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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.

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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^2 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 20th 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^2, whereas Colombia, in second place, has only 43.8 plant species per 1 000 km^2 (Obando, 2007). Similarly, Costa Rica has 28.2 species of vertebrates (excluding fishes) per 1 000 km^2, whereas Ecuador, the second most biodiverse vertebrate country per km^2 in the world, has 9.2 species per 1 000 km^2, and the third most biodiverse vertebrate country, Malaysia, has only 4.4 vertebrate species per 1 000 km^2 (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^2 worldwide, 22.47 international ecotourists/km^2 in the year 2007, with the African sub-Saharan countries as the next places with most ecotourists per km^2 (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) and from the Missouri Botanical Garden electronic database (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).

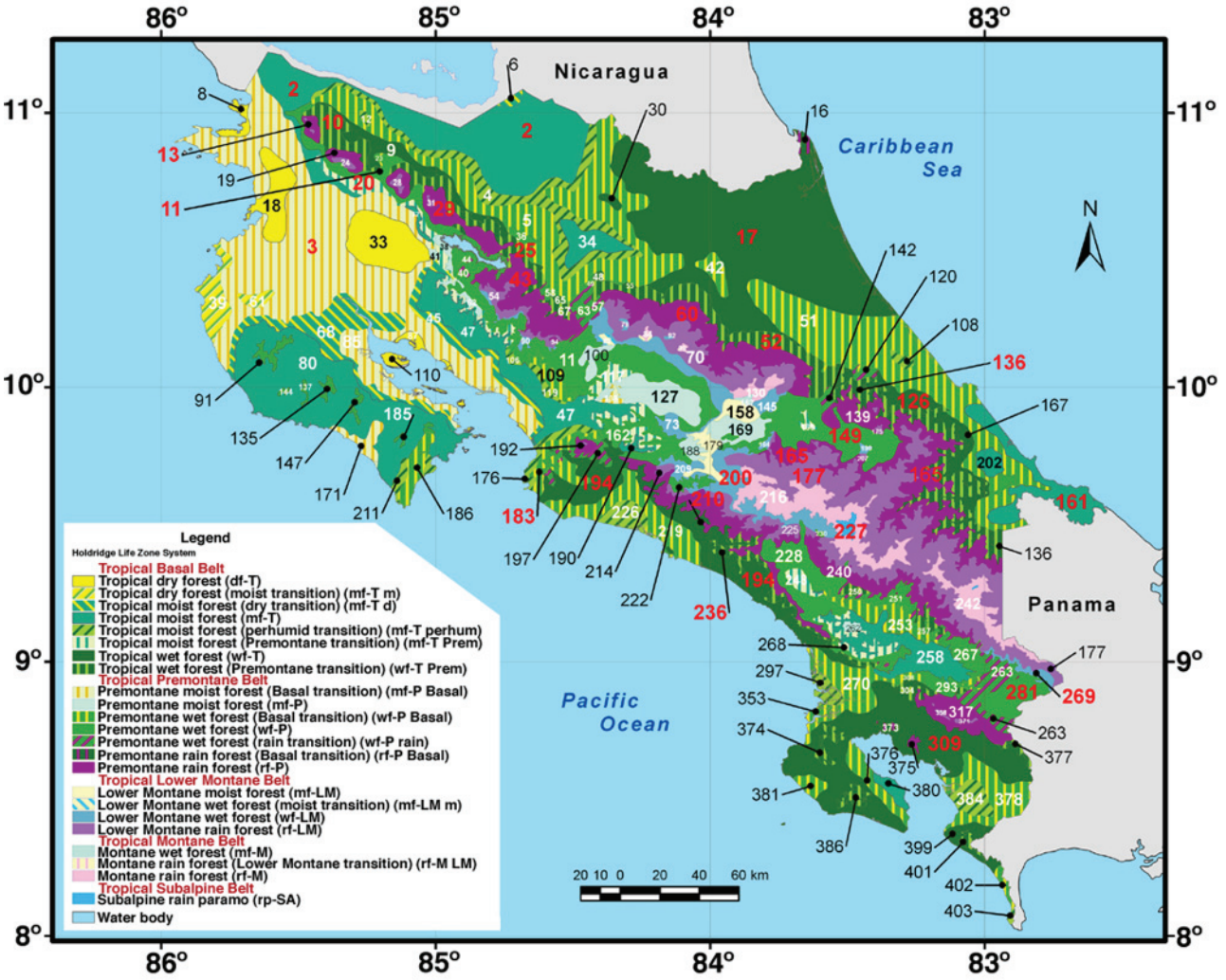

Figure 2. Numbering the Holdridge Life Zone polygons in Costa Rica. Numbers in red represent life zones with 5 or more years of collecting, which are considered as well represented.

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). 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 ≥ 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.

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

a) Araceae

Areas of priority zones Total area	Priority 1 6111 km^2	% (*)	Priority 2 3344 km^2	% (*)	Priority 3 0 km^2	% (*)	Priority 4 3326 km^2	% (*)	Priority 5 0 km^2	% (*)	Priority 6 733 km^2	% (*)	Total 13514 km^2	Total % (*)
State Farms	0.00	0.00	0.00	0.00	0.00	0.00	3.89	0.12	0.00	0.00	0.00	0.00	3.89	0.03
Wetlands	56.52	0.92	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	56.53	0.42
National Park	702.48	11.50	1 718.69	51.39	0.00	0.00	199.42	6.00	0.00	0.00	113.42	15.47	2 734.01	20.23
National Refuge	990.87	16.21	11.23	0.34	0.00	0.00	33.10	1.00	0.00	0.00	0.00	0.00	1 035.20	7.66
Biological Reserve	0.00	0.00	13.53	0.40	0.00	0.00	68.02	2.05	0.00	0.00	70.47	9.61	152.01	1.12
Forest Reserve	544.03	8.90	528.51	15.80	0.00	0.00	25.49	0.77	0.00	0.00	47.43	6.47	1 145.48	8.48
Protection Zone	43.58	0.71	171.20	5.12	0.00	0.00	274.37	8.25	0.00	0.00	50.41	6.88	539.56	3.99
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^2) and percentage* under protection by priority category	2 337.48	38.25	2 443.16	73.05	0.00	0.00	604.30	18.17	0.00	0.00	281.73	38.43	5 666.68	41.93

b) Arecaceae

Areas of priority zones Total area	Priority 1 1851 km^2	% (*)	Priority 2 3036 km^2	% (*)	Priority 3 4519 km^2	% (*)	Priority 4 4744 km^2	% (*)	Priority 5 0 km^2	% (*)	Priority 6 0 km^2	% (*)	Total 14150 km^2	Total % (*)
State Farms	0.00	0.00	0.00	0.00	40.96	0.91	0.02	0.00	0.00	0.00	0.00	0.00	40.99	0.29
Wetlands	44.59	2.41	0.01	0.00	11.93	0.26	0.38	0.01	0.00	0.00	0.00	0.00	56.92	0.40
National Park	415.53	22.45	546.67	18.01	311.31	6.89	1742.08	36.72	0.00	0.00	0.00	0.00	3 015.59	21.31
National Refuge	35.79	1.93	20.42	0.67	955.08	21.13	53.60	1.13	0.00	0.00	0.00	0.00	1 064.89	7.53
Biological Reserve	0.00	0.00	83.99	2.77	0.00	0.00	68.02	1.43	0.00	0.00	0.00	0.00	152.01	1.07
Forest Reserve	465.47	25.15	181.66	5.98	78.57	1.74	726.80	15.32	0.00	0.00	0.00	0.00	1 452.49	10.26
Protection Zone	0.00	0.00	119.99	3.95	43.58	0.96	348.72	7.35	0.00	0.00	0.00	0.00	512.29	3.62
National Monument	0.00	0.00	0.00	0.00	0.00	0.00	1.38	0.03	0.00	0.00	0.00	0.00	1.38	0.01
Total area (in km^2) and percentage* under protection by priority category	961.38	51.95	952.73	31.38	1 441.44	31.90	2 941.01	61.99	0.00	0.00	0.00	0.00	6 296.55	44.49

c) Bromeliaceae

Areas of priority zones Total area	Priority 1 3177 km²	% (*)	Priority 2 0 km²	% (*)	Priority 3 2504 km²	% (*)	Priority 4 902 km²	% (*)	Priority 5 661 km²	% (*)	Priority 6 8854 km²	% (*)	Total 16098 km²	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 km²) 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 Total area	Priority 1 1593 km²	% (*)	Priority 2 0 km²	% (*)	Priority 3 259 km²	% (*)	Priority 4 7425 km²	% (*)	Priority 5 2360 km²	% (*)	Priority 6 2591 km²	% (*)	Total 14228 km²	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 km²) 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

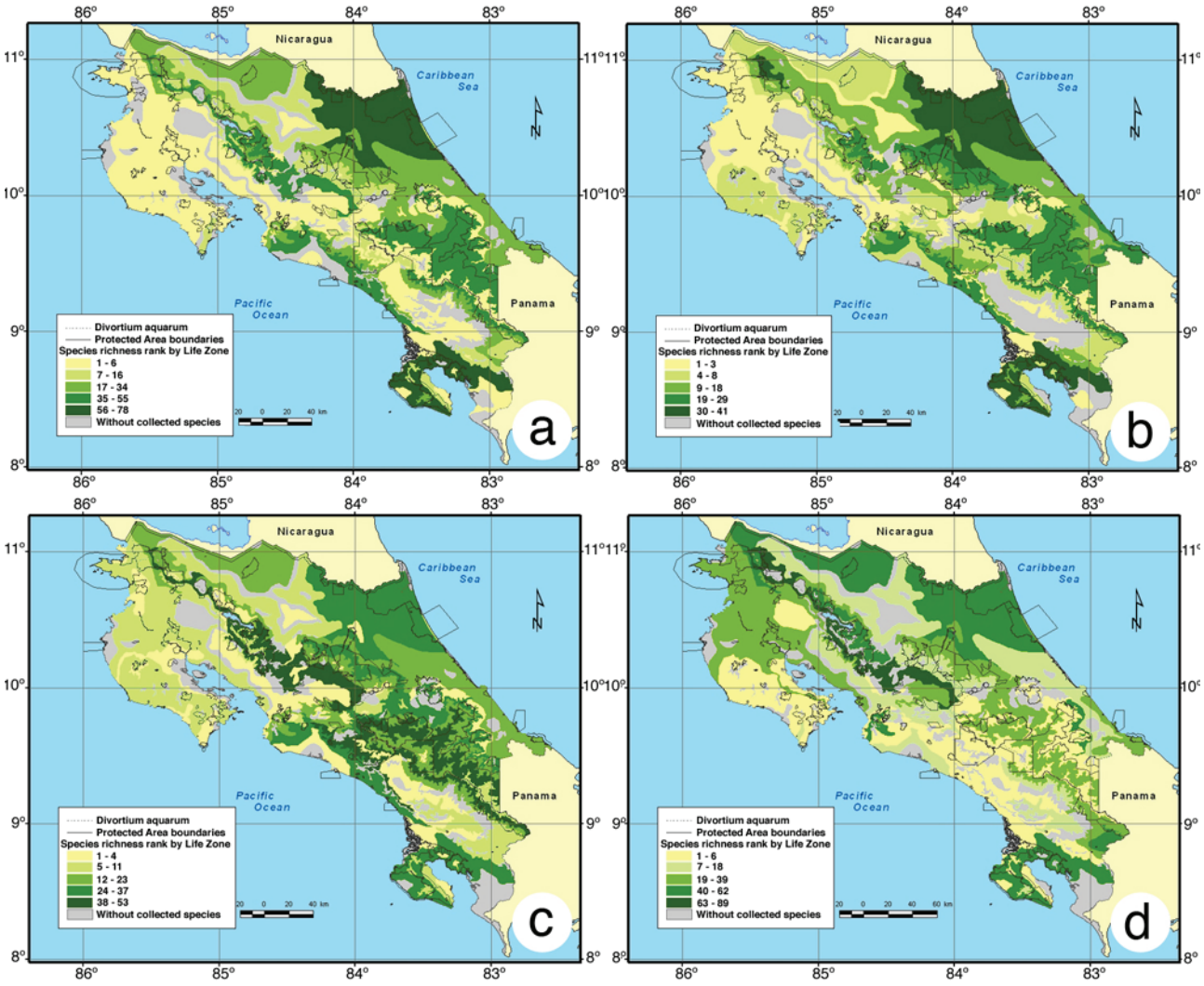

Figure 3. Distributions of species richness ranks for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

Protection of life zone areas: Costa Rica has a total mainland area of 51 042.8 km^2. Out of these, 12 422.4 km^2 (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

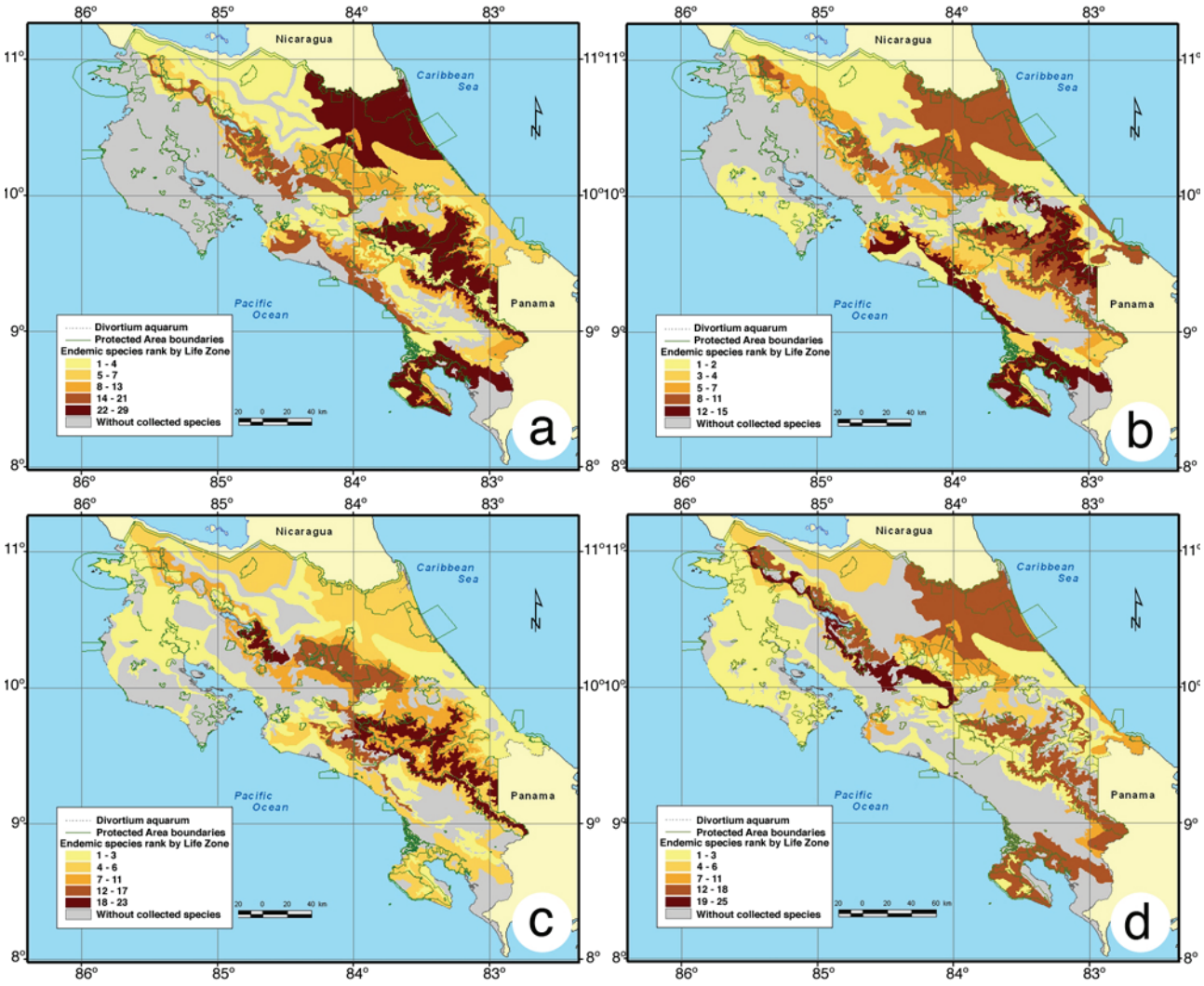

Figure 4. Distributions of endemism ranks for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae. Divortium aquarum = watershed divide.

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 Scrabaeinae 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

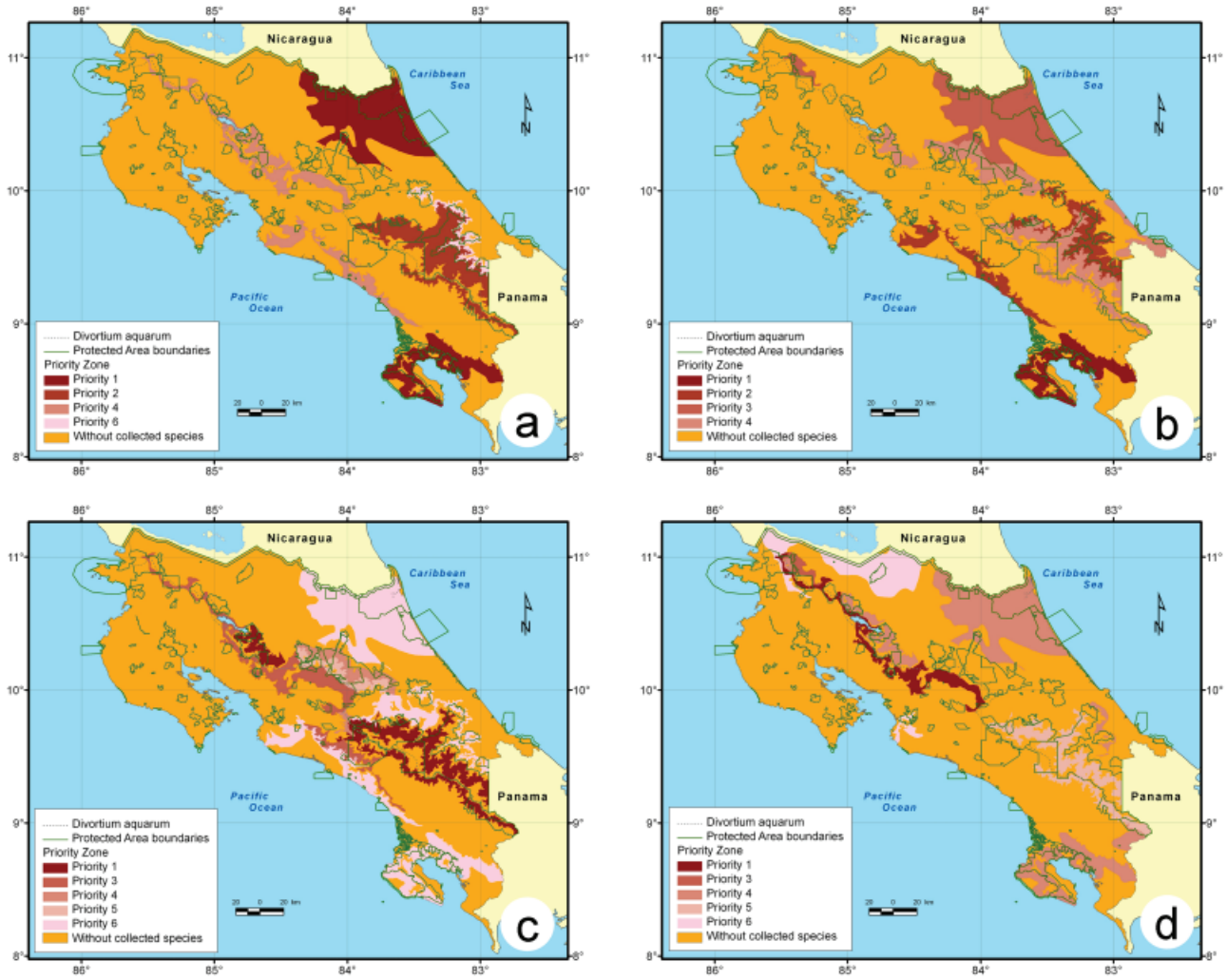

Figure 5. Distributions of conservation priority zones for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

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

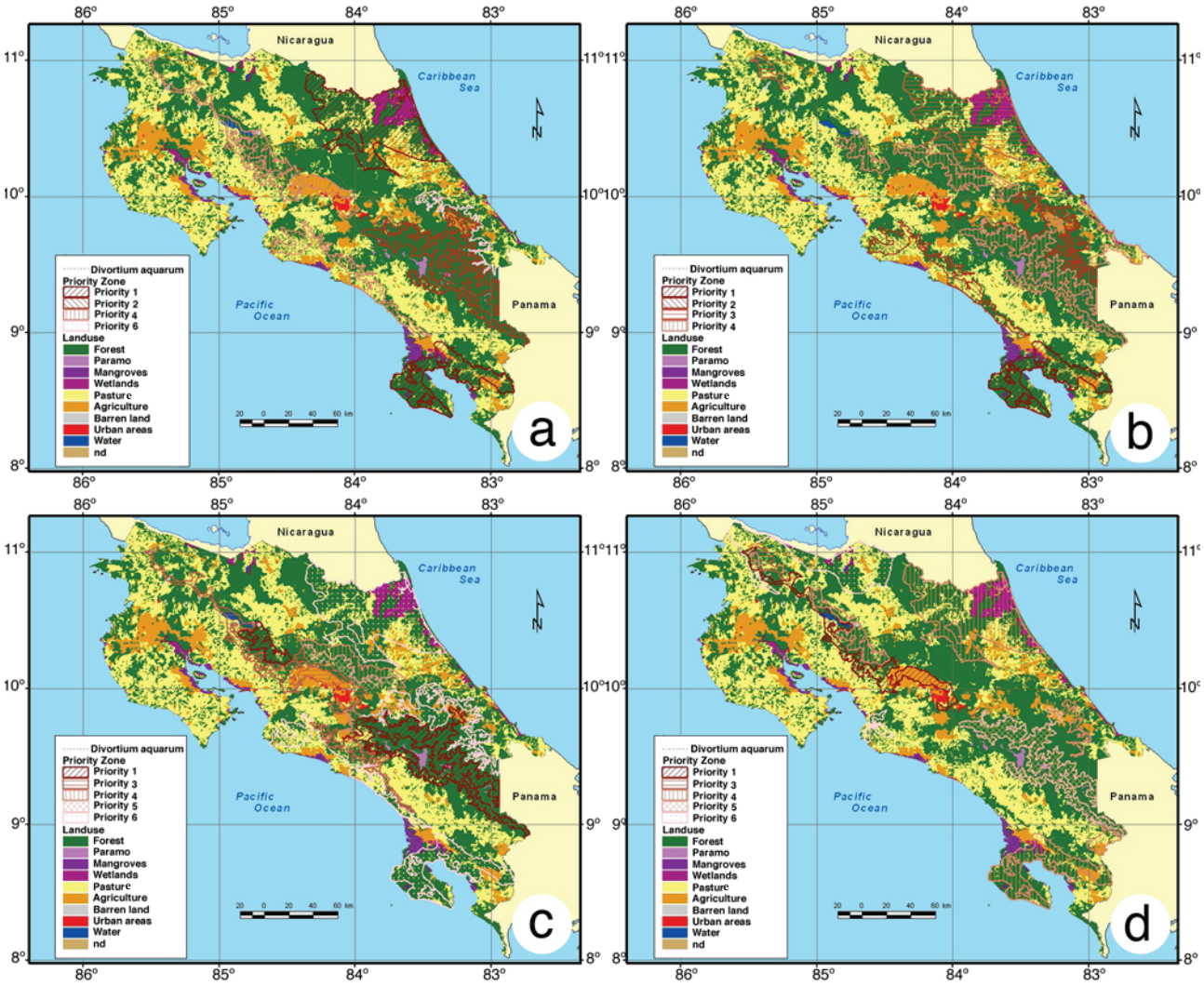

Figure 6. Land use within identified priority areas for (a) Araceae, (b) Arecaceae, (c) Bromeliaceae, and (d) Scarabaeinae in Costa Rica. Divortium aquarum = watershed divide.

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

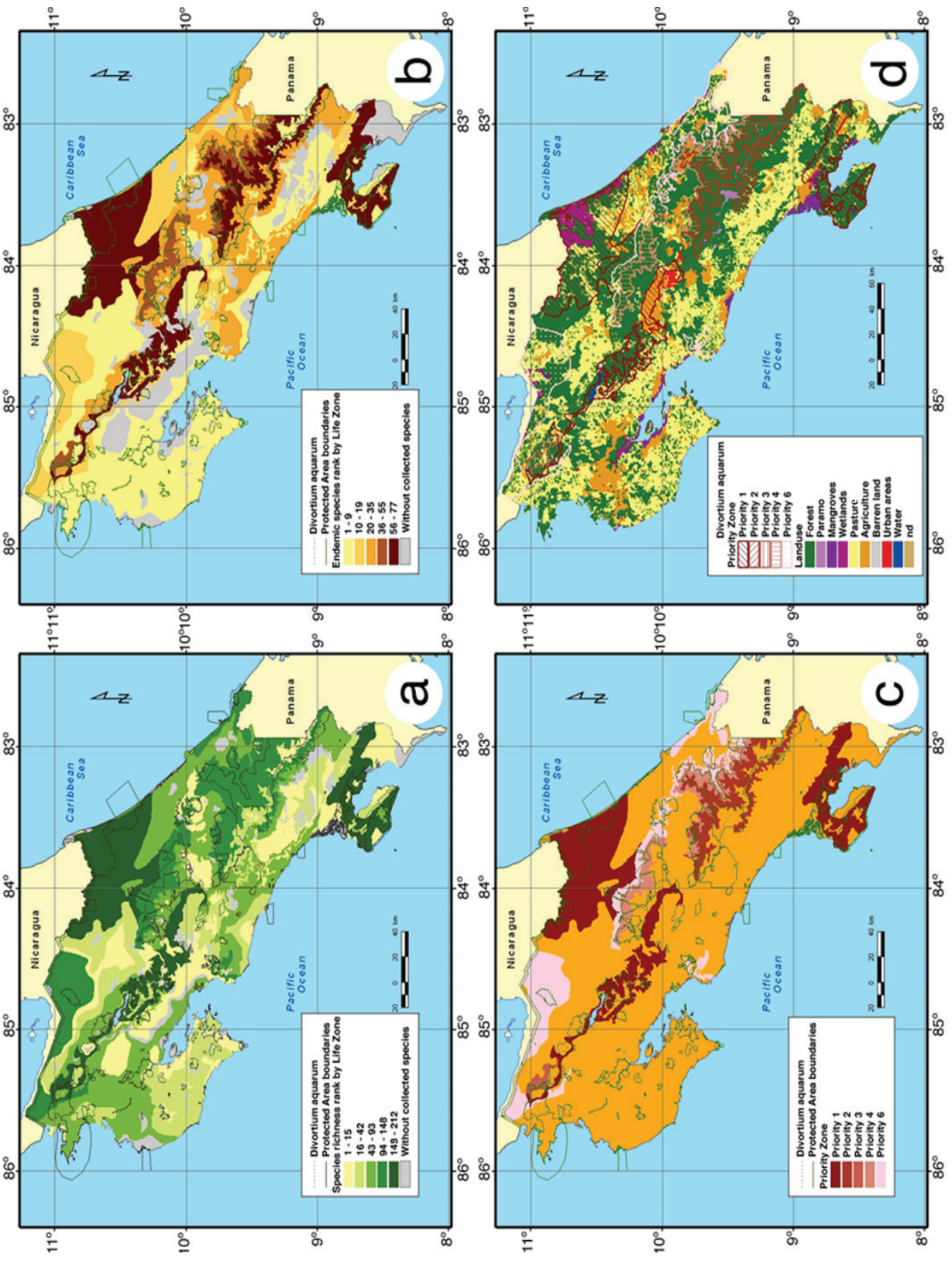

Figure 7. Overall species (a) and endemic (b) species richness ranks, priority zones (c) and current land use/ land cover mosaic (d) based on the totality of the studied taxa and their overlap with the established protected areas. Areas in grey represent zones where no taxa have yet been recorded. Note 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 Kussmaul, 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 being 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 diferent land use conditions

a) Araceae

Areas of priority zones Total area	Priority 1 6111 km²	% (*)	Priority 2 3344 km²	% (*)	Priority 3 0 km²	% (*)	Priority 4 3326 km²	% (*)	Priority 5 0 km²	% (*)	Priority 6 733 km²	% (*)	Total 13514 km²	Total % (*)
Area of land use categories (1992) in km²														
Forest	3915	64.40	3119	93.38	0	0.00	1534	46.21	0	0.00	655	89.47	9223	68.46
Paramo	0	0.00	8	0.23	0	0.00	0	0.00	0	0.00	0	0.00	8	0.06
Mangroves	35	0.57	0	0.00	0	0.00	5	0.15	0	0.00	0	0.00	40	0.29
Wetlands	728	11.98	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	728	5.40
Pasture	1032	16.98	35	1.05	0	0.00	1194	35.97	0	0.00	20	2.79	2282	16.94
Agriculture	330	5.43	169	5.05	0	0.00	464	13.99	0	0.00	57	7.74	1020	7.57
Barren land	0	0.00	0	0.00	0	0.00	30	0.92	0	0.00	0	0.00	30	0.23
Urban areas	4	0.07	0	0.00	0	0.00	23	0.70	0	0.00	0	0.00	27	0.20
Water	34	0.57	0	0.00	0	0.00	69	2.07	0	0.00	0	0.00	103	0.76
na**	0	0.00	10	0.30	0	0.00	0	0.00	0	0.00	0	0.00	10	0.08

b) Arecaceae

Areas of priority zones Total area	Priority 1 1851 km²	% (*)	Priority 2 3036 km²	% (*)	Priority 3 4519 km²	% (*)	Priority 4 4744 km²	% (*)	Priority 5 0 km²	% (*)	Priority 6 0 km²	% (*)	Total 14150 km²	Total % (*)
Area of land use categories (1992) in km²														
Forest	1423	77.45	2118	69.94	2662	59.16	3968	83.83	0	0.00	0	0.00	10172	72.51
Paramo	0	0.00	0	0.00	0	0.00	8	0.16	0	0.00	0	0.00	8	0.05
Mangroves	35	1.88	5	0.17	0	0.00	0	0.00	0	0.00	0	0.00	40	0.28
Wetlands	36	1.95	0	0.00	692	15.38	33	0.70	0	0.00	0	0.00	761	5.43
Pasture	200	10.90	698	23.03	920	20.45	467	9.87	0	0.00	0	0.00	2285	16.29
Agriculture	141	7.66	202	6.67	190	4.22	167	3.52	0	0.00	0	0.00	699	4.98
Barren land	0	0.00	0	0.00	0	0.00	15	0.33	0	0.00	0	0.00	15	0.11
Urban areas	3	0.16	0	0.00	1	0.03	0	0.00	0	0.00	0	0.00	4	0.03
Water	0	0.00	0	0.00	34	0.76	0	0.00	0	0.00	0	0.00	34	0.25
na**	0	0.00	6	0.19	0	0.01	4	0.09	0	0.00	0	0.00	10	0.07

c) Bromeliaceae

Areas of priority zones Total area	Priority 1 3177 km²	% (*)	Priority 2 0 km²	% (*)	Priority 3 2504 km²	% (*)	Priority 4 902 km²	% (*)	Priority 5 661 km²	% (*)	Priority 6 8854 km²	% (*)	Total 16098 km²	Total % (*)
Area of land use categories (1992) in km²														
Forest	2884	90.88	0	0.00	1192	47.59	793	87.46	617	93.41	5548	62.94	11035	68.71
Paramo	10	0.33	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	10	0.07
Mangroves	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	40	0.45	40	0.25
Wetlands	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	728	8.26	728	4.53
Pasture	182	5.74	0	0.00	720	28.76	83	9.11	40	6.10	1815	20.59	2841	17.69
Agriculture	77	2.43	0	0.00	482	19.24	31	3.42	0	0.00	626	7.10	1216	7.57
Barren land	15	0.49	0	0.00	15	0.60	0	0.00	3	0.49	0	0.00	34	0.21
Urban areas	0	0.00	0	0.00	27	1.07	0	0.00	0	0.00	6	0.07	33	0.20
Water	0	0.00	0	0.00	69	2.74	0	0.00	0	0.00	35	0.40	104	0.65
na**	4	0.14	0	0.00	0	0.00	0	0.00	0	0.00	17	0.19	21	0.13

d) Scarabaeinae

Areas of priority zones Total area	Priority 1 1593 km²	% (*)	Priority 2 0 km²	% (*)	Priority 3 259 km²	% (*)	Priority 4 7426 km²	% (*)	Priority 5 2360 km²	% (*)	Priority 6 2591 km²	% (*)	Total 14229 km²	Total % (*)
Area of land use categories (1992) in km²														
Forest	559	35.08	0	0.00	171	65.84	4896	65.93	2266	96.13	1279	49.51	9170	64.45
Paramo	0	0.00	0	0.00	0	0.00	0	0.00	8	0.32	0	0.00	8	0.05
Mangroves	0	0.00	0	0.00	0	0.00	35	0.47	0	0.00	0	0.00	35	0.24
Wetlands	0	0.00	0	0.00	0	0.00	731	9.84	0	0.00	97	3.76	828	5.82
Pasture	490	30.79	0	0.00	88	34.08	1290	17.37	29	1.22	1065	41.22	2963	20.82
Agriculture	437	27.43	0	0.00	0	0.08	408	5.49	51	2.15	129	4.98	1025	7.20
Barren land	15	0.95	0	0.00	0	0.00	15	0.20	0	0.00	4	0.15	34	0.24
Urban areas	23	1.46	0	0.00	0	0.00	4	0.05	0	0.00	0	0.01	28	0.19
Water	69	4.31	0	0.00	0	0.00	48	0.65	0	0.00	9	0.36	126	0.89
na**	0	0.00	0	0.00	0	0.00	0	0.00	4	0.18	0	0.00	5	0.03

(*) 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

Araceae	Number	%
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
Arecaceae	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
Bromeliaceae	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
Scarabaeinae	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^2 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^2), 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^2 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^2) with 65% of its area under protection, while priority area 6 (4 519 km^2) is the least protected category with 21%. All priority areas add up to 17 099 km^2, 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^2 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*
Anthurium acutangulum	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
Anthurium acutifolium	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
Anthurium alatipedunculatum	309, 374, 381, 386	wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
Anthurium alticola	136	wf-T Prem	Not endemic
Anthurium angustispadix	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
Anthurium antonioanum	177	rf-LM	Endemic shared with Panama
Anthurium austin-smithii	17, 52, 54, 165	rf-LM, rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
Anthurium bakeri	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
Anthurium bittneri	177	rf-LM	Endemic of Costa Rica
Anthurium bradeanum	2, 17, 25, 42, 165	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
Anthurium brenesii	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
Anthurium brownii	9, 10, 11, 20, 25, 136, 194, 309	mf-T Prem, wf-P, wf-T, wf-T Prem	Not endemic
Anthurium burgeri	317	rf-P	Endemic of Costa Rica
Anthurium caperatum	43, 52, 165, 177, 204, 209, 210, 240	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
Anthurium carnosum	24, 177, 200, 209, 242, 269	rf-LM, rf-M, wf-LM	Endemic shared with Panama
Anthurium clavatum	177, 204	rf-LM, rf-P	Endemic of Costa Rica
Anthurium clavigerum	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
Anthurium clidemioides	17, 309	wf-T	Endemic shared with Panama
Anthurium concinnatum	70, 73, 99, 177, 200, 204, 216, 242	rf-LM, rf-M, rf-P, wf-LM	Endemic shared with Panama
Anthurium consobrinum	2, 9, 10, 11, 17, 25, 37, 52	mf-T, wf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua and Panama
Anthurium cotobrusii	240, 281	rf-P, wf-P	Endemic shared with Panama
Anthurium cubense	2, 11, 80, 183, 186, 194	mf-T, wf-P, wf-P Basal, wf-T	Not endemic
Anthurium cucullispathum	11, 165	rf-P, wf-P	Endemic shared with Panama
Anthurium cuspidatum	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
Anthurium davidsoniae	20, 165, 177, 204	mf-T Prem, rf-LM, rf-P	Endemic shared with Panama
Anthurium durandii	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
Anthurium dwyerii	60	rf-P	Not endemic

Anthurium erythrostachyum	210	rf-P	Endemic shared with Panama
Anthurium eximium	183, 194, 210, 309, 317, 374, 386	rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
Anthurium fatoense	136, 149, 161, 165	mf-T, rf-P, wf-P, wf-T Prem	Endemic shared with Panama
Anthurium flexile	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
Anthurium formosum	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
Anthurium friedrichsthalii	17, 37, 42, 54, 126, 136, 194, 203, 309	rf-LM, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
Anthurium gracile	2, 9, 17, 37, 51, 161, 167, 309, 380	mf-T, wf-P Basal, wf-T	Not endemic
Anthurium hacumense	183, 194, 210, 309, 375, 381	rf-P, wf-P Basal, wf-T	Not endemic
Anthurium hoffmannii	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
Anthurium hornitense	165	rf-P	Endemic shared with Panama
Anthurium interruptum	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
Anthurium kunthii	51, 161	mf-T, wf-P Basal	Not endemic
Anthurium lancifolium	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
Anthurium lentii	52, 60, 165, 177, 204, 216	rf-LM, rf-M, rf-P, wf-T Prem	Not endemic
Anthurium limonense	34	mf-T	Endemic of Costa Rica
Anthurium llanense	161, 165	mf-T, rf-P	Endemic shared with Panama
Anthurium longistipitatum	177	rf-LM	Endemic shared with Panama
Anthurium louisii	165, 177	rf-LM, rf-P	Endemic of Costa Rica
Anthurium michelii	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
Anthurium microspadix	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
Anthurium monteverdense	54	rf-LM	Endemic of Costa Rica
Anthurium obtusilobum	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
Anthurium obtusum	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
Anthurium ochranthum	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
Anthurium oerstedianum	192, 194, 197, 203, 237, 240, 317, 386	rf-P, wf-P rain, wf-T, wf-T Prem	Endemic of Costa Rica
Anthurium orteganum	149	wf-P	Not endemic

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

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

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

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

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

Stenospermation marantifolium	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
Stenospermation robustum	43, 60, 136, 309	rf-P, wf-T, wf-T Prem	Not endemic
Stenospermation sessile	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
Stenospermation spruceanum	25, 43, 165, 177	rf-LM, rf-P, wf-T Prem	Not endemic
Syngonium angustatum	2, 3	mf-P Basal, mf-T	Not endemic
Syngonium armigerum	136	wf-T Prem	Endemic of Costa Rica
Syngonium castroi	309	wf-T	Endemic of Costa Rica
Syngonium hastiferum	309	wf-T	Endemic of Costa Rica
Syngonium hoffmannii	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
Syngonium laterinervium	309, 386	wf-T, wf-T Prem	Endemic shared with Panama
Syngonium macrophyllum	9, 17, 60, 309	rf-P, wf-T	Not endemic
Syngonium mauroanum	251	wf-P	Endemic shared with Panama
Syngonium oduberi	309, 317, 376	rf-P, wf-P Basal, wf-T	Endemic of Costa Rica
Syngonium peliocladum	17, 51	wf-P Basal, wf-T	Endemic shared with Panama
Syngonium podophyllum	10, 11, 17, 136, 186, 194, 203, 309	wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
Syngonium rayi	17, 210	rf-P, wf-T	Endemic shared with Panama
Syngonium schottianum	9, 17, 42, 43	rf-P, wf-P Basal, wf-T	Not endemic
Syngonium standleyanum	43	rf-P	Endemic shared with Nicaragua
Syngonium triphyllum	2, 37, 43, 51, 161, 183, 194, 197, 309, 376	mf-T, rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
Syngonium wendlandii	162, 183, 203, 212	wf-P, wf-P Basal, wf-P rain	Endemic of Costa Rica
Urospatha grandis	17, 42, 161	mf-T, wf-P Basal, wf-T	Not endemic
Xanthosoma dealbatum	183, 194, 263, 309	wf-P Basal, wf-P rain, wf-T	Endemic of Costa Rica
Xanthosoma mexicanum	11, 47, 68, 80, 91, 119, 127, 171, 183, 258	mf-P, mf-P Basal, mf-T, mf-T d, mf-T perhum, wf-P, wf-P Basal	Not endemic
Xanthosoma robustum	374	wf-T Prem	Not endemic
Xanthosoma undipes	11, 60, 149, 165, 177, 263, 309	rf-LM, rf-P, wf-P, wf-P rain, wf-T	Not endemic
Xanthosoma wendlandii	3, 11, 20, 47, 80, 183, 197, 203	mf-P Basal, mf-T, mf-T Prem, wf-P, 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*
Acoelorraphe wrightii	2	mf-T	Not endemic
Acrocomia aculeata	18, 68, 190, 376	df-T, mf-T, mf-T d, wf-P Basal	Not endemic
Aiphanes aculeata	309	wf-T	Not endemic
Aiphanes hirsuta	317	rf-P	Not endemic
Asterogyne martiana	9, 10, 17, 34, 37, 42, 52, 60, 161, 194, 309, 373, 374, 386	mf-T, rf-P, rf-P Basal, wf-P Basal, wf-T, wf-T Prem	Not endemic
Astrocaryum alatum	4, 10, 161, 167, 183	mf-T, mf-T perhum, wf-P Basal, wf-T, wf-T Prem	Not endemic
Astrocaryum confertum	42	wf-P Basal	Endemic shared with Panama
Astrocaryum standleyanum	161, 219, 376	mf-T, wf-P Basal	Not endemic
Attalea butyracea	3, 80, 183, 203, 253	mf-P Basal, mf-T, wf-P Basal, wf-P rain	Not endemic
Bactris ana-juliae	210	rf-P	Endemic of Costa Rica
Bactris baileyana	171, 183, 194, 309, 376	mf-P Basal, wf-P Basal, wf-T	Endemic shared with Panama
Bactris caudata	165, 166	mf-T Prem, rf-P	Endemic shared with Nicaragua and Panama
Bactris coloradonis	17, 52, 136	wf-T, wf-T Prem	Not endemic
Bactris dianeura	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
Bactris gasipaes	161, 309	mf-T, wf-T	Not endemic
Bactris glandulosa	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
Bactris gracilior	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
Bactris grayumii	10, 17, 21, 37	wf-T, wf-T Prem	Endemic shared with Nicaragua
Bactris guineensis	3, 171	mf-P Basal	Not endemic
Bactris herrerana	194, 309, 386	wf-T, wf-T Prem	Endemic of Costa Rica
Bactris hondurensis	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
Bactris longiseta	4, 9, 17	mf-T perhum, wf-T	Endemic of Costa Rica
Bactris major	2, 3, 17, 80, 183, 309, 376, 384	mf-P Basal, mf-T, mf-T perhum, wf-P Basal, wf-T	Not endemic
Bactris maraja	161, 309	mf-T, wf-T	Not endemic
Bactris militaris	17, 161, 270	mf-T, wf-P Basal, wf-T	Endemic shared with Panama
Bactris polystachya	161	mf-T	Endemic of Costa Rica
Calyptrogyne condensata	161	mf-T	Endemic shared with Panama

Calyptrogyne ghiesbreghtiana	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
Calyptrogyne herrerae	165	rf-P	Endemic of Costa Rica
Calyptrogyne trichostachys	5, 9, 10, 11, 19, 29, 43, 165	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
Chamaedorea amabilis	43, 52, 136, 149	rf-P, wf-P, wf-T Prem	Endemic shared with Panama
Chamaedorea anemophila	10, 165	rf-P, wf-T Prem	Endemic shared with Panama
Chamaedorea binderi	194, 263	wf-P rain, wf-T	Endemic of Costa Rica
Chamaedorea brachyclada	194, 237, 240, 263, 309, 317, 374	rf-P, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
Chamaedorea costaricana	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
Chamaedorea crucensis	177, 225, 269, 281	rf-LM, wf-LM, wf-P	Endemic of Costa Rica
Chamaedorea dammeriana	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
Chamaedorea deckeriana	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
Chamaedorea geonomiformis	60, 149, 165, 225, 309, 374	rf-LM, rf-P, wf-P, wf-T, wf-T Prem	Not endemic
Chamaedorea graminifolia	177	rf-LM	Endemic shared with Nicaragua
Chamaedorea hodelii	60, 70, 165, 177, 204	rf-LM, rf-P	Endemic of Costa Rica
Chamaedorea incrustata	225	rf-LM	Endemic of Costa Rica
Chamaedorea lucidifrons	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
Chamaedorea macrospadix	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
Chamaedorea matae	183, 194, 203, 309, 374, 386	wf-P Basal, wf-P rain, wf-T, wf-T Prem	Endemic shared with Panama
Chamaedorea palmeriana	60, 70, 136, 165, 177	rf-LM, rf-P, wf-T Prem	Endemic shared with Panama
Chamaedorea parvifolia	54, 59, 70, 200, 209, 216, 269	rf-LM, rf-M, wf-LM	Endemic of Costa Rica
Chamaedorea pinnatifrons	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
Chamaedorea piscifolia	210	rf-P	Endemic of Costa Rica
Chamaedorea pittieri	200, 216	rf-M, wf-LM	Endemic shared with Panama
Chamaedorea pumila	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
Chamaedorea pygmaea	177, 225, 269	rf-LM, wf-LM	Not endemic
Chamaedorea robertii	43, 60	rf-P	Endemic shared with Panama

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

Geonoma longevaginata	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
Geonoma monospatha	188, 192	mf-P, rf-P	Endemic shared with Panama
Geonoma oxycarpa	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
Geonoma procumbens	10, 17, 19	rf-P, wf-T, wf-T Prem	Not endemic
Geonoma scoparia	309, 373	rf-P Basal, wf-T	Endemic of Costa Rica
Geonoma talamancana	165, 177	rf-LM, rf-P	Endemic of Costa Rica
Hyospathe elegans	60, 120, 165	rf-P, wf-P rain	Not endemic
Iriartea deltoidea	10, 43, 52, 60, 161, 309, 376, 386	mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Manicaria saccifera	37	wf-T	Not endemic
Neonicholsonia watsonii	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
Oenocarpus mapora	194, 309	wf-T	Not endemic
Pholidostachys pulchra	17, 52, 60, 127, 381	mf-P, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Prestoea acuminata	60, 67, 70, 165, 177, 200, 269, 358	rf-LM, rf-P, wf-LM, wf-T Prem	Not endemic
Prestoea decurrens	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
Prestoea ensiformis	109, 194	wf-P Basal, wf-T	Not endemic
Prestoea longepetiolata	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
Prestoea schultzeana	309, 317	rf-P, wf-T	Not endemic
Raphia taedigera	37, 309, 373	rf-P Basal, wf-T	Not endemic
Reinhardtia gracilis	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
Reinhardtia koschnyan	4, 34	mf-T, mf-T perhum	Not endemic
Reinhardtia latisecta	9, 10, 17, 309	wf-T, wf-T Prem	Not endemic
Reinhardtia simplex	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
Sabal mauritiiformis	219	wf-P Basal	Not endemic
Socratea exorrhiza	17, 52, 60, 161, 167	mf-T, rf-P, wf-T, wf-T Prem	Not endemic
Synechanthus fibrosus	17, 51, 60, 126, 165, 263	rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
Synechanthus warscewiczianus	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
Welfia georgii	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*
Aechmea angustifolia	10, 17, 34, 51, 52, 136, 161, 194, 231, 309, 376	mf-T, wf-P Basal, wf-T, wf-T Prem	Not endemic
Aechmea aquilega	166	mf-T Prem	Not endemic
Aechmea bracteata	2, 17, 161	mf-T, wf-T	Not endemic
Aechmea castelnavii	183, 194, 270	wf-P Basal, wf-T	Not endemic
Aechmea dactylina	2, 203, 216, 309, 219	mf-T, rf-M, wf-P Basal, wf-P rain, wf-T	Not endemic
Aechmea lueddemaniana	2, 10, 13	mf-T, rf-P, wf-T Prem	Not endemic
Aechmea magdalenae	2, 11, 37, 80, 136, 161, 183, 272, 309	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Aechmea mariae-reginae	17, 43, 52, 136, 167, 177	rf-LM, rf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
Aechmea mexicana	43, 136, 149, 162, 194, 204, 216, 269	rf-M, rf-P, wf-LM, wf-P, wf-T, wf-T Prem	Not endemic
Aechmea nudicaulis	17, 19, 37, 42, 136, 161, 38	mf-P, mf-T, rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Aechmea penduliflora	13	rf-P	Not endemic
Aechmea pittieri	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
Aechmea pubescens	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
Aechmea tillandsioides	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
Aechmea tonduzii	210, 240, 263, 317, 386	rf-P, wf-P rain, wf-T Prem	Endemic shared with Panama
Aechmea veitchii	165, 177, 200, 204	rf-LM, rf-P, wf-LM	Not endemic
Ananas ananassoides	258	mf-T	Not endemic
Androlepis skinneri	17, 19, 40, 177	rf-LM, rf-P, wf-P rain, wf-T	Not endemic
Araeococcus pectinatus	194, 203, 210, 309, 374, 376	rf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
Billbergia macrolepis	250	wf-T Prem	Not endemic
Bromelia hemispherica	11, 194	wf-P, wf-T	Not endemic
Bromelia pinguin	3, 20, 68, 171, 18, 8, 174, 211	df-T, mf-P Basal, mf-T d, mf-T perhum, mf-T Prem	Not endemic
Bromelia plumieri	3, 11, 80, 258	mf-P Basal, mf-T, wf-P	Not endemic
Catopsis berteroniana	2, 52	mf-T, wf-T Prem	Not endemic
Catopsis hahni	188	mf-P	Not endemic
Catopsis juncifolia	17, 51, 60, 136	rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Catopsis morreniana	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

Catopsis nitida	11, 54, 59, 60, 73, 162, 179, 200, 204, 145	mf-LM, rf-LM, rf-P, wf-LM, wf-P	Not endemic
Catopsis nutans	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
Catopsis paniculata	59, 73, 127, 136, 177, 179, 209	mf-LM, mf-P, rf-LM, wf-LM, wf-T Prem	Not endemic
Catopsis pedicellata	2	mf-T	Not endemic
Catopsis sessiliflora	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
Catopsis wangerinii	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
Greigia columbiana	216, 242	rf-M	Not endemic
Greigia sylvicola	11, 70, 165, 177, 216, 242, 252	p-SA, rf-LM, rf-M, rf-P, wf-P	Endemic shared with Panama
Guzmania angustifolia	43, 52, 54, 136, 200, 240, 269	rf-LM, rf-P, wf-LM, wf-T Prem	Not endemic
Guzmania blassii	29, 43, 177, 200, 204, 210, 216, 227	p-SA, rf-LM, rf-M, rf-P, wf-LM	Endemic of Costa Rica
Guzmania circinnata	177	rf-LM	Not endemic
Guzmania compacta	2, 10, 19, 43, 59, 200	mf-T, rf-P, wf-LM, wf-T Prem	Endemic shared with Nicaragua and Panama
Guzmania condensata	60, 177, 200	rf-LM, rf-P, wf-LM	Not endemic
Guzmania coriostachya	11, 40, 43, 59, 60	rf-P, wf-LM, wf-P, wf-P rain	Not endemic
Guzmania desautelsii	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
Guzmania donnellsmithii	2, 10, 19, 43, 52, 136, 269	mf-T, rf-P, wf-LM, wf-T Prem	Endemic shared with Nicaragua and Panama
Guzmania glomerata	10, 17, 43, 51, 165, 177, 200	rf-LM, rf-P, wf-LM, wf-P Basal, wf-T, wf-T Prem	Not endemic
Guzmania herrerae	5, 11, 25, 43, 149	rf-P, wf-P, wf-P Basal, wf-T Prem	Endemic of Costa Rica
Guzmania lingulata	13, 17, 37, 43, 52, 136, 161, 194, 210, 231, 309, 375	mf-T, rf-P, wf-T, wf-T Prem	Not endemic
Guzmania monostachia	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
Guzmania musaica	136, 165	rf-P, wf-T Prem	Not endemic
Guzmania nicaraguensis	11, 40, 43, 177	rf-LM, rf-P, wf-P, wf-P rain	Not endemic
Guzmania obtusiloba	43, 70, 165, 204	rf-LM, rf-P	Not endemic
Guzmania patula	177, 194, 210, 263, 374, 280	rf-LM, rf-P, wf-P rain, wf-T, wf-T Prem	Not endemic
Guzmania plicatifolia	25, 43, 54, 59, 165, 177, 200, 204	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
Guzmania polycephala	43, 60, 177	rf-LM, rf-P	Endemic shared with Panama
Guzmania sanguinea	11, 13	rf-P, wf-P	Not endemic
Guzmania scandens	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*
Guzmania scherzeriana	11, 17, 43, 51, 52, 136, 204, 210, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Guzmania skotakii	149, 204	rf-P, wf-P	Endemic of Costa Rica
Guzmania spectabilis	70, 165, 194	rf-LM, rf-P, wf-T	Endemic of Costa Rica
Guzmania sprucei	35, 43, 51, 60, 136	rf-P, wf-P Basal, wf-T Prem	Not endemic
Guzmania stenostachya	13, 25, 43, 165, 177, 200, 204	rf-LM, rf-P, wf-LM, wf-T Prem	Endemic shared with Panama
Guzmania subcorymbosa	10, 24, 29, 43	rf-LM, rf-P, wf-T Prem	Not endemic
Guzmania zahnii	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
Mezobromelia pleiosticha	149, 210	rf-P, wf-P	Not endemic
Pitcairnia arcuata	10, 11, 43, 136, 309, 317, 386	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
Pitcairnia atrorubens	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
Pitcairnia brittoniana	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
Pitcairnia calcicola	3, 64, 68, 91	mf-P Basal, mf-T d, wf-P	Endemic of Costa Rica
Pitcairnia funkiae	10, 25	wf-T Prem	Endemic of Costa Rica
Pitcairnia guzmanoides	177, 179	mf-LM, rf-LM	Not endemic
Pitcairnia halophila	171, 194, 309, 219	mf-P Basal, wf-P Basal, wf-T	Endemic of Costa Rica
Pitcairnia heterophylla	11, 13, 24, 73, 192, 209, 210, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic
Pitcairnia kalbreyeri	54, 165, 179, 204, 187	mf-LM, rf-LM, rf-P, wf-P	Not endemic
Pitcairnia lyman-smithiana	204	rf-P	Endemic shared with Panama
Pitcairnia maidifolia	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
Pitcairnia megasepala	258, 309, 253, 373	mf-T, rf-P Basal, wf-P Basal, wf-T	Not endemic
Pitcairnia membranifolia	73	wf-LM	Endemic of Costa Rica
Pitcairnia quesneloides	386	wf-T Prem	Not endemic
Pitcairnia saxicola	209	wf-LM	Not endemic
Pitcairnia valerioi	29, 43, 52, 60	rf-P, wf-T Prem	Endemic shared with Panama
Pitcairnia wendlandii	43, 136, 149, 165, 166, 200, 204	mf-T Prem, rf-P, wf-LM, wf-P, wf-T Prem	Not endemic
Puya dasylirioides	149, 216	rf-M, wf-P	Endemic of Costa Rica
Puya floccosa	177, 240	rf-LM, rf-P	Not endemic
Racinaea adpressa	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

Racinaea contorta	10, 42, 52, 60, 136	rf-P, wf-P Basal, wf-T Prem	Endemic shared with Nicaragua and Panama
Racinaea rothschuhiana	149, 169	mf-P, wf-P	Not endemic
Racinaea schumanniana	70, 73, 177, 200, 209, 92	rf-LM, wf-LM	Not endemic
Racinaea spiculosa	43, 73, 149, 177, 179, 200, 204, 79	mf-LM, rf-LM, rf-P, wf-LM, wf-P	Not endemic
Ronnbergia hathewayi	17, 42, 51, 52, 60, 136	rf-P, wf-P Basal, wf-T, wf-T Prem	Endemic shared with Panama
Tillandsia abdita	73, 162, 209	wf-LM, wf-P	Endemic of Costa Rica
Tillandsia acostae	17, 51, 52, 149, 194, 210, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Tillandsia anceps	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
Tillandsia balbisiana	2, 17, 176, 183, 258, 309, 380	mf-T, mf-T perhum, wf-P Basal, wf-T	Not endemic
Tillandsia biflora	177, 200, 216, 242, 269	rf-LM, rf-M, wf-LM	Not endemic
Tillandsia brachycaulos	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
Tillandsia bulbosa	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
Tillandsia butzii	11, 59, 73, 179, 209, 269, 145	mf-LM, wf-LM, wf-P	Not endemic
Tillandsia caput-medusae	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
Tillandsia cauliflora	210	rf-P	Endemic of Costa Rica
Tillandsia complanata	60, 73, 177, 200	rf-LM, rf-P, wf-LM	Not endemic
Tillandsia excelsa	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
Tillandsia fasciculata	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
Tillandsia festucoides	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
Tillandsia filifolia	51, 52, 149,166	mf-T Prem, wf-P, wf-P Basal, wf-T Prem	Not endemic
Tillandsia flexuosa	376	wf-P Basal	Not endemic
Tillandsia insignis	11, 25, 43, 54, 60, 165, 177, 204	rf-LM, rf-P, wf-P, wf-T Prem	Endemic shared with Panama
Tillandsia ionantha	3	mf-P Basal	Not endemic
Tillandsia juncea	11, 20, 43, 59, 73, 162, 194, 240, 281	mf-T Prem, rf-P, wf-LM, wf-P, wf-T	Not endemic
Tillandsia lampropoda	73, 179	mf-LM, wf-LM	Not endemic
Tillandsia leiboldiana	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
Tillandsia longifolia	73, 177, 200, 209	rf-LM, wf-LM	Not endemic

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

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

Species	*Number of Life Zone polygons*	*Life Zones*	*Endemism*
Werauhia ringens	17, 52	wf-T, wf-T Prem	Not endemic
Werauhia rubra	73	wf-LM	Endemic shared with Panama
Werauhia rugosa	179, 200	mf-LM, wf-LM	Endemic of Costa Rica
Werauhia sanguinolenta	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
Werauhia singuliflora	43, 60, 177	rf-LM, rf-P	Endemic of Costa Rica
Werauhia stenophylla	52	wf-T Prem	Endemic shared with Panama
Werauhia subsecunda	59, 70, 73	rf-LM, wf-LM	Endemic shared with Panama
Werauhia tiquirensis	162	wf-P	Endemic of Costa Rica
Werauhia tonduziana	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
Werauhia umbrosa	13, 59, 177, 210	rf-LM, rf-P, wf-LM	Endemic shared with Panama
Werauhia uxoris	200, 210, 216	rf-M, rf-P, wf-LM	Endemic of Costa Rica
Werauhia vietoris	179	mf-LM	Endemic of Costa Rica
Werauhia viridiflora	11, 13, 17, 177, 194, 200, 204, 209, 210, 240, 269, 309	rf-LM, rf-P, wf-LM, wf-P, wf-T	Not endemic
Werauhia viridis	70, 99, 209, 145	rf-LM, rf-M, wf-LM	Endemic of Costa Rica
Werauhia vittata	11, 17, 43, 52, 60	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
Werauhia vulcanicola	24	rf-LM	Endemic of Costa Rica
Werauhia werckleana	11, 59, 73, 209, 210, 269, 281	rf-P, wf-LM, wf-P	Not endemic
Werauhia williamsii	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*
Agamopus lampros	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
Anomiopus panamensis	2, 10, 17, 183, 281, 309	mf-T, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Ateuchus aeneomicans	183, 203, 281, 309, 372	wf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
Ateuchus candezei	10, 11, 13, 42, 51, 161, 167	mf-T, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Ateuchus fetteri	11, 13	rf-P, wf-P	Endemic of Costa Rica
Ateuchus ginae	24, 160	rf-LM, mf-T Prem	Endemic shared with Nicaragua and Panama
Ateuchus hendrichsi	13	rf-P	Endemic of Costa Rica
Ateuchus howdeni	183, 309	wf-P Basal, wf-T	Not endemic
Ateuchus rodriguezi	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
Ateuchus solisi	10, 167	wf-T, wf-T Prem	Endemic of Costa Rica
Ateuchus zoebischi	10, 13, 25, 52, 167	rf-P, wf-T, wf-T Prem	Endemic of Costa Rica
Bdelyrus seminudus	10, 29, 43, 167, 177, 309	rf-LM, rf-P, wf-T, wf-T Prem	Not endemic
Canthidium angusticeps	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
Canthidium annagabrielae	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
Canthidium ardens	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
Canthidium aurifex	11, 13, 60, 183, 211, 219, 309, 376	mf-T perhum, rf-P, wf-P, wf-P Basal, wf-T	Not endemic
Canthidium centrale	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
Canthidium discopygidiale	11, 13, 43, 59, 60	rf-P, wf-LM, wf-P	Endemic shared with Panama
Canthidium emoryi	177, 204	rf-LM, rf-P	Endemic of Costa Rica
Canthidium guanacaste	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
Canthidium haroldi	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*
Canthidium hespenheidei	2, 5, 10, 11, 17, 29, 37, 42, 43, 52, 136, 161, 167, 183, 203, 309	mf-T, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
Canthidium laetum	2, 3, 11, 18, 68, 127	df-T, mf-P, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
Canthidium leucopterum	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
Canthidium macroculare	281, 309	wf-P, wf-T	Not endemic
Canthidium marianelae	10, 11, 13, 29, 59, 70	rf-LM, rf-P, wf-LM, wf-P, wf-T Prem	Endemic of Costa Rica
Canthidium marielae	309	wf-T	Endemic of Costa Rica
Canthidium pallidoalatum	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
Canthidium perceptibile	11, 13, 29, 59, 263, 281	rf-P, wf-LM, wf-P, wf-P rain	Not endemic
Canthidium planovultum	73, 177, 209, 216, 269	rf-LM, rf-M, wf-LM	Endemic shared with Panama
Canthidium priscillae	29	rf-P	Endemic of Costa Rica
Canthidium pseudopuncticolle	2, 11	mf-T, wf-P	Not endemic
Canthidium tenebrosum	73, 177, 204, 209	rf-LM, rf-P, wf-LM	Endemic shared with Panama
Canthidium tuberifrons	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
Canthidium variolosum	177, 263, 269, 281	rf-LM, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
Canthidium vespertinum	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
Canthidium n. sp	165, 177	rf-P, rf-LM	Endemic
Canthon aberrans	11, 43, 59, 70, 177, 204	rf-LM, rf-P, wf-LM, wf-P	Not endemic
Canthon aequinoctialis	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
Canthon angustatus	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
Canthon caelius	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
Canthon cyanellus	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
Canthon deyrollei	2, 3, 11, 18, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
Canthon euryscelis	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

Canthon hartmanni	11, 13, 177, 263, 281	rf-LM, rf-P, wf-P, wf-P rain	Endemic shared with Panama
Canthon humboldti	183, 192, 203, 309, 381	rf-P, wf-P Basal, wf-P rain, wf-T	Endemic of Costa Rica
Canthon indigaceus chevrolati	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
Canthon juvencus	253, 258, 309	mf-T, wf-P Basal, wf-T	Not endemic
Canthon lituratus	258	mf-T	Not endemic
Canthon meridionalis	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
Canthon moniliatus	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
Canthon morsei	2, 3, 18, 183, 211	df-T, mf-P Basal, mf-T, mf-T perhum, wf-P Basal	Not endemic
Canthon mutabilis	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
Canthon septemmaculatum	228, 258	mf-T, wf-P	Not endemic
Canthon silvaticus	17, 37, 42, 51, 161, 167	mf-T, wf-P Basal, wf-T	Endemic of Costa Rica
Canthon subhyalinus subhyalinus	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
Canthon vazquezae	3, 11, 13, 29, 43, 59, 127, 149, 165, 204, 240	mf-P, mf-P Basal, rf-P, wf-LM, wf-P	Not endemic
Copris costaricensis costaricensis	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
Copris incertus	10, 17, 25, 42, 43, 51, 52, 60, 167, 183, 210, 309	rf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Copris laeviceps	17, 167	wf-T	Not endemic
Copris lugubris	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
Copris subpunctatus	70, 73, 127, 179, 216, 89	mf-LM, mf-LM m, mf-P, rf-LM, rf-M, wf-LM	Endemic shared with Panama
Copris tridentatus	160	mf-T Prem	Endemic of Costa Rica
Coprophanaeus chiriquensis	177, 204, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Not endemic
Coprophanaeus gilli	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*
Coprophanaeus kohlmanni	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
Coprophanaeus pecki	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
Coprophanaeus pluto boucardi	2, 3, 11, 18, 29, 127	df-T, mf-P, mf-P Basal, mf-T, rf-P, wf-P	Endemic shared with Nicaragua
Coprophanaeus solisi	183, 309	wf-P Basal, wf-T	Endemic of Costa Rica
Coprophanaeus telamon corythus	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
Cryptocanthon denticulum	165, 177	rf-P, rf-LM	Endemic shared with Panama
Cryptocanthon lindemanae	309	wf-T	Endemic of Costa Rica
Cryptocanthon osaensis	309	wf-T	Endemic of Costa Rica
Cryptocanthon solisi	60	rf-P	Endemic of Costa Rica
Deltochilum gibbosum	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
Deltochilum lobipes	2, 3, 11, 18, 52, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P, wf-T Prem	Not endemic
Deltochilum mexicanum	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
Deltochilum parile	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
Deltochilum pseudoparile	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
Deltochilum scabriusculum	80	mf-T	Not endemic
Deltochilum valgum	17, 183, 203, 309	wf-P Basal, wf-P rain, wf-T	Not endemic
Dichotomius agenor	183, 203, 190	mf-T, wf-P Basal, wf-P rain	Not endemic
Dichotomius amicitiae	177, 200, 233, 263, 269, 281, 309	rf-LM, wf-LM, wf-P, wf-P rain, wf-T	Endemic shared with Panama
Dichotomius annae	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
Dichotomius centralis	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
Dichotomius costaricensis	The type mentions only Costa Rica as the original locality	It seems possible that the species is a cave dweller	Not endemic
Dichotomius danieli	9, 10, 11, 17, 25, 43, 52	rf-P, wf-P, wf-T, wf-T Prem	Endemic of Costa Rica

Dichotomius favi	17, 42, 161, 167	mf-T, wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
Dichotomius rodrigoi	309, 386	wf-T, wf-T Prem	Endemic of Costa Rica
Dichotomius satanas	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
Dichotomius yucatanus	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
Eurysternus caribaeus	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
Eurysternus hamaticollis	183, 192, 203, 309	rf-P, wf-P Basal, wf-P rain, wf-T	Not endemic
Eurysternus magnus	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
Eurysternus mexicanus	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
Eurysternus plebejus	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
Eurysternus streblus	309, 386	wf-T, wf-T Prem	Not endemic
Eurysternus velutinus	10, 43, 52, 149, 309	rf-P, wf-P, wf-T, wf-T Prem	Not endemic
Malagoniella astyanax	2, 3, 18, 68, 85	df-T, mf-P Basal, mf-T, mf-T d	Not endemic
Megathoposoma candezei	9, 10, 11, 17, 42, 52, 167, 183, 192, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Ontherus azteca	10, 11, 13, 17, 160, 183	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Ontherus brevipennis	10, 219, 309	wf-P Basal, wf-T, wf-T Prem	Not endemic
Ontherus pseudodidymus	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
Ontherus sextuberculatus	11, 17, 29, 51, 52, 60, 149, 309	rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Endemic of Costa Rica
Onthophagus acuminatus	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
Onthophagus andersoni	11, 13, 59, 281	rf-P, wf-LM, wf-P	Endemic of Costa Rica
Onthophagus anthracinus	11, 59, 73, 162, 179, 89	mf-LM, mf-LM m, wf-LM, wf-P	Not endemic
Onthophagus atriglabrus	11, 13, 29, 43, 60, 127, 263, 281, 317	mf-P, rf-P, wf-P, wf-P rain	Not endemic
Onthophagus atrosericeus	73, 177, 200, 216	rf-LM, rf-M, wf-LM	Not endemic

Species	*Number of Life Zone polygons*	*Life Zones*	*Endemism*
Onthophagus batesi	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
Onthophagus championi	2, 3, 18, 47, 68, 183, 190	df-T, mf-P Basal, mf-T, mf-T d, wf-P Basal	Not endemic
Onthophagus chryses	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
Onthophagus coriaceoumbrosus	160, 183, 281, 309	mf-T Prem, wf-P, wf-P Basal, wf-T	Endemic shared with Panama
Onthophagus coscineus	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
Onthophagus crinitus	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
Onthophagus cryptodicranius	17, 42, 167	wf-P Basal, wf-T	Endemic shared with Nicaragua and Panama
Onthophagus cyanellus	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
Onthophagus dicranius	183, 219, 309	wf-P Basal, wf-T	Not endemic
Onthophagus dorsipilulus	177	rf-LM	Endemic shared with Panama
Onthophagus gazellinus	10, 11, 43	rf-P, wf-P, wf-T Prem	Endemic shared with Nicaragua
Onthophagus genuinus	11, 17, 43, 52	rf-P, wf-P, wf-T, wf-T Prem	Endemic of Costa Rica
Onthophagus grataehelenae	73, 162, 177, 204, 263, 269, 281	rf-LM, rf-P, wf-LM, wf-P, wf-P rain	Endemic shared with Panama
Onthophagus hopfneri	3, 18, 47, 68, 159	df-T, mf-P Basal, mf-T, mf-T d	Not endemic
Onthophagus incensus	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
Onthophagus inediapterus	269	wf-LM	Endemic of Costa Rica
Onthophagus landolti	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
Onthophagus limonensis	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
Onthophagus marginicollis	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
Onthophagus micropterus	177, 216	rf-LM, rf-M	Endemic of Costa Rica
Onthophagus nemorivagus	10, 13, 17, 29, 43, 52, 60, 149, 167	rf-P, wf-P, wf-T, wf-T Prem	Endemic of Costa Rica
Onthophagus notiodes	60, 149	rf-P, wf-P	Endemic of Costa Rica

Onthophagus nubilus	240	rf-P	Endemic of Costa Rica
Onthophagus nyctopus	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
Onthophagus orphnoides	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
Onthophagus praecellens	2, 5, 10, 11, 17, 18, 20, 29, 42, 43, 51, 68, 127, 149, 160, 167, 183, 203, 211, 219, 228, 263, 281, 309	df-T, mf-P, mf-T, mf-T d, mf-T perhum, mf-T Prem, rf-P, wf-P, wf-P Basal, wf-P rain, wf-T, wf-T Prem	Not endemic
Onthophagus propraecellens	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
Onthophagus quetzalis	13, 29	rf-P	Endemic of Costa Rica
Onthophagus sharpi	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
Onthophagus singulariformis	52	Wf-Tprem	Endemic to Costa Rica
Onthophagus solisi	10, 13, 20, 29, 43	mf-T Prem, rf-P, wf-T Prem	Endemic of Costa Rica
Onthophagus stockwelli	10, 11, 161, 167	mf-T, wf-P, wf-T, wf-T Prem	Not endemic
Onthophagus tapirus	11, 17, 20, 37, 52, 136, 161, 167	mf-T, mf-T Prem, wf-P, wf-T, wf-T Prem	Endemic shared with Nicaragua
Onthophagus viridivinosus	2, 17, 37	mf-T, wf-T	Endemic shared with Nicaragua
Oxysternon silenus smaragdinum	136	wf-T Prem	Not endemic
Pedaridium bottimeri	161	mf-T	Endemic shared with Panama
Pedaridium bradyporum	51, 149, 183	wf-P, wf-P Basal	Endemic of Costa Rica
Pedaridium pilosum	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
Phanaeus beltianus	10, 11, 17, 20, 43, 51, 52	mf-T Prem, rf-P, wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Phanaeus changdiazi	183	wf-P Basal	Endemic shared with Panama
Phanaeus demon excelsus	3, 18, 68, 127	df-T, mf-P, mf-P Basal, mf-T d	Not endemic
Phanaeus eximius	2, 3, 11, 18	df-T, mf-P Basal, mf-T, wf-P	Not endemic
Phanaeus hermes	240, 253, 258	mf-T, rf-P, wf-P Basal	Not endemic
Phanaeus pyrois pyrois	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*
Phanaeus wagneri wagneri	3, 11, 18, 47, 68, 127, 143	df-T, mf-P, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
Pseudocanthon perplexus	3, 18, 179	df-T, mf-LM, mf-P Basal	Not endemic
Scatimus erinnyos	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
Scatimus ovatus	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
Sisyphus mexicanus	2, 3, 11, 18, 68	df-T, mf-P Basal, mf-T, mf-T d, wf-P	Not endemic
Sulcophanaeus noctis cupricollis	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
Sulcophanaeus noctis noctis	183, 281, 309, 386	wf-P, wf-P Basal, wf-T, wf-T Prem	Not endemic
Sulcophanaeus velutinus	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
Trichillum arcus	10, 11, 20, 25, 42	mf-T Prem, wf-P, wf-P Basal, wf-T Prem	Endemic of Costa Rica
Uroxys boneti	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
Uroxys deavilai	2, 3, 11, 18	df-T, mf-P Basal, mf-T, wf-P	Not endemic
Uroxys depressifrons	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
Uroxys dybasi	10, 11, 13, 43, 59, 73, 162	rf-P, wf-LM, wf-P, wf-T Prem	Endemic shared with Panama
Uroxys gatunensis	309	wf-T	Not endemic
Uroxys gorgon	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
Uroxys metagorgon	149	wf-P	Endemic shared with Panama
Uroxys microcularis	3	mf-P Basal	Not endemic
Uroxys micros	2, 10, 11, 18, 20, 29, 162	df-T, mf-T, mf-T Prem, rf-P, wf-P, wf-T Prem	Not endemic
Uroxys nebulinus	29, 70, 162, 177, 204	rf-LM, rf-P, wf-P	Not endemic
Uroxys platypyga	10, 11, 167	wf-T, wf-T Prem	Not endemic
Uroxys transversifrons	17, 43, 52, 60, 149	rf-P, wf-P, wf-T, wf-T Prem	Not endemic