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1. 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). An appropriate action to this end 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, the writing of biogeographic atlases can be proposed as a practical tool for biodiversity conservation (Prendergast et al., 1993; Morrone, 2000) and hotspot identification (area that combines a high biodiversity with a high threat degree by humans; Myers, 1988; Kappelle, 2008). A very important task of biogeographic atlases is the study of diversity and endemism patterns in order to protect rare and endangered species. As Lomolino et al. (2006) indicate two major tasks of this process are: (1) to document the intensities and locations of hotspots for a particular taxonomic group and (2) to determine to what degree do different taxon-specific hotspots overlap. Although levels of endemism and species richness are frequently positively correlated (Balmford & Long, 1995), unfortunately, many times there is little overlap in the species richness and endemity areas (Bibby et al., 1992; Prendergast et al., 1993; Araujo, 2002; Cox & Moore, 2005; Lomolino et al., 2006). This fact forces the analysis of distribution patterns region by region in order to understand what the approximate situation is and being able to identify biodiversity hotspots (Myers et al., 2000). As Gaston (2000) and Gaston & Spicer (2004) indicate, species distribution is not very uniform across the world and must therefore be mapped. Peaks of diversity exert widespread fascination, especially regarding the origin of high numbers. After all, conservation planning is based on spatial biodiversity distribution (Margules & Pressey, 2000).

Another aspect of the use of biodiversity atlases that has not been previously mentioned is their possible importance as a tool for following distributional changes caused by climatic effects, especially in mountainous areas, such as Costa Rica. The study and knowledge of the aforementioned situation in Costa Rica is of utmost importance. Costa Rica belongs to one (Middle America) of the 36 world hotspots, as defined by Mittermeier et al., (2004). Costa Rica is not a big country (Fig. 1). It has 51,042.8 km² of continental and insular land surface, representing 0.03 % of the Earth surface (Jiménez, 1995; Ministerio del Ambiente y Energía, 2000). In the ranking of world diversity, Costa Rica occupies the 20th place,
approximately. As such, it is not considered a megadiverse country, since only twelve countries build up the list in this category. 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 Rica could probably occupy the first place in the world (Valerio, 1999, 2006; Obando, 2002, 2007). This country possesses approximately 3.6 % of the total expected world 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 (insects: 66 946 species, plants: 11 451 species, other invertebrates: 5253 species) (Obando 2007). To give a comparative idea of species density, Costa Rica has 234.8 plant species per 1000 km$^2$, whereas Colombia, in second place, has only 43.8 plant species per 1000 km$^2$ (Obando, 2007). If we consider orchids alone, Costa Rica has 25.5 species per 1000 km$^2$, whereas Colombia has 2.6 species per 1000 km$^2$ (Valerio, 1999). Similarly, Costa Rica has 28.2 species of vertebrates (excluding fishes) per 1000 km$^2$, whereas Ecuador, the second most biodiverse vertebrate country per km$^2$ in the world, has 9.2 species per 1000 km$^2$, and the third most biodiverse vertebrate country, Malaysia, has only 4.4 vertebrate species per 1000 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 % 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 degree 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 (1102 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 two great groups, four 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. 2); a fifth area has been identified in Coco Island, in the Pacific Ocean (Elizondo et al., 1989). From the ecosystem point of view, cloud forests are the most endemic ecosystems (Obando, 2002). This study defined a biodiversity atlas indicating the areas of high species richness and endemism for Costa Rica, using freshwater fishes (Pisces), insects (Coleoptera: Scarabaeidae: Dynastinae and Coleoptera: Scarabaeidae: Scarabaeinae) and plants (Araceae, Arecaceae and Bromeliaceae). Adequate representation of biodiversity is ideally achieved by the use of multiple taxonomic groups (Stork & Samways, 1995; Pawar et al., 2007; Larsen et al., 2011). However, due to time funding, collection and taxonomic constraints for many 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; Rondini & Boitani, 2006; Pawar et al., 2007). Despite the popularity of the surrogacy approach, its efficacy remains unclear (Moore et al., 2003; Graham & Hijmans, 2006; Lamoreux et al., 2006).

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 also congruence; in other cases the relationships are not clear (Mittermeier et al., 2004).
The analysis focused on continental Costa Rica; Coco Island was not included because neither Scarabaeinae, nor Dynastinae material has been collected from that locality. This atlas represents an effort to help define those areas most in need of conservation and sustainable use in Costa Rica. The atlas will also help define those areas that have been under sampled and therefore future collecting efforts can be directed to these information voids. This study is also an expansion and continuation of previous gap analyses which used beetles and plants (Kohlmann & Wilkinson, 2007; Kohlmann et al., 2007; Kohlmann et al., 2010); the 2007 study has been considered a pioneer study in Costa Rica by Arias et al. (2008), because it represents the first attempt to use the actual distribution of all species of a specific taxonomic group.

2. Biodiversity mapping

2.1 Taxon information
Information regarding dung scarab beetle distribution (coordinates) was taken from the collections and electronic database of the National Biodiversity Institute (INBio, www.inbio.ac.cr). This institution has been collecting plants and insects in Costa Rica for the last 20 years. The dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) have been particularly well studied in relation to their systematics (Kohlmann et al., 2007, 2010). So far, 177 native taxa of Scarabaeinae have been reported in Costa Rica. In relation to the dynastine scarab beetles (Coleoptera: Scarabaeidae: Dynastinae) information was also taken from the electronic database of INBio, as well from the regional study written by Ratcliffe (2003). A total of 125 species were considered. Fish information and distributions were based on the seminal study made by Bussing (1998). Different to Bussing’s holistic study that also considers marine species that penetrate into freshwater or contrariwise, like sharks, sawfishes, tarpons and eels, only strict freshwater fishes (111 species) were considered in this study in order to better reflect local biodiversity. Regarding the three plant families, Araceae, Arecaceae and Bromeliaceae, their distribution information (coordinates) was also taken from the collections and electronic database of the National Biodiversity Institute (INBio).

Additional information was incorporated from the publication “Manual de Plantas de Costa Rica. Gimnospermas y Monocotiledóneas (Agavaceae-Musaceae)”, published by Hammel et al. (2003). Furthermore, extra information was obtained from the Missouri Botanical Garden electronic database (www.mobot.org). The total number of plant species considered for this study was: Araceae, 229 species; Arecaceae, 107 species; Bromeliaceae, 187 species. No introduced species, neither animals nor plants, were considered for this study. Concluding, the six 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, therefore complying with Müller’s (1981) three tenets for making this group particularly well-suited for the present biogeographic analysis.

2.2 Vegetation base map
One of the most popular systems used in Costa Rica and in twelve other countries (Meza, 2001) for the classification of vegetation is the Life Zone System developed by Holdridge (1967). This system divides Costa Rica into 12 Life Zones and 11 Transition Zones based on environmental factors such as humidity, rainfall and temperature (Fig. 3). This system is thus independent of floristic relationships and the same zones can then reappear in different regions of the world. According to Hall (1984), this system takes into account not only
variations caused by latitude, but also by altitude, and is therefore especially useful for tropical mountainous countries (Meza, 2001).

Fig. 1. View of Costa Rica looking northwest as seen from the Space Shuttle (taken from Kohlmann et al., 2002).

According to this classification, the five most extensive vegetation types are: tropical wet forest (wf-T) (10.5 % of the total country area), premontane wet forest (wf-P) (7.2 %), lower montane wet forest (wf-LM) (5.9 %), premontane rain forest (rf-P) (5.6 %) and tropical moist forest (mf-T) (5.5 %) (Obando, 2002). There are some limitations to this system. The Holdridge life zone system can potentially vary along other environmental axes, besides total precipitation and temperature, such as edaphic conditions and this could impact species abundance and endemism. For example, bioclimatic regions such as the Pacific dry forest comprise long belts along mountain/volcanic ranges, and by assuming that these long belts share the same biodiversity category a potential risk can be generated of losing resolution when assigning conservation priority zones.

2.3 GIS Analysis

Some of the advantages of digital mapping techniques using Geographic Information Systems (GIS), comprise that they are faster, more efficient, and more powerful and versatile than traditional analog cartography. Some of many advantages of these 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 that reason we have followed a GIS-oriented process for the elaboration of our biogeography atlas. For the GIS analysis the following processes were done using Arcview® 3.1 (ESRI, 2002), ArcGIS® 9.2 (ESRI 2006) and Microsoft Excel® (2002):

1. Establishment and cleansing of the data bases for each taxon in relation to taxon names, type of endemism and location of collecting sites. Information layers were generated using the collecting sites for each species.
2. Depuration of referential geographic information. The layers containing the National System of Coordinates were transformed to geographic coordinates (the same datum

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Fig. 2. 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 (taken from Kohlmann et al., 2002).
was always used: Fundamental de Ocotepeque). For distributional referencing, each Holdridge life zone polygon was numbered (Fig. 3).

3. For each taxon the collecting sites were superimposed on the Holdridge life zones and out of this product the number of collections and taxa, as well as the total number of taxa and endemics and type of endemicty (endemics known to occur only in Costa Rica, endemics shared with Panama, endemics shared with Nicaragua, endemics shared with Nicaragua and Panama, total number of endemics for Costa Rica) were obtained for each life zone polygon. Each polygon was associated with the number of collections per taxon, the total number of collections and taxa. Layers for the total number of taxa and each type of endemism were produced for the groups.

4. The collecting sites were overlaid on the Holdridge life zones for the total number of taxa and endemics, as well as each of the possible endemism situation, following Morrone’s (2000) suggestions regarding the formal preparation of a biogeographic atlas. 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 rank levels of species richness and endemism by life zone were calculated in accordance with a previous classification used for Costa Rica, as defined by Kohlmann et al. (2007, 2010). Accordingly, five levels were distinguished for both categories. Concerning species richness these limits are: up to 7 % of the maximum species richness in a single Life Zone (class one), up to 20 % (class two), up to 44 % (class three), up to 70 % (class four) and more than 70 % (class five). For the sake of this analysis and comparative purposes, only the two most numerous ranks (ranks 4 and 5) were used. Thus this system allows us to focus the analysis on the richer and therefore more representative areas. Concerning endemism the limits for the five classes are: up to 12 % of maximum number of endemic species in a single Life Zone for class 1, with 24 %, 46 %, 72 %, and over 72 % for classes 2 through 5, respectively. For each taxonomic group these relative values were converted into absolute values of species richness and endemism. For the sake of this analysis and comparative purposes, only the two most numerous ranks were used, following the logic outlined in the previous discussion on species richness.

6. A conservation priority map was elaborated overlaying layers of maps of species numbers and endemics over a map of protected areas. These two maps (species richness and endemics) indicated each one five different number of taxa classes (1-5), where class 5 is the class with the highest number of taxa. Subsequently, two conservation priority zones were defined in a gap analysis map by overlaying the species number and endemics map on the protected areas map. Conservation priority zones were defined according to the following scheme: priority conservation zone 1 is defined by a species richness and endemicty rank of 5, conservation priority zone 2 is defined by an endemicty rank of 5 and a species richness rank of <5.

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 endemicty 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 endemicty areas 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 endemicty over species richness in the definition process follows well
established recommendations expressed by Mittermeier et al. (2004), because the endemics are irreplaceable.

3. Conclusion

3.1 Distribution of collection localities
The collection localities indicate that the northern part of Costa Rica, as well as the Central Pacific, are under collected; due mostly to the fact that these areas have been highly altered by agricultural activities. Other areas that also require more collecting effort are the Nicoya peninsula of Northwestern Costa Rica and the higher parts of the Talamanca Cordillera to the southeast; the lack of roads in these regions is one of the main barriers to collecting in these areas. The selection of collecting sites is often biased. Unfortunately, as already indicated, not all areas of Costa Rica have been collected with equal intensity. In order to deal with under sampled areas, as well as to know the areas with a good collecting record, and for comparative purposes, regions with a collecting effort of five or more years were arbitrarily chosen for this study (Fig. 3). The subsequent analyses will be based on these regions. Life zones areas depicted in grey in several maps (Figs. 7-8), represent zones where no collecting efforts have been undertaken, thus indicating regions where collecting should be directed in the future.

Fig. 3. 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 in this study as well represented (taken from Kohlmann et al., 2010).
3.2 Protection of life zone areas

Costa Rica has a total mainland area of 51,042.8 km². Out of these, 12,422.4 km² (24.3 %) are under some sort of official governmental protection. Noteworthy is that a 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 area under protection are: 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.

3.3 Distribution of species richness by life zone

Figure 4 indicates species richness per group per life zone in Costa Rica. Only the life zones highlighted with a star have been well sampled (i.e. more than five years of collecting), therefore, they can be adequately compared. Figure 4 also clearly shows where no members of the taxa under study have been found so far. It should be noted that the highest species richness areas do not coincide for all the taxa in the same place. Araceae, Arecaceae, and Bromeliaceae (Fig. 4) show the same areas of highest species richness in the premontane rain forest (rf-P) and the Scarabaeinae and Dynastinae show an area of highest species diversity coinciding in the premontane wet forest (wf-P) along the different mountain systems; whereas Pisces shows its highest species richness area in the premontane wet forest (Basal transition) (wf-P Basal). In the second highest species richness rank we have that Pisces, Dynastinae, Araceae and Arecaceae coincide in the tropical wet forest (wf-T). Scarabaeinae and Dynastinae show their second highest species richness levels in the premontane rain forest (rf-P) and the lower montane rain forest (wf-LM), respectively.

The overall highest species richness life zones in descending order are: the tropical wet forest (wf-T), the premontane rain forest (rf-P), the premontane wet forest (wf-P), the tropical wet forest (premontane transition) (wf-T Prem), and the premontane wet forest (basal transition) (mf-P Basal). The tropical wet forest (wf-T) (approx. 0 masl – 500 masl, average temperature 24 °C) is generally considered to be the most species rich ecosystem in Costa Rica (Fogden & Fogden, 1997; Valerio, 1999). The premontane rain forest (rf-P) and the premontane wet forest (wf-P) (approx. 500 masl – 1750 masl, average temperature between 17 °C and 24 °C) cover one of the largest geographical areas in the country, where the upper altitudinal limit corresponds spatially with the frost line or with the so-called “coffee line” (Valerio, 2006).

3.4 Distribution of endemicity by life zone

Figure 5 shows the overall number per group of endemic species per life zone. We basically mapped the total number of endemic species (strictly endemic plus shared with Nicaragua and/or Panama) by life zone. Interestingly, coincidences of the highest endemicity areas exist for almost all taxa in the same life zone (Fig. 5). The common areas are the premontane rain forest (rf-P) between the Araceae, Arecaceae, Bromeliaceae, Dynastinae, and Scarabaeinae. Only Pisces has its highest endemicity area in the premontane wet forest (Basal transition) (wf-P Basal).

The overall highest number of endemics by life zone in descending order are: the premontane rain forest (rf-P), the tropical wet forest (wf-T), the premontane wet forest (wf-P), the premontane wet forest (Basal transition) (wf-P Basal), and the lower montane rain forest (mf-P Basal).
forest (rf-LM). Several coincidences occur for the second rank. Pisces, Araceae, and Arecaceae coincide in the tropical wet forest (wf-T), Scarabaeinae and Dynastinae in the premontane wet forest (wf-P). 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 results end up supporting Obando’s (2002) conclusion that the cloud forest is the most endemics-rich ecosystem of Costa Rica.

3.5 Representativeness of the protected areas
As previously indicated above, 24.3 % of the total mainland area represents some sort of a governmentally protected area. An analysis of the totality of the species for each of the studied groups (Araceae, 229; Arecaceae, 107; Bromeliaceae, 187; Dynastinae, 125; Scarabaeinae, 177; and Pisces, 111) indicates that: 205 (89.5 %), 95 (88.8 %), 156 (83.3 %), 108 (86.4 %), 165 (93.2 %), and 99 (89.2 %) species, respectively, are present in protected areas. Likewise, an analysis for the total number of endemics for each of the six groups under study (Araceae, 116; Arecaceae, 57; Bromeliaceae, 80; Dynastinae, 68; Scarabaeinae, 68; and Pisces, 62) indicates that 97 (83.6 %), 40 (70.2 %), 64 (80 %), 55 (80.8 %), 64 (94.1 %), and 53 (85.5 %) species, respectively, are present in protected areas.

3.6 Areas of highest species richness per life zone
There are three zones with highest species richness (Fig. 6) according to the overlay of the six groups under study: the first two are the tropical wet forests (wf-T) (approximately 0 masl – 500 masl) in the northeastern corner, bordering Nicaragua (although most probably the central and southern Caribbean coast might also have high numbers that shall become evident after a more intense collection programme is applied), and the Osa Peninsula region. It would appear that the high species richness of these lowland forests tend 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 (wf-P) (approximately 500 masl – 1750 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 & Kussmaul, 2000), thus contradicting all the tenets (time, species-area, and modified species-area relationship) of the island biogeography theory. 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 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).
Fig. 4. Distribution of species richness by life zone. Life zones highlighted with a star have been sampled for more than five years and are therefore well-sampled.

Fig. 5. Distribution of endemic species by life zone. Life zones highlighted with a star have been sampled for more than five years and are therefore well-sampled.
3.7 Areas of highest endemism per life zone

The areas of highest endemism (Fig. 7) according to the overlay analysis show a great spatial correspondence with the previous analysis, containing the same aforementioned three areas. A similar situation had 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) (approx. 1000 – 2000 masl) on both slopes of 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 & Solís, 2006).

Obando (2002) reports in her study the existence of five major areas of endemism in Costa Rica. These areas are represented by Coco Island, which was not considered in this study; the Golfo Dulce region (Fig. 2, O), the Cordillera Central (Fig. 2, C), the Talamanca mountain range (Fig. 2, T), and the Central Pacific region (Fig. 2, P). This study supports previously proposed areas of endemism, with the exception of the Central Pacific region. However, three 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. 7). 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 reason 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, a place with rare and unusual species (not necessarily an area of endemism). At the same time, the Caribbean lowlands have a relatively recent origin (Pliocene-Pleistocene) according to 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).

3.8 Distribution of priority conservation areas

Two conservation categories were defined (Fig. 8). As a reminder suffice to say that a complementarity system was used (Williams et al., 1996), where areas of greatest species and endemicty richness defined the priority conservation categories. In the present case, endemicity was prioritized over species richness, following Mittermeier et al., (2004). Tropical wet forests (wf-T) on the Nicaraguan border and the Osa Peninsula, as well as premontane wet forest (wf-P) along the Central, Tilarán and Guanacaste Cordilleras were determined as priority 1 conservation areas. On the other hand, premontane rain forest (rf-P) on the Tilarán Cordillera and lower montane rain forest (rf-LM) on both slopes of the Talamanca Cordillera were determined as priority 2 conservation areas.

3.9 Number of endemics

Regarding the percentage (26 % - 45 %) of regional (Nicaragua-Costa Rica-Panama) (Table 1) endemic values, they are fairly high, as compared to the 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. These figures also compare well with the estimates that Obando (2002) established for plant endemism (12 %) in Costa Rica.
Mammals and birds on the contrary present low values of endemism of 0.8 % and 2.5 %, respectively, according to Obando (2002), being one reason for not developing a conservation analysis using only these groups, as is usually done. The use of other groups, like insects, plants and freshwater fishes, can give a much more detailed picture of areas of endemism.

Fig. 6. Overall species richness ranks, based on the totality of the studied groups and their overlap with the established protected areas. Areas in grey represent zones where no collecting has been undertaken. Divortium aquarum = watershed divide.

4. Discussion

4.1 Representativeness of protected areas
The representativeness analysis indicates that a high number (Araceae 89 %, Arecaceae 89 %, Bromeliaceae 83 %, Dynastinae 86 %, Scarabaeinae 95 %, and Pisces 89 %) 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 %, Dynastinae 80 %, Scarabaeinae 97 %, and Pisces 85 %) in these protected areas. It is possible that the number for plants may be slightly
underestimated, because the dung beetles have been more thoroughly collected. It can be argued that the representation of both, species richness and endemics, in protected areas is already high.

Fig. 7. Overall endemic species richness ranks, based on the totality of the studied groups and their overlap with the established protected areas. Areas in grey represent zones where no collecting has been undertaken. Divortium aquarum = watershed divide.

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. It is interesting to compare the above results with a similar analysis undertaken by McLean & Meyer (2010), where they estimate that 71 % of the original biodiversity of Costa Rica is still preserved inside protected areas and only 46 % of this same biodiversity is preserved in the whole country! Their analysis was not based on actual counting, but using a model called Mean Species Abundance (MSA), that combines various pressures on biodiversity (land use, infrastructure, fragmentation, and climate change). This study by McLean & Meyer (2010) does arrive to
the same conclusion presented by Kohlmann et al. (2010), that land use is the main threat impacting the loss of biodiversity, especially pastures and agriculture. This same study (McLean & Meyer, 2000) also concludes that the zones indicated in this study as priority conservation zones are also the areas showing the greatest remaining biodiversity in Costa Rica.

Fig. 8. Distribution of conservation priority zones based on the overlay of species and endemic species richness ranks. Divortium aquarum = watershed divide.

4.2 Distribution of priority conservation areas
Information taken from the two previous maps (Figs. 7 and 8) serves as a base for the present gap analysis creating a conservation priority map (Fig. 8). Priority zone 1 indicates the areas where the highest species richness (rank 5) and the highest endemics (rank 5) numbers coincide. 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 zone 2 indicates the areas where the highest endemicty level (rank 5) coincides with areas below the highest species richness level (rank<5). Two areas are defined in this category: the lower
montane rain forest (rf-LM) on the Talamanca mountain range and the premontane rain forest (rf-P) on the Tilarán Cordillera.

4.3 Representativeness and complementarity

In the past, the majority of the species richness and endemcity studies of Costa Rica have relied basically on vertebrate distribution analysis, especially birds and big-sized vertebrates as indicator indexes of human impacts on the biodiversity, and more recently plants have 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 three plant families, two beetle subfamilies, and freshwater fishes instead. This analysis suggests the existence of three previously undetected endemcity areas (Fig. 7) that had not been registered using 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 endemcity (Fig. 8), 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 incredible work done by the INBio (Obando, 2007). Still, some areas have been under collected, but the available information allows us to elucidate general patterns.

| Taxonomic group | Total number of species | Endemics |
|-----------------|-------------------------|----------|
|                 |                         | Total by group | %   |
| Araceae         | 229                     | 116       | 50.6 |
| Arecaceae       | 107                     | 57        | 53.2 |
| Bromeliaceae    | 187                     | 80        | 42.7 |
| Dynastinae      | 125                     | 66        | 52.8 |
| Scarabaeinae    | 177                     | 68        | 38.4 |
| Pisces          | 111                     | 62        | 55.8 |
| **Total**       | **936**                 | **449**   | **48.9** |

Table 1. Total number of species and regional endemics by taxonomic group.

This analysis represents a complementary representation and contribution to the excellent proposal presented by the National System of Conservation Areas (Sistema Nacional de Áreas de Conservación (SINAC, 2007b) of Costa Rica. This analysis did follow a different conceptual and methodological approach by defining a conservation strategy oriented toward the necessity of representativeness 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 relevance that are conservation-compatible by basing its conservation planning strategy mostly on a phytogeographic system (Zamora, 2008), 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 & 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 & Brooks, 2007: 719), where surrogacy is defined as: “extent to which conservation planning based on a particular set of biodiversity features (surrogates) effectively represents another set (targets)” (Rodrigues & Brooks, 2007: 714). Additionally, Pawar et al. (2007) did a very interesting conservation biogeography hierarchical analysis of cross-taxon distributional congruence in North-East India, using amphibians, reptiles and birds from tropical rainforest sites. They found that inherent life-history characteristics shared by certain groups contribute to observed patterns of congruence. They also found that examining biologically distinct subsets of larger groups can improve the resolution of congruence analysis, thus refining area-prioritization initiatives by revealing fine-scale discordances between otherwise concordant groups and vice versa and therefore providing a better resolution even with single-group data. This congruence can then be used as a diversity surrogate simplifying the task of area prioritization and conservation and efficient use of resources. 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 need for cross-taxon analyses and area prioritization efforts.

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