

# Is higher-taxon analysis an useful surrogate of species richness in studies of Neotropical mammal diversity?

Carlos Eduardo Viveiros Grelle

Laboratório de Zoologia de Vertebrados, Setor de Zoologia, DBAV, IBRAG, UERJ, Av. São Francisco Xavier, 524 Maracanã, 20559-900  
Rio de Janeiro, RJ, Brazil

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## Abstract

The usefulness of higher-taxon analysis was investigated at genus-, family-, and order-levels; to estimate the species richness of mammals from localities in the Amazon and Central America. The dataset allowed the test of higher-taxon approach through all orders of mammals, and within the most speciose orders: Didelphimorphia, Chiroptera, Primates, and Rodentia. Analyses with all orders together, Didelphimorphia, Chiroptera, and Rodentia showed that family and order richness were not related with species richness. In all cases, there were significant and positive relationships between generic and species richness. Within Primates, family richness was related to the number of species, but weaker than the relationship between generic and species richness. In summary, higher-taxon approach, at the generic level, is a useful surrogate of species richness for mammals that occur in the Amazon and Central America. © 2002 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Studies on spatial patterns of species diversity are fundamental to biological conservation. For instance, species richness is frequently used to select areas for conservation (e.g. Pressey and Nichols, 1989; Prendergast et al., 1993; Pressey et al., 1993; Howard et al., 2000). This is, however, a hard task for many taxonomic groups, mainly in highly speciose regions such as the Neotropics, one of the most species-rich regions on Earth (e.g. Myers et al., 2000). Frequently there are many problems in alpha-taxonomy, with many complex groups of species (super-species) waiting to be untangled. Besides this, many new species are still being discovered, described, and rearranged, showing the high fluidity of Neotropical taxonomy. This is true even for vertebrates in the Neotropics. Recently, for example, Patterson (2000) published a revision of new species of Neotropical mammals described, or rearranged, from 1992 to 1999. His list comprised 57 species, and species continue to accumulate. Referring only to Brazilian species, nine species can be added to his list: the marsupial

*Monodelphis unistriata* (Lemos et al., 2000), the primates *Callithrix manicorensis* and *Callithrix acariensis* (van Rossmalen et al., 2000), and the rodents *Neacomys musseri*, *Neacomys minutus*, *Rhipidomys gardneri*, *Mesomys occultus* (Patton et al., 2000), *Oryzomys seuanezi* (Weksler et al., 1999) and *Akodon paranaensis* (Christoff et al., 2000).

According to Cole et al. (1994) there are 1096 species, 309 genera, 50 families, and 12 orders of mammals inhabiting the Neotropics. Patterson (1994) listed 1145 species—by including recent descriptions and revisions. But these number of species, and genera, should be considered outdated. For instance, the mammal list of Brazil, the most speciose country of Neotropics, catalogued 483 continental species (Fonseca et al., 1996). Some authorities estimate, however, that the number of species of some groups, such as rodents, can be inflated 100–120% (Vivo, 1996). Thus, the mammalian taxonomy in Brazil, and probably in the Neotropics, appears to be far from resolved, and there is no doubt that conservation strategies should be drawn up from a dataset of species without taxonomic problems. As quoted by May (1990) “taxonomy is the destiny”. However, the question is that frequently we cannot wait for a “resolved taxonomy”, with all good species named

E-mail address: grellece@uerj.br (C.E.V. Grelle).

and their range limited. Conservation biology is a “crisis discipline” and it is essential to consider “what is feasible, what is too crude to be useful, and what is unnecessarily detailed” (Fjelds , 2000).

Some years ago, Gaston and Williams (1993) suggested that patterns of species richness could be studied from higher taxonomic level than species. This cheap and quick methodology has proved to be useful, since there are correlation between higher-taxon richness (mainly at genus-level) and species richness (Gaston and Williams, 1993; Williams and Gaston, 1994; Gaston and Blackburn, 1995; Balmford et al., 1996b, 2000). But, on the other hand, some studies have found that higher-taxon analyses are weak predictors of species richness (Andersen, 1995; Prance, 1994; Fjelds , 2000), suggesting that higher-taxon is not a Rosetta Stone to estimate the patterns of richness.

Here, I have tested the usefulness of higher-taxon analysis; at genus-, family-, and order-level; to estimate the spatial pattern of mammal species richness in the Neotropics. The number of species per site in the lowland Amazon and Central America (93–139 species) show that these are, probably, the biologically richest areas known (Voss and Emmons, 1996). As good quality data are now becoming available, it is now possible to investigate the relationship among species richness and higher-taxon richness (genus, family and order) through sites in South (Amazon) and Central America. Furthermore, I have tested the reliability of higher-taxon analysis as surrogate of species richness within the four most speciose orders of Neotropical mammals: Didelphimorphia, Chiroptera, Primates, and Rodentia.

## 2. Methods

Hutterer et al. (1995) and, principally, Voss and Emmons (1996) compiled the most comprehensive lists of mammalian communities from the Amazon and Central America regions from primary reports. There, the number of species ranges from 93 (Cunucunuma) to 139 species (Cocha Cashu/Paktiza). I have used their dataset to examine the relationship among species richness and richness of higher-taxa (genus, family and order) through all orders of mammals. Furthermore, I have selected other localities well inventoried for some groups to study the reliability of higher-taxon analysis within the most speciose orders of mammals in Neotropics. The data from four localities in Brazilian Amazon sampled by Patton et al. (2000) were used for analyses within Didelphimorphia (genus-level) and Rodentia (genus and family-level) orders. Data from Urucu (Peres, 1999) was used for analyses with marsupials, primates and rodents. The inventories by Peres (1997) provided additional data for analysis within Primates (genus and family-level). Although there are

other sampled localities in Amazon, the most comprehensive studies were used, with available data of species, genera and family (Table 3 in Peres, 1997).

There are different proposals for taxonomy of Neotropical mammals, including family-level, and here I followed those used in Wilson and Reeder (1993).

A gazetteer of localities (and the source of information) is in Table 1. Species composition, further details of localities, and original sources of data can be found in Hutterer et al. (1995), Patton et al. (2000), Peres (1997, 1999), and Voss and Emmons (1996).

Variables such as sampling effort and spatial autocorrelation can confuse the analysis on the usefulness of higher-taxon as surrogates of species richness, but the importance of these variables has been reduced in the present paper. First, because it was possible to choose many sites that were sampled using the same sampling protocol, and I have selected and compiled the data for the best inventoried localities in the Amazon and Central America. Second, most of localities studied are isolated from each other, reducing the possible effects of spatial autocorrelation in analyses performed here.

All data were log<sub>10</sub>-transformed to approach normality. Analyses through all orders were made with three contrasts: species richness versus genus richness, species richness versus family richness, and species richness versus order richness. A Bonferroni correction of *P*-value was applied in all multiple contrasts. In these cases, *P*-value was corrected (i.e.  $\alpha = 0.05/3$ ).

## 3. Results

Analyses showed that generic richness was more related to species richness than to families or order richness. Specifically, for analysis through all orders, species richness was positively related with genera richness ( $R^2 = 0.81$ ,  $F = 29.099$ ,  $P = 0.001$ ,  $n = 9$ , Fig. 1). On the other hand, family and order-level were not correlated with species richness, being weak surrogates to higher-taxon analysis ( $R^2 = 0.14$ ,  $F = 1.111$ ,  $P = 0.327$ ,  $n = 9$ , and  $R^2 = 0.06$ ,  $F = 0.42$ ,  $P = 0.536$ ,  $n = 9$ , respectively).

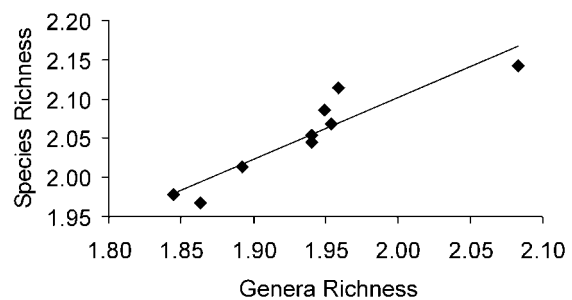


Fig. 1. Relationship between generic richness and species richness of Neotropical mammals, in nine localities. Each dot is a locality. All data were log<sub>10</sub> transformed.

Table 1

Localities, coordinate, order analysed (see the text), and source of mammalian communities from South and Central America

Locality, Country	Latitude	Longitude	Order analysed	Source
La Selva, Costa Rica	10°26' N	83°59' W	All	Voss and Emmons, 1996
Arataye, French Guiana	ca. 4°05' N	ca. 52°40' W	All	Voss and Emmons, 1996
Cunucunuma, Peru	3°39' N	65°46' W	All	Voss and Emmons, 1996
PBS <sup>a</sup> , Peru	9°37' S	74° 56' W	All	Hutterer et al., 1995
BCI <sup>b</sup> , Panamá	9°09' N	79°51' W	All	Voss and Emmons, 1996
Balta, Peru	10°08' S	71°13' W	All	Voss and Emmons, 1996
CCBS/Pakitza <sup>c</sup> , Peru	ca. 11°54' S	ca. 71°22' W	All	Voss and Emmons, 1996
Cuzco Reserve, Peru	12°33' S	69°03' W	All	Voss and Emmons, 1996
River Xingú, Brazil	ca. 3°39' S	ca. 52°22' W	All	Voss and Emmons, 1996
Kartabo, Guyana	6°23' N	58°41' W	Did <sup>e</sup> , Prim <sup>f</sup> , Rod <sup>g</sup>	Voss and Emmons, 1996
MCSE Reserves <sup>d</sup> , Brazil	2°30' S	66°00' W	Did <sup>e</sup> , Prim <sup>f</sup> , Rod <sup>g</sup>	Voss and Emmons, 1996
Urucu, Brazil	4°50' S	65°16' W	Did <sup>e</sup> , Prim <sup>f</sup> , Rod <sup>g</sup>	Peres, 1999
Headwaters, River Juruá, Brazil	ca. 8°40' S	ca. 72°47' W	Did <sup>e</sup> , Rod <sup>g</sup>	Patton et al., 2000
Upper Central, River Juruá, Brazil	ca. 6°45' S	ca. 70°51' W	Did <sup>e</sup> , Rod <sup>g</sup>	Patton et al., 2000
Upper Central, River Juruá, Brazil	ca. 6°45' S	ca. 70°51' W	Did <sup>e</sup> , Rod <sup>g</sup>	Patton et al., 2000
Lower Central, River Juruá, Brazil	ca. 6°35' S	ca. 68°55' W	Did <sup>e</sup> , Rod <sup>g</sup>	Patton et al., 2000
Mouth, River Juruá, Brazil	ca. 3°19' S	ca. 66°00' W	Did <sup>e</sup> , Rod <sup>g</sup>	Patton et al., 2000
Porongaba, Brazil	8°40' S	72°47' W	Primates	Peres, 1997
Sobral, Brazil	8°22' S	72°49' W	Primates	Peres, 1997
Condor, Brazil	6°45' S	70°51' W	Primates	Peres, 1997
Penedo, Brazil	6°50' S	70°45' W	Primates	Peres, 1997
Altamira, Brazil	6°35' S	68°54' W	Primates	Peres, 1997
Barro Vermelho I, Brazil	6°28' S	68°46' W	Primates	Peres, 1997
Fortuna, Brazil	5°05' S	67°10' W	Primates	Peres, 1997
Igarapé Jaraquí, Brazil	4°21' S	66°31' W	Primates	Peres, 1997
Vira Volta, Brazil	3°17' S	66°14' W	Primates	Peres, 1997
Vai Quem Quer, Brazil	3°19' S	66°01' W	Primates	Peres, 1997
Kaxinawá Reserve, Brazil	9°23' S	71°52' W	Primates	Peres, 1997
Riozinho, Brazil	4°38' S	66°54' W	Primates	Peres, 1997
Sacado, Brazil	6°45' S	70°51' W	Primates	Peres, 1997
Nova Empresa, Brazil	6°48' S	70°44' W	Primates	Peres, 1997
Boa Esperanca, Brazil	6°32' S	68°55' W	Primates	Peres, 1997
Barro Vermelho II, Brazil	6°28' S	68°46' W	Primates	Peres, 1997
Lago da Fortuna, Brazil	5°05' S	67°10' W	Primates	Peres, 1997

<sup>a</sup> Panguana biological station.<sup>b</sup> Barro Colorado Island.<sup>c</sup> Cocha Cashu biological station/Pakitza.<sup>d</sup> Minimal critical size of ecosystems.<sup>e</sup> Didelphimorphia.<sup>f</sup> Primates.<sup>g</sup> Rodentia.

Within Didelphimorphia, genera richness was strongly correlated with number of species ( $R^2=0.78$ ,  $F=55.38$ ,  $P=0.000$ ,  $n=16$ , Fig. 2a), and the same was observed for the bats ( $R^2=0.64$ ,  $F=12.369$ ,  $P=0.010$ ,  $n=9$ , Fig. 2b). In Chiroptera, family-level was not related with number of species ( $R^2=0.068$ ,  $P=0.499$ ,  $n=9$ ). Species richness of Primates was also positively, strongly, correlated with genera richness ( $R^2=0.96$ ,  $F=612.677$ ,  $P=0.000$ ,  $n=29$ , Fig. 2c) and, quite surprisingly, with family richness ( $R^2=0.37$ ,  $F=16.069$ ,  $P=0.000$ ,  $n=29$ , Fig. 2d), although there are only two families of Primates analysed (Callitrichidae and Cebidae). The number of rodent species was weakly, but significantly, related with genera ( $R^2=0.45$ ,  $F=11.211$ ,  $P=0.005$ ,  $n=16$ , Fig. 2e), but it was not associated with family richness ( $R^2=0.15$ ,  $P=0.142$ ,  $n=16$ ).

#### 4. Discussion

Contrasts through all orders and within the most speciose orders (Didelphimorphia, Chiroptera, Primates, and Rodentia) showed different patterns of higher-taxon analyses. This suggests that results for mammals as a class do not apply to individual orders. For instance, family-level of Chiroptera and Rodentia were not correlated with species richness. On the one side, analysis within Primates order revealed that genera- and family-level were good surrogates of species richness. However, strengths of these relationships are different, indicating that generic-level is more related to species richness than family-level for Primates.

Obviously, these analyses depend on systematic arrangement, as already argued elsewhere (Crozier,

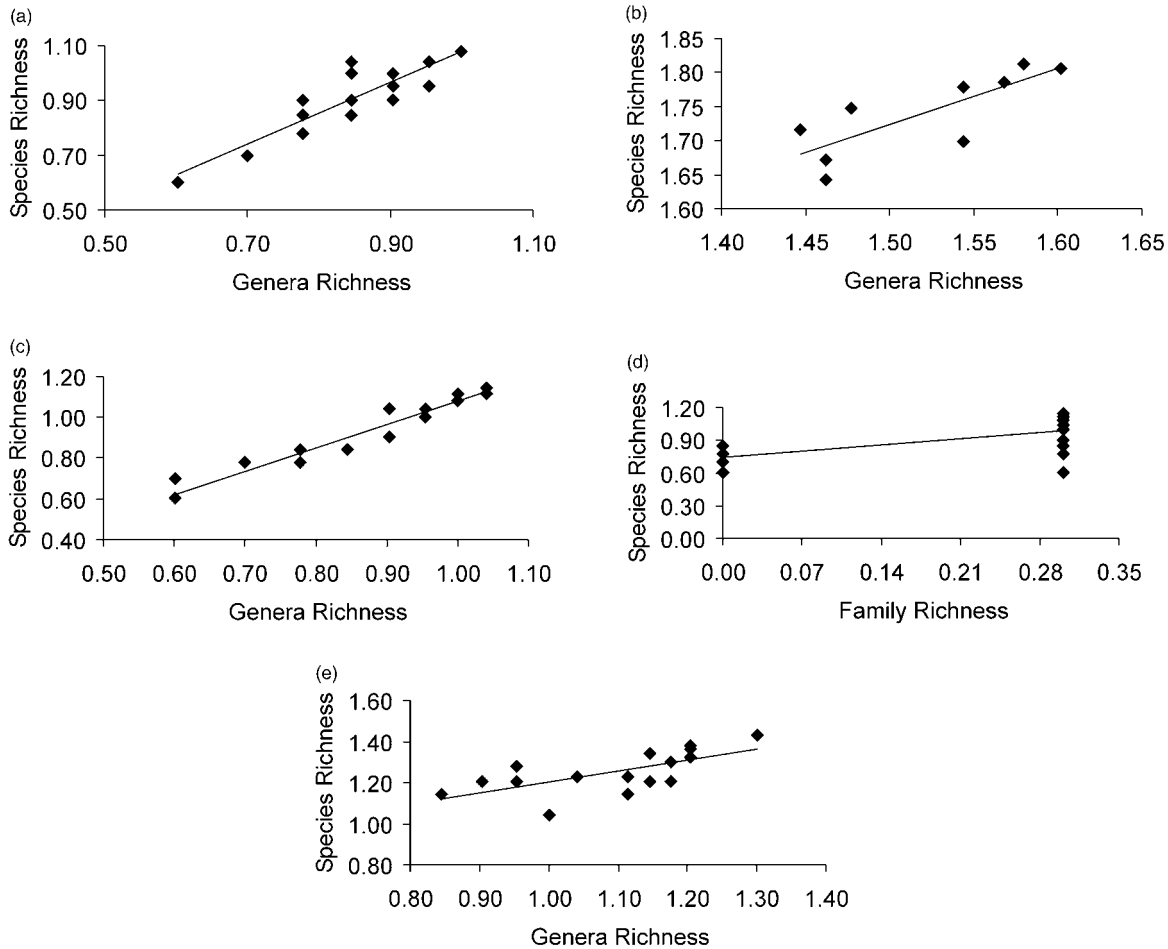


Fig. 2. (a) Relationship between generic richness and species richness of marsupials; (b) relationship between generic richness and species richness of bats; (c) relationship between generic richness and species richness of primates; (d) relationship between family richness and species richness of primates; and (e) relationship between generic richness and species richness of rodents. Each dot is a locality. All data were log<sub>10</sub> transformed.

1997; Gaston and Williams, 1993) and, consequently, taxonomic arrangement can influence the results of higher-taxon analysis. This, however, can be tested examining other taxonomic proposals of Neotropical Primates. Recently, some authors have advocated that there are five families of Primates occurring in the Neotropics (Rylands et al., 2000). To test this, I examined the relationship between species richness and family richness dividing Neotropical Primates in five families (Callitrichidae, Cebidae, Aotidae, Pitheciidae, and Atelidae) according to studies based on genetics, morphology, physiology, and behaviour (Rylands et al., 2000). I found a positive association between species richness and family richness ( $R^2=0.59$ ,  $F=39.818$ ,  $P=0.000$ ,  $n=29$ ) using the classification of Rylands et al. (2000). But, it should be noted that the relationship between species richness and family richness was again weaker than correlation at genus level for Primates.

Some studies have used the higher-taxon analysis to evaluate the area selection (e.g. Balmford et al., 1996a, b, 2000; Williams and Araújo, 2000). The datasets utilised here could be used for area selection, picking the ideal

regions for conservation, but this approach will be explored elsewhere (Grelle, in preparation).

Interestingly, the relationship between species richness and generic richness in Primates ( $R^2=0.96$ ) was stronger than that of Didelphimorphia ( $R^2=0.78$ ), Chiroptera ( $R^2=0.64$ ) and Rodentia ( $R^2=0.45$ ). This can be explained by the low number of species of each genus in the different orders. Specifically, in primates two (*Saguinus* and *Cebus*) out of 12 genera have two, or occasionally three, species per locality, whereas the other genera have only one species per locality. Marsupials have a similar trend: one species per genus per locality. Only some genera such as *Caluromys* and *Phyllander*, and less frequently *Marmosops* and *Micoureus*, have two species per locality. Conversely, there are, in general, at least two species of bats in the following genera per locality: *Saccopteryx*, *Noctilio*, *Pteronotus*, *Mimon*, *Phylloderma*, *Tonatia*, *Glossophaga*, *Sturnira*, *Uroderma*, *Thyroptera*, *Eptesicus*, *Molossus*, and *Myotis*. In addition, some genera (*Artibeus*, *Carollia*, *Platyrrhinus*, *Tonatia*, *Micronycteris*, *Vampyressa*, and *Phyllostomus*) have three or more species/locality. In Rodentia,

there are two or more species for a set of genera per locality. Some genera of Sigmodontinae (*Oryzomys*, *Oecomys*, and *Neacomys*) frequently have two, or more, species/locality. For instance, the genera *Oecomys* and *Oryzomys* can have three, four, or even five, species/locality, as in Lower Rio Xingú, Balta, and Cuzco. In the family Echimyidae, some genera (*Proechimys*, *Echimyis*, and *Mesomys*) have two or three species occurring in sympatry, and some localities (Balta, Cocha Cashu/Pakitza) can have four species of *Proechimys* (see these data in: Table 1 in Hutterer et al., 1995; Table 3 in Peres, 1997; Appendix in Peres, 1999; Appendix 1–10 in Voss and Emmons, 1996).

These differences between the number of species/genus per locality through orders weakly suggest a higher turnover of primate and marsupial species than of bats and rodents. As suggested earlier, the pattern appears to be one species/genera in primates and marsupials. In a community ecology perspective, this can be interpreted as a result of different assembly rules organising (or not) these communities. Apparently, primates and marsupials, through localities studied here, follow a known pattern found in small mammal community at Australia (Fox, 1989).

Ideally, the study of patterns of biodiversity should be carried out using species-based datasets, including, utopically, genetic knowledge of organisms. However, this would require an unpredictable amount of time, and, in some cases, higher-taxon can be a shortcut. In conclusion, the analyses performed here showed that generic-level could be used as a reasonable surrogate for species richness. This is true for analyses through all orders of Neotropical mammals, as well as within speciose orders like Didelphimorphia, Chiroptera, Primates, and Rodentia. Family- and order-level, however, should not be used as surrogates since these levels are not related, or only weakly correlated with species richness as in case of family-level within Primates. Thus, for mammals of lowland Amazon and Central America, generic richness can be considered useful in the studies of species spatial patterns for conservation in the Neotropics.

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