Connecting two continents: species richness, functional traits and extinction risk in the Panamanian Isthmus-Choco continuum

Conectando dos continentes: riqueza de especies, caracteres funcionales y el riesgo de extinción en el continuo del Istmo de Panamá-Chocó

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Abstract

Macroecological analyses provide a powerful tool for evaluating the animal communities and the conservation status of an ecoregion. Using this approach in smaller scales allows reaching solid results in how the species richness, functional traits and extinction risk are changing throughout a specific region. The connectivity area between the Costa Rican Seasonal forest and the Chocó Darién Moist Forest represents the bridge between the Mesoamerican region and the Andean tropical region. This area has historical importance based on the role played in the great mammal exchange, currently containing over 327 species of mammals and possessing well preserved forest patches as well as highly deforested areas. Species composition follows a clear pattern within a geographic logic, but extinction risk and functional traits do not follow the same pattern. Here we provide exploratory and preliminary analyses of the ecological continuum between Costa Rica and Colombia, based on a macro-ecological perspective, in order to provide insights on current biogeographical and threat patterns as a basis for ecological understanding and conservation planning.

Keywords: Chocó; Costa Rica; Darién; Extinction risk; Mammal diversity; Panamá Isthmus; Species turnover.

Resumen

Los análisis macroecológicos proporcionan una potente herramienta para evaluar las comunidades de animales y el estado de conservación de una ecoregión. Utilizar el enfoque macroecológico en escalas menores que las usuales, permite llegar a resultados concretos sobre la forma en que la riqueza de especies, las características funcionales y el riesgo de extinción están cambiando a lo largo de una región específica. La región entre el bosque estacional de Costa Rica y el bosque húmedo del Chocó Darién representa el puente de unión entre la región de Mesoamérica y la región andina tropical. Además de la importancia histórica que desempeñó esta misma región durante el gran intercambio faunístico americano, la región actualmente alberga más de 327 especies de mamíferos y enmarca un mosaico compuesto por cultivos mixtos, grandes áreas de bosque con altos niveles de conservación y zonas altamente deforestadas. Se encontró un patrón claro en cuanto a la continuidad a nivel de la composición de especies en términos geográficos, mas no así a nivel funcional y de riesgo de extinción. Aquí presentamos los análisis exploratorios y preliminares de la continuidad ecológica entre Costa Rica y Colombia, con base en una perspectiva macroecológica, con el fin de proporcionar información sobre los actuales patrones biogeográficos y de amenazas como base para la comprensión ecológica y la planificación de la conservación.

Palabras clave: Chocó; Costa Rica; Darién; Diversidad de mamíferos; Istmo de Panamá; Recambio de especies.

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Introduction

Understanding the mechanisms of geographical variation in species richness across an specific taxa represents a major challenge for ecology and conservation strategies (McGill 2003, Jetz *et al.* 2009, Soberon and Ceballos 2011). Macroecological analyses have acquired a great deal of importance over the last two decades, mainly due to that large scale analyses allow a different perspective to evaluate the animal communities and the conservation status of an ecoregion. This is important in designing new management strategies for the regions transcending the political borders of the countries. The techniques have been generally applied in assessing how the communities are structured in large scales and have proven to be very successful in describing general patterns, but the same approach has not been used to understand the processes that are linked to the patterns in the structuring of communities at smaller scales (Beck *et al.* 2012).

Smaller scale analysis with a macroecological approach will allow reaching consistent results (Rondinini *et al.* 2011), especially when determining how the species richness, functional traits and extinction risk are changing throughout a specific area. The region between the Costa Rican Seasonal forest and the Chocó Darien Moist Forest represents the connecting bridge between the Mesoamerican region and the Andean tropical region. Besides the historical importance that this same region played in the great mammal interchange, currently the region harbors over 327 species of mammals and possess well preserved forest patches as well as highly deforested areas along the landscape (Sánchez-Azofeifa *et al.* 2001).

Over the years, the research has focused in the comparisons made between ecoregions analyzing how the species composition changes from one site to another. Although these classical approach is useful, due to species introduction and local extinctions, there is a great deal of redundancy in the communities across a large region. Here is when it becomes important to evaluate the functional traits and groups of an animal community in order to obtain more plausible comparisons between the sites (Vitousek *et al.* 1997, McGill *et al.* 2006, Messier *et al.* 2010). Thereby to understand these functional traits, we need more research and understanding of the deficiencies in the current data gaps, the missing data on species, distribution and phylogenetic relatedness since this aspects make more difficult to assess the global and regional biodiversity patterns and underlying processes. This exploratory analysis is based on current knowledge (including biogeographical patterns and threats) and the idea is to relate all this information with the current challenges in the management and conservation planning of the ecological realms. Here we provide an exploratory and preliminary analysis of the ecological continuum between Costa Rica and Colombia, based on a macroecological perspective, in order to provide insights on current biogeographical and threats patterns as a basis for ecological understanding and conservation planning.

Materials and methods

Study area. Our study focused on the mammal fauna present on five ecoregions defined by the World Wildlife Fund (WWF; Olson *et al.* 2001), covering from Costa Rica towards northwestern between Panama and Colombia (Figure 1). The ecoregions analyzed were the Chocó-Darién moist forests (C-D MF), Costa Rican seasonal moist forests (CR SMF), the Isthmian-Atlantic moist forests (I-A MF), the Isthmian-Pacific moist forests (I-P MF) and the Talamancan montane forests (T MF). This continuum represents the connection between the two sub-continents, North and South America. We selected these ecoregions based on ecological and ecosystem affinities (in terms of biomes), including the area where more shared ecological affinities could be expected. Of the five ecoregions, the largest one corresponds to Chocó-Darién moist forests, whilst the smallest is the Costa Rican seasonal moist forests, been this ecoregion and the Isthmian-Pacific moist forests the most threatened according to WWF classification (Table 1; Olson *et al.* 2001, Olson & Dinerstein 2002). So, even that the ecoregions shared a common geological past and stand close of each other, the conservation needs and the threats differ greatly from one to another.

Methods. Based on the five ecoregions studied, we analyzed the composition of mammal assemblages based in three variables: species composition,

Table 1. Ecoregions analyzed and their characteristics (WWF 2009)

Ecoregion name	Area (km²)	Global status	Biome
C-D MF	73.556,27	Relatively Stable/Intact	Tropical and subtropical moist broadleaf forests
CR SMF	10.699,08	Critical/Endangered	
I-A MF	58.761,68	Vulnerable	
I-P MF	29.177,08	Critical/Endangered	
T MF	16.287,19	Relatively Stable/Intact	

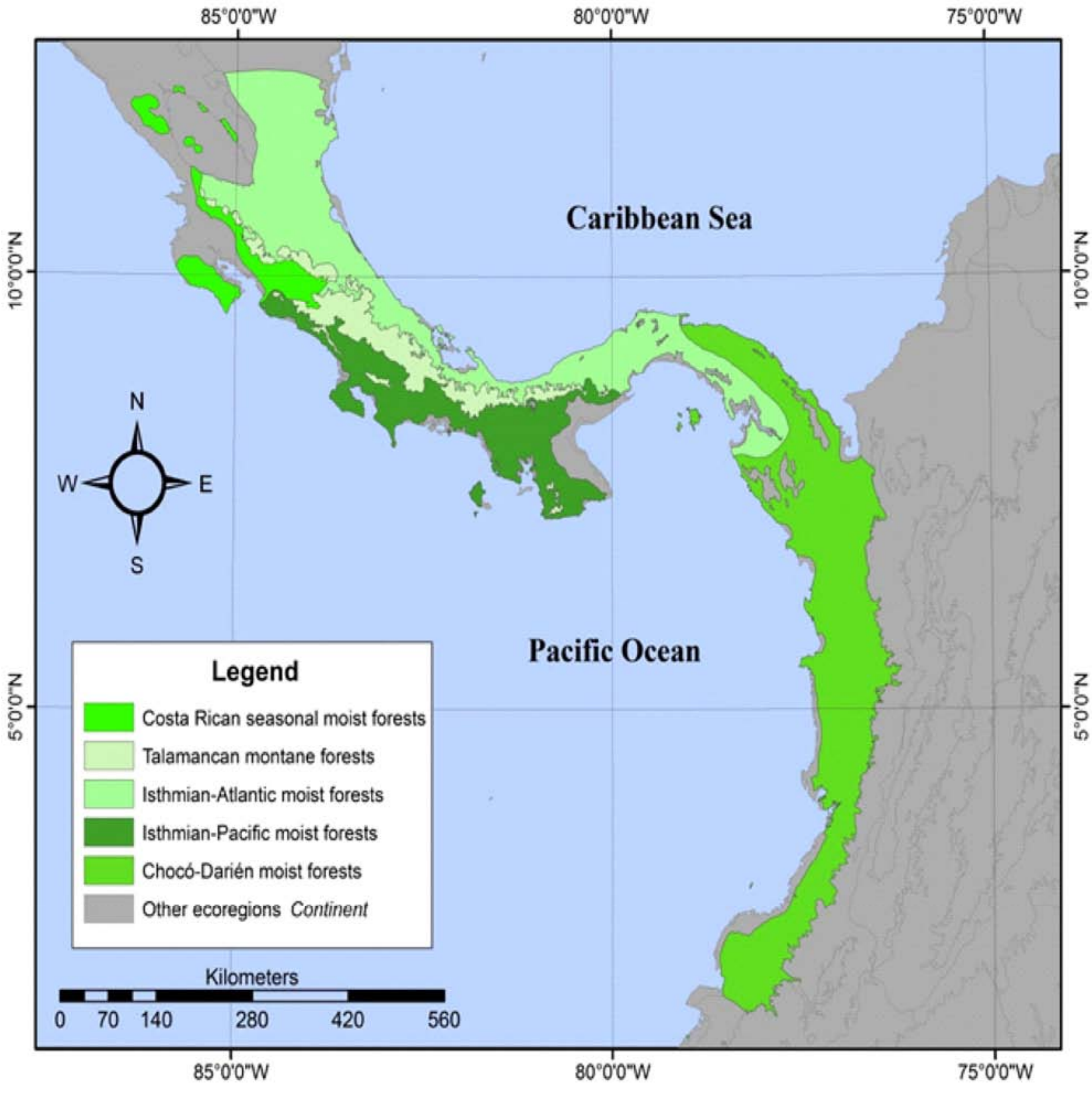

Figure1. Ecoregions used for macroecological analyses in the Costa Rica-Panamá-Colombia isthmus.

life traits and extinction risk. We extracted the geographic information for the five ecoregions from the WWF Ecoregions Database (WWF 2009), and used the distribution polygons for all mammals from the IUCN Red List of Threatened Species (IUCN 2012). We extracted those species present on each ecoregion by a spatial overlapping using ArcGIS (ESRI 2009). After obtaining the species composition, we classified each species according to the following traits: Mass (five categories: small, small-medium, medium, medium-large and large), guild realm (three categories: herbivore, carnivore and omnivore) and habits (five categories: terrestrial, aquatic, fossorial, arboreal and volant) based on previous databases (Davidson *et al.* 2009, Jones *et al.* 2009) and our updates. Also, each species was classified according to its conservation status following the IUCN Red List of Threatened Species categorization, available at IUCN (2012).

We explored the species composition on each ecoregion and compared the compositions across the five of them using cluster analyses (Jaccard mean average distance for species richness and traits and Euclidian Average linkage for threat categories). Also, a Simple Linear Regression was used to relate the area of each ecoregion and the species richness. Contingency tables were used to explore the relationship between the number of traits and number of species on each threat category and the ecoregions. All the statistical analyses were performed in Infostat (Di Rienzo *et al.* 2011).

Results

A total of 327 species of mammals were obtained for the five ecoregions. The Chocó-Darién moist forests was the ecoregion with the highest richness, followed by the Isthmian-Atlantic moist forests, while the Costa Rican seasonal moist forests showed the lowest species richness (Table 2, Figure 1). In this sense the area of the ecoregion significantly explained the number of species present in each area (Lineal regression: R^2=0,8036, p=0,0394).

The relationship and similarity between the ecoregions according to the number of species on each area, showed a significant relationship between the Talamancan Montane Forests and the Isthmian Pacific Moist Forests, decreasing the association respectively with the rest of ecoregions, while the Chocó-Darién Moist Forests were the most distinctive (Figure 2).

In terms of functional traits, for all ecoregions the most abundant traits (number of species) were carnivores, volant and small, showing a significant decreasing pattern according to species richness (Figure 3). No significant relationship was found between the number of species of each trait and the ecoregion (p>0,99).

The relationship between the richness of each trait relating all the ecoregions showed significant relationship between the Isthmian-Pacific moist forests with Costa Rican Seasonal moist forests and the Talamancan montane forests with the Isthmian-

Table 2. Total richness and number of species per mammal order in the five ecoregions of the isthmus.

Order	C-D MF	CR SMF	I-A MF	I-P MF	T MF
Artiodactyla	6	4	4	4	4
Carnivora	22	20	20	18	18
Chiroptera	135	104	100	93	93
Cingulata	2	2	2	2	2
Didelphimorphia	14	8	8	7	7
Insectivora	1	4	4	3	3
Lagomorpha	1	3	3	2	2
Pilosa	5	5	5	5	5
Primates	11	4	3	3	3
Paucituberculata	2	0	0	0	0
Pterissodactyla	1	1	1	1	1
Rodentia	57	45	40	34	34
Total	257	200	190	172	172

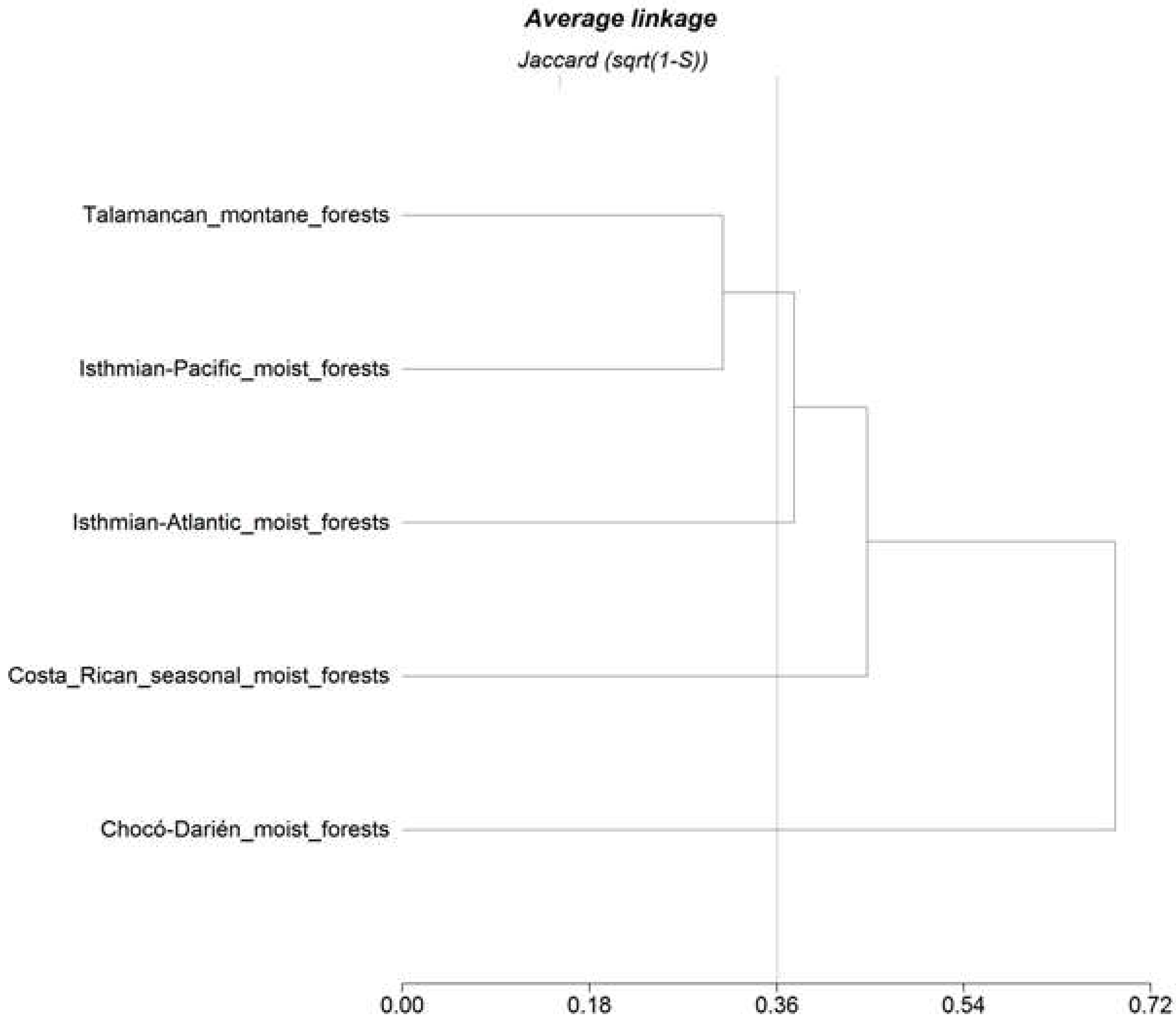

Figure 2. Cluster analyses based on Jaccard average distance for each ecoregion according to species richness.

Atlantic moist forests, while the Chocó-Darién moist forests was significantly different from the rest (Figure 4).

In terms of threats and conservation status, the vast majority of species on each ecoregion belonged to the Least Concern category (LC), followed by Data Deficient (DD) and Near Threatened (NT) (Figure 5). No significant relationship was found between the IUCN category and ecoregions (Contingency Table: $p<0,3713$). Although, the association between ecoregions based on the number of species on each category showed a significant relationship between the Isthmian-Pacific moist forests and Costa Rican Seasonal moist forests followed by the Talamancan Montane Forests (Figure 6).

Discussion

Mammal richness in the isthmus varies significantly among ecoregions, however, with no significant differences among the different orders. While the C-D MF is the ecoregion with the highest richness and T MF has the lowest, there is not a consistent gradient neither North-South nor South-North direction. Despite the geographic position of all the ecoregions and the closeness among them, differences in the number of species can be found in terms of species composition between the regions. One possible explanation is related with elevation and environmental factors. Rahbek (1995) demonstrated that diversity decreases with elevation, although for mammals there is consistent evidence that the highest richness is nested in mid-elevation (McCain 2005, Belmaker and Jetz 2011), and the mammal assemblages in high elevations are composed of complementary species (i.e. species that are less similar in their functional traits; Safi *et al.* 2011).

Our results indicate that the T MF ecoregion, located right in between of I-A MF and I-P MF, showed the highest similarity, significantly differencing those on the extremes (C-D MF and CR SMF), showing an interrupted pattern towards the middle. This represents an interesting trend showing

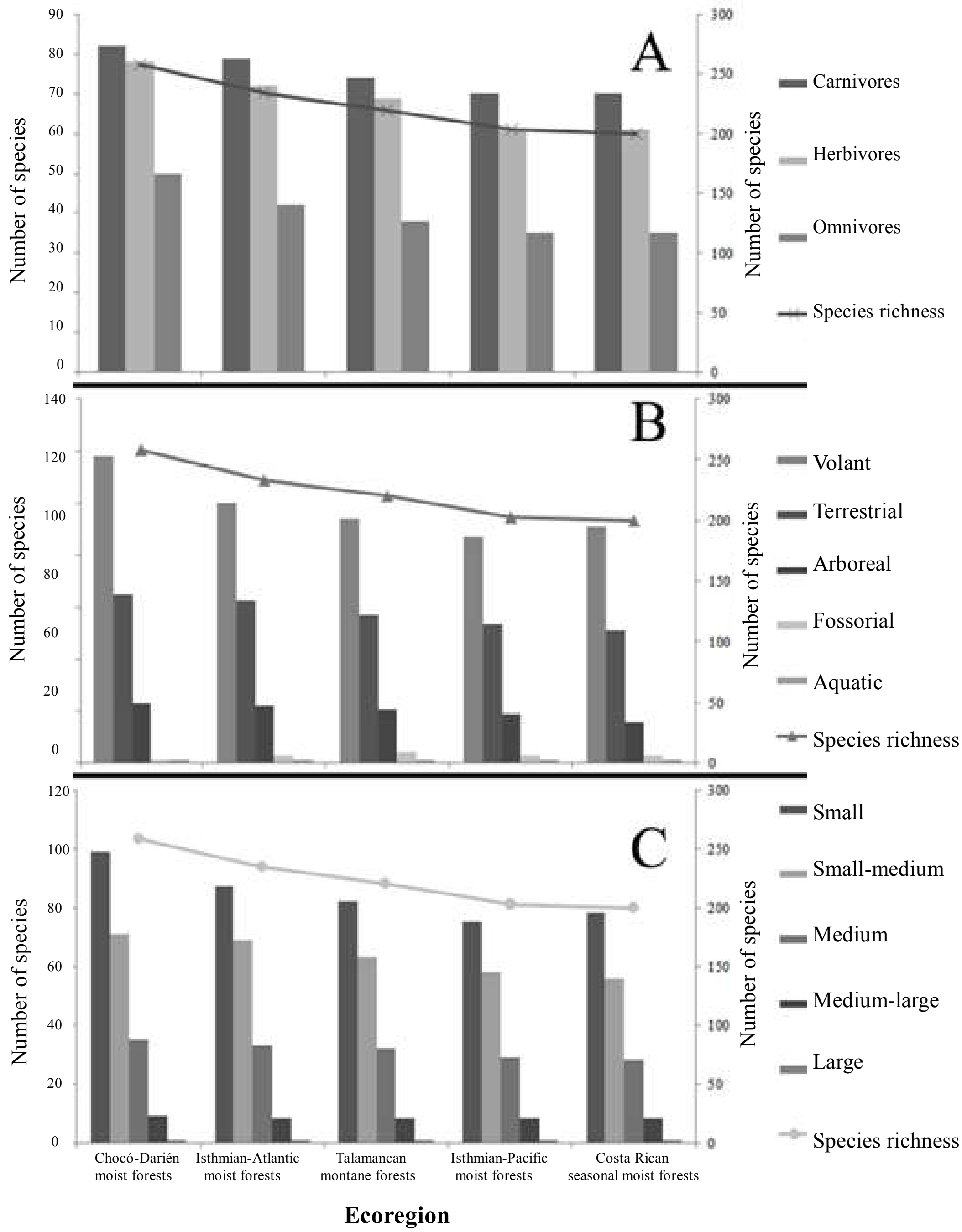

Figure 3. Number of species on each trait in the five ecoregions. (A) Trophic Realm, (B) Habit and (C) Body size.

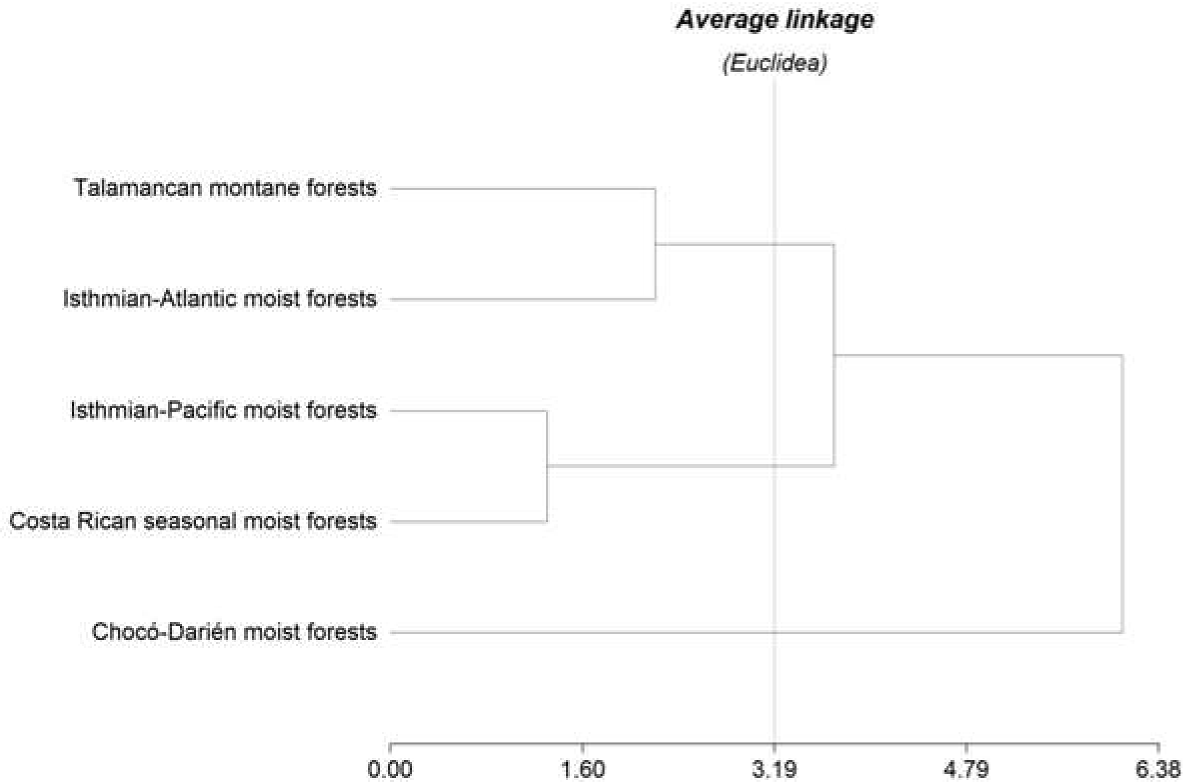

Figure 4. Cluster analyses based on Euclidean average distance for each ecoregion according to traits richness.

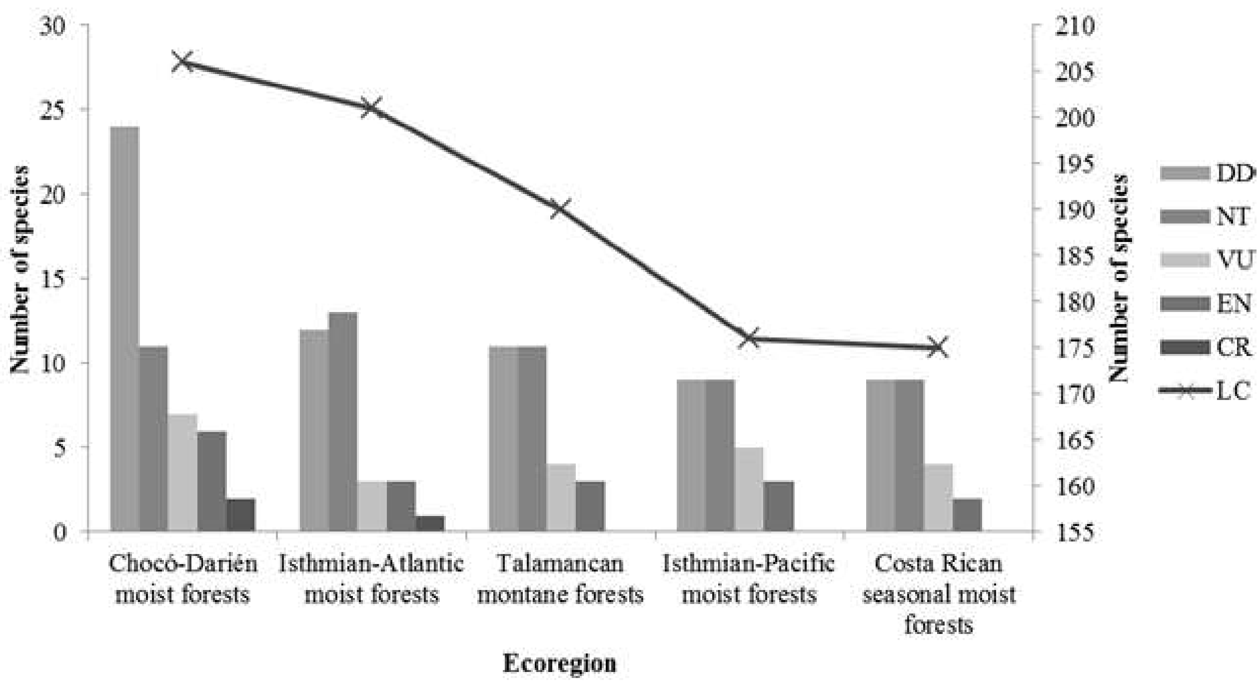

Figure 5. Number of species on each IUCN Red List of Threatened species category per ecoregion.

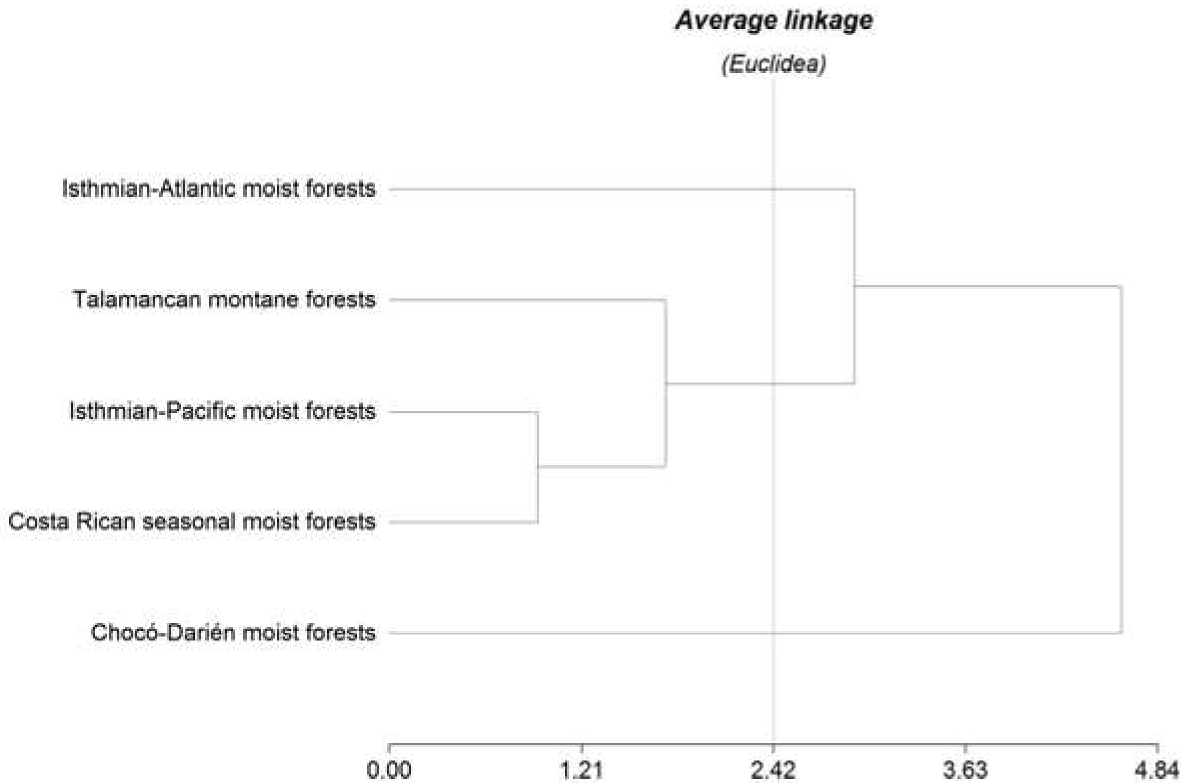

Figure 6. Cluster analyses based on Euclidean average distance for each ecoregion according to species richness on each Red List category.

a turning point in the ecoregions with significant differences towards the «connection» between both sub-continents, with C-D MF representing the South American component and CR SMF the Central American counterpart. The T MF and the I-P MF showed the highest correlation in terms of Species Richness; this may be explained by the fact that this particular region is more or less well preserved and the continuity of this is maintained by conservation areas such as the La Amistad binational park between Costa Rica and Panamá (United Nations Environmental Programme/World Conservation Monitoring Centre 2011).

However, it is interesting how this pattern do not follow the same trend in terms of species traits and threat status. Whilst according to species richness T MF, I-A MF and I-P MF are highly similar and differentiated from the two extremes and in terms of species traits the pattern follows a South-North trend, decreasing the number of species, especially for carnivores, volant and small mammals. In this case, the clusters are formed differently, with a highest association between T MF and I-A MF, even higher for CR SMF and I-P MF and both clusters totally differentiated from the C-D MF. This trend indicates a rupture on the functional patterns of the mammal assemblages from South America, relating all the Central American ecoregions and showing a threshold exactly located in the Panamanian isthmus. This rupture may be explained by environmental factors such as rainfall and more importantly latitude with some groups being more diverse south of the Panamanian isthmus threshold. Lyons & Willig (2002) showed the species richness decreased with latitude for bats and marsupials. Although our study is covered in a much smaller scale the same pattern is expected, and this may be an explanation for the rupture on functional patters shown in our analyses. Furthermore, it is possible that this tendency can be also related with the level of disturbance for some of the ecoregions, influencing how some species and functional traits are significantly reduced, changing the composition of the assemblage.

In terms of conservation status, the same South-North pattern arises, but with the interesting trend of equal Data Deficient and Near Threatened species for all Central American ecoregions, but in the C-D MF, representing a huge gap of knowledge, mostly described by the number of Data Deficient species. The number of Least Concern species also decreases from South to North, probably related with the conservation status of the ecoregion itself. The cluster analyses for threat categories also organizes the Central American ecoregions together and separate them from C-D MF, but showed a different pattern, also clustering T MF with I-A MF, but organizing CR SMF and I-P MF more highly associated. Land use changes and other human activities represent a major threat for all the tropical ecosystems, for example the effects on biodiversity of the pineapple and oil palm plantations in Costa Rica and Panama are not fully understood, but the global tendency shows that the oil plantations are a major driver of deforestation worldwide even though that much of of the studies have been conducted in southeast Asia (Koh and Wilcove 2007, Carlson *et al.* 2012).

The interesting patterns found for the herein three variables analyzed, highly relates with a potential turning point on the mammal fauna from the two subcontinents, highlighting the differences and importance of the region in terms of small-scales variation. Even when the species richness varies among ecoregions because the assemblage structure might vary with the size of ecoregions, in smaller areas like I-P MF and CR SMF the extinctions probabilities increase because this ecoregions are more vulnerable to environmental disturbances, while in larger areas like C-D MF and A-I MF the structure of the assemblages potentially is more stable (Cardillo 2011). It seems that traits are better proxies of the differences, which implies interesting patterns in terms of species assemblages and ecosystem functioning. Macroecological analysis have shown that the functional diversity tends to be more stable across a particular ecoregion than among ecoregions or vast areas (Safi *et al.* 2011), so it is necessary to understand the variability between and within biogeographical units.

The analysis of conservation status is also very interesting as it indicates how despite geographic proximity some ecoregions have significantly higher knowledge, but also, how geographic restrictions together with human activities, conducts to completely different threat patterns. The future of tropical dry and moist rainforest is threaten by five major anthropogenic forces: hunting, wood extraction, land use changes, atmospheric and climate changes (Miles *et al.* 2006, Wright 2010). The continuum showed differences not only in terms of species richness and traits, but also in terms of data gaps, risk and conservation status in general. For most Central American ecoregions analyzed, the general conservation status is deficient, with the exception of C-D MF and T MF, both that represent the two extremes in terms of species richness and trait composition. It seems clear that the analysis of species composition can lead to better understanding of ecological realms, accounting for differences even when small scales are analyzed. However, this specific region also shows an incredible variability, highlighting how species richness and uniqueness is so heterogeneous in tropical ecoregions.

With the environmental threats hanging over our heads like the Damocles sword, immediate actions must be taken to ensure the preservation of the tropical forests. Regional actions must integrate the local stakeholders and make them real conservation actors, in order to ensure the long-term participation in conservation programs (Harvey *et al.* 2008). This idea is not nearly new, Janzen (1986) urged the scientific community to establish this relationship, but yet here we stand more than 25 years later still stating the importance of this connection but without any real strategies.

Conclusions

Current knowledge suggests that the distribution of biodiversity should be a priority for political and biological processes since is directly related to human well-being (ecosystem services). With this work, we showed how a freely available set of variables (richnness, functional traits and extinction risk) can provide interesting regional-scale results, giving new tools to the decision makers to conservation planning. Additionally, we have shown successfully that standard techniques taken form macroecological approaches can be applied to minor scales yielding consistent results. The information extracted from this kind of analyses has a major role in terms of conservation planning and species distribution understanding.

Our analysis of the conservation status shows that throughout the region the knowledge gaps are common. Given the constant ecological threats affecting the region, studies filling this information gaps must be a high priority for researchers and authorities in the area. It seems some of the ecoregions are subject to different levels of human disturbance, and this can be reflected not only on the status of the ecoregion itself, but in terms of the risk for the species present on each. Since some of these ecoregions are potentially more affected or vulnerable to threats, we highly recommend assessing and addressing the urgent threats to this ecoregions, especially those in Mesoamerica, in order to reduce mammal conservation risks and ensure the long term persistence of the assemblages, both in terms of species and functional diversity.

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