, 60, 136, 149, 162, 165, 166, 179, 192, 197, 204, 210, 216, 225, 233, 269, 309, 100	mf-LM, mf-P, mf-T Prem, rf-LM, rf-M, rf-P, wf-LM, wf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Tillandsia longifolia</i>	73, 177, 200, 209	rf-LM, wf-LM	Not endemic

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Tillandsia makoyana</i>	3, 10, 20, 18, 174	df-T, mf-P Basal, mf-T Prem, wf-T Prem	Not endemic
<i>Tillandsia monadelpha</i>	2, 5, 9, 10, 17, 25, 126, 136, 149, 161, 194, 231, 309, 374, 373	mf-T, rf-P Basal, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
<i>Tillandsia multicaulis</i>	11, 60, 70, 73, 177, 179, 200, 209, 214, 281, 100, 145	mf-LM, mf-P, rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Tillandsia oerstediana</i>	169, 240, 269, 317	mf-P, rf-P, wf-LM	Endemic shared with Panama
<i>Tillandsia paucifolia</i>	3, 5, 8, 174	df-T, mf-P Basal, wf-P Basal	Not endemic
<i>Tillandsia pruinosa</i>	11, 17, 169, 142	mf-P, wf-P, wf-P rain, wf-T	Not endemic
<i>Tillandsia punctulata</i>	11, 13, 50, 73, 162, 177, 200, 209, 210, 214, 269, 145	mf-P, rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Tillandsia schiedeana</i>	11, 13, 20, 68, 80, 127, 149, 160, 162, 166, 178, 183	mf-P, mf-T, mf-T d, mf-T Prem, rf-P, wf-P Basal	Not endemic
<i>Tillandsia singularis</i>	10, 25, 43, 60, 136	rf-P, wf-T Prem	Endemic shared with Panama
<i>Tillandsia subulifera</i>	2, 258, 309	mf-T, wf-T	Not endemic
<i>Tillandsia tricolor</i>	11, 73, 126, 162, 169, 179, 209, 210, 317, 100	mf-LM, mf-P, rf-P, wf-LM, wf-P, wf-T	Not endemic
<i>Tillandsia usneoides</i>	11, 17, 34, 51, 73, 149, 179, 200, 309, 376, 38	mf-LM, mf-P, mf-T, wf-LM, wf-P, wf-P Basal, wf-T	Not endemic
<i>Tillandsia urticulata</i>	25, 149, 169, 179, 38	mf-LM, mf-P, wf-P, wf-T Prem	Not endemic
<i>Tillandsia variabilis</i>	43, 169, 177	mf-P, rf-LM, rf-P	Not endemic
<i>Tillandsia venusta</i>	11, 17, 149	wf-P, wf-T	Endemic shared with Panama
<i>Vriesea chontalensis</i>	17, 51, 136, 149, 165, 177, 192, 210	rf-LM, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua
<i>Vriesea heliconioides</i>	9, 17, 136, 161, 183, 194, 197, 203, 309	mf-T, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Vriesea incurva</i>	11, 60, 73, 162, 165, 177, 179, 200, 210, 240, 269, 79, 145	mf-LM, rf-LM, rf-P, wf-LM, wf-P	Not endemic
<i>Vriesea monstrum</i>	2, 9, 136	mf-T, wf-T, wf-T Prem	Not endemic
<i>Werauhia acuminata</i>	13, 165, 177, 179, 200, 309	mf-LM, rf-LM, rf-P, wf-LM, wf-T	Endemic of Costa Rica
<i>Werauhia ampla</i>	73, 179, 209	mf-LM, wf-LM	Endemic of Costa Rica
<i>Werauhia apiculata</i>	228	wf-P	Endemic shared with Panama
<i>Werauhia attenuata</i>	11, 43	rf-P, wf-P	Endemic of Costa Rica
<i>Werauhia balanophora</i>	13, 42, 70, 177, 179	mf-LM, rf-LM, rf-P, wf-P Basal	Endemic of Costa Rica
<i>Werauhia barii</i>	177, 179, 200	mf-LM, rf-LM, wf-LM	Endemic of Costa Rica
<i>Werauhia bicolor</i>	73, 177, 200, 216	rf-LM, rf-M, wf-LM	Endemic of Costa Rica
<i>Werauhia bracteosa</i>	179	mf-LM	Endemic of Costa Rica
<i>Werauhia brunei</i>	200, 209	wf-LM	Endemic of Costa Rica



<i>Werauhia burgeri</i>	60, 177, 194, 210, 216, 263, 317	rf-LM, rf-M, rf-P, wf-P rain, wf-T	Endemic shared with Panama
<i>Werauhia camptoclada</i>	179	mf-LM	Endemic of Costa Rica
<i>Werauhia capitata</i>	149, 165, 263	rf-P, wf-P, wf-P rain	Endemic shared with Panama
<i>Werauhia comata</i>	13, 43, 52, 59, 165, 177, 200, 204	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
<i>Werauhia cooperiana</i>	11, 70	rf-LM, wf-P	Endemic of Costa Rica
<i>Werauhia dodsonii</i>	60, 192, 197, 210, 309, 374	rf-P, wf-P rain, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Werauhia gladioliflora</i>	17, 25, 43, 52, 59, 169, 194, 210, 309	mf-P, rf-P, wf-LM, wf-T, wf-T Prem	Not endemic
<i>Werauhia graminifolia</i>	43, 51, 60, 177, 204	rf-LM, rf-P, wf-P Basal	Not endemic
<i>Werauhia greenbergii</i>	11, 43, 210	rf-P, wf-P	Not endemic
<i>Werauhia haberii</i>	54	rf-LM	Endemic of Costa Rica
<i>Werauhia hainesiorum</i>	179, 200	mf-LM, wf-LM	Endemic of Costa Rica
<i>Werauhia hygrometrica</i>	54, 70, 75, 165, 177, 179, 204, 210, 57	mf-LM, rf-LM, rf-P, wf-LM, wf-P rain	Not endemic
<i>Werauhia kathyae</i>	43, 60, 165, 177, 200, 204	rf-LM, rf-P, wf-LM	Endemic of Costa Rica
<i>Werauhia kupperiana</i>	17, 25, 43	rf-P, wf-T, wf-T Prem	Endemic shared with Panama
<i>Werauhia latissima</i>	70	rf-LM	Endemic shared with Panama
<i>Werauhia laxa</i>	70	rf-LM	Endemic shared with Panama
<i>Werauhia leucophylla</i>	177, 200	rf-LM, wf-LM	Endemic shared with Panama
<i>Werauhia luis-gomezii</i>	216, 242	rf-LM, wf-LM	Endemic shared with Panama
<i>Werauhia lymann-smithii</i>	70, 73, 149	rf-M	Endemic of Costa Rica
<i>Werauhia macrantha</i>	200, 242	rf-LM, wf-LM, wf-P	Endemic of Costa Rica
<i>Werauhia macrochlamys</i>	10, 13, 73, 177, 179, 209, 214, 240	rf-M, wf-LM	Endemic of Costa Rica
<i>Werauhia marnier-lapostollei</i>	43, 194, 197, 210, 309	mf-LM, rf-LM, rf-P, wf-LM, wf-T Prem	Endemic of Costa Rica
<i>Werauhia moralesii</i>	43	rf-P, wf-P rain, wf-T	Endemic shared with Panama
<i>Werauhia nephrolepis</i>	73, 179, 200, 209, 214	rf-P	Endemic shared with Panama
<i>Werauhia notata</i>	59, 70, 177, 179	mf-LM, rf-LM, wf-LM	Not endemic
<i>Werauhia orientensis</i>	70, 73, 99, 149, 183, 200, 216, 242, 103, 130, 145	mf-LM, rf-LM, wf-LM	Endemic of Costa Rica
<i>Werauhia osaensis</i>	194, 309, 376, 386	rf-LM, rf-M, rf-M LM, wf-LM, wf-P, wf-P Basal	Endemic shared with Panama
<i>Werauhia paniculata</i>	204	wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Werauhia pedicellata</i>	54, 73, 177, 179, 200, 204, 209, 216, 240	rf-P	Endemic shared with Panama
<i>Werauhia picta</i>	73	mf-LM, rf-LM, rf-M, rf-P, wf-LM	Not endemic
<i>Werauhia pittieri</i>	73, 99, 177, 200, 216, 269	wf-LM	Endemic shared with Panama
		rf-LM, rf-M, wf-LM	Endemic shared with Panama

Species	Number of Life Zone polygons	Life Zones	Endemism
<i>Werauhia ringens</i>	17, 52	wf-T, wf-T Prem	Not endemic
<i>Werauhia rubra</i>	73	wf-LM	Endemic shared with Panama
<i>Werauhia rugosa</i>	179, 200	mf-LM, wf-LM	Endemic of Costa Rica
<i>Werauhia sanguinolenta</i>	2, 5, 10, 194, 203, 258, 309, 38	mf-P, mf-T, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
<i>Werauhia singuliflora</i>	43, 60, 177	rf-LM, rf-P	Endemic of Costa Rica
<i>Werauhia stenophylla</i>	52	wf-T Prem	Endemic shared with Panama
<i>Werauhia subsecunda</i>	59, 70, 73	rf-LM, wf-LM	Endemic shared with Panama
<i>Werauhia tiquitrensis</i>	162	wf-P	Endemic of Costa Rica
<i>Werauhia tonduziana</i>	2, 11, 43, 60, 70, 73, 162, 179, 200, 210	mf-LM, mf-T, rf-LM, rf-P, wf-LM, wf-P	Endemic of Costa Rica
<i>Werauhia umbrosa</i>	13, 59, 177, 210	rf-LM, rf-P, wf-LM	Endemic shared with Panama
<i>Werauhia usoris</i>	200, 210, 216	rf-M, rf-P, wf-LM	Endemic of Costa Rica
<i>Werauhia vietoris</i>	179	mf-LM	Endemic of Costa Rica
<i>Werauhia viridiflora</i>	11, 13, 17, 177, 194, 200, 204, 209, 210, 240, 269, 309	rf-LM, rf-P, wf-LM, wf-P, wf-T	Not endemic
<i>Werauhia viridis</i>	70, 99, 209, 145	rf-LM, rf-M, wf-LM	Endemic of Costa Rica
<i>Werauhia vittata</i>	11, 17, 43, 52, 60	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
<i>Werauhia vulcanicola</i>	24	rf-LM	Endemic of Costa Rica
<i>Werauhia werckleana</i>	11, 59, 73, 209, 210, 269, 281	rf-P, wf-LM, wf-P	Not endemic
<i>Werauhia williamsii</i>	70, 73, 177, 179, 200, 216, 242	mf-LM, rf-LM, rf-M, wf-LM	Endemic shared with Panama

Appendix 4. Scarabaeinae species by Life Zone number, type, and endemism status in Costa Rica.

Species	Number of Life Zone polygons	Life Zones	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 of Costa Rica
<i>Ateuchus ginae</i>	24, 160	rf-LM, mf-T Prem	Endemic shared with Nicaragua and Panama
<i>Ateuchus hendrichsi</i>	13	rf-P	Endemic of 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 of Costa Rica
<i>Ateuchus zoebischi</i>	10, 13, 25, 52, 167	rf-P, wf-T, wf-T Prem	Endemic of Costa Rica
<i>Bdelynus 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 of 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

Species	Number of Life Zone polygons	Life Zones	Endemism
<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-LM, wf-LM, 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 leucopteryum</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 mariamelae</i>	10, 11, 13, 29, 59, 70	rf-LM, rf-P, wf-LM, wf-P, wf-T Prem	Endemic of Costa Rica
<i>Canthidium marielae</i>	309	wf-T	Endemic of Costa Rica
<i>Canthidium pallidolatum</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 of Costa Rica
<i>Canthidium pseudopuncticollis</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 variosum</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>Canthidium n. sp</i>	165, 177	rf-P, rf-LM	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 of 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 juveneus</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 monilitatus</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 of 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, 127, 179, 216, 89	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 of Costa Rica
<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

Species	Number of Life Zone polygons	Life Zones	Endemism
<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>Coprophanaeus pluto 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 solisi</i>	183, 309	wf-P Basal, wf-T	Endemic of Costa Rica
<i>Coprophanaeus 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 denticulum</i>	165, 177	rf-P, rf-LM	Endemic shared with Panama
<i>Cryptocanthon lindemanae</i>	309	wf-T	Endemic of Costa Rica
<i>Cryptocanthon osaensis</i>	309	wf-T	Endemic of Costa Rica
<i>Cryptocanthon solisi</i>	60	rf-P	Endemic of Costa Rica
<i>Deltochilum gibbosum</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</i>	80	mf-T	Not endemic
<i>Deltochilum valgum</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 amicitiae</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 annae</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 of 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 of 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 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</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 of 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 of 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 atriglabrus</i>	11, 13, 29, 43, 60, 127, 263, 281, 317	mf-P, rf-P, wf-P, wf-P rain	Not endemic
<i>Onthophagus atroserriceus</i>	73, 177, 200, 216	rf-LM, rf-M, wf-LM	Not endemic

Species	Number of Life Zone polygons	Life Zones	Endemism
<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 cryptodicranius</i>	17, 42, 167	wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
<i>Onthophagus cyanellus</i>	11, 73, 89, 127, 158, 162, 177, 179, 200, 216, 269, 281	mf-LM, mf-LM m, mf-P, rf-LM, rf-M, wf-LM, wf-P	Not endemic
<i>Onthophagus dicranius</i>	183, 219, 309	wf-P Basal, wf-T	Not endemic
<i>Onthophagus dorsipitulus</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 of Costa Rica
<i>Onthophagus grataehelena</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 of 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 of 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 of Costa Rica
<i>Onthophagus notiodes</i>	60, 149	rf-P, wf-P	Endemic of Costa Rica



<i>Onthophagus nubilus</i>	240		rf-P	Endemic of Costa Rica
<i>Onthophagus nycotopus</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 perthum, 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 of 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 of 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 botimeri</i>	161		mf-T	Endemic shared with Panama
<i>Pedaridium brachyporum</i>	51, 149, 183		wf-P, wf-P Basal	Endemic of 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 changliazi</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, 160, 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

Species	Number of Life Zone polygons	Life Zones	Endemism
<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>Sisypus 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 of 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 decavilai</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