

Original article

Anuran species richness, complementarity and conservation conflicts in Brazilian Cerrado

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Abstract

Broad-scale correlations between species richness and human population suggest that processes driving species richness, mainly related to high ecological productivity, may also drive human populations. However, it is still under debate if this coincidence implies conflicts between biodiversity conservation and human development. In this paper, we analyzed the relationships among human population size, species richness and irreplaceability in Brazilian Cerrado. We analyzed a dataset with 131 species of anurans distributed in 181 cells with 1° of spatial resolution covering the biome. We found a positive correlation between human population size and anuran species richness ($r = 0.46$; $P = 0.033$ with 19.5 geographically effective degrees of freedom, v^*), but the irreplaceability of each cell was poorly correlated with human population size ($r = 0.075$; $P = 0.323$; $v^* = 173.9$). The 17 cells in the 97 optimal reserve networks contained a total human population ranging from 2942,195 to 4319,845 people, representing on average 11.8% of the human population in the entire Cerrado grid. The comparison of these observed values with 10,000 values from randomly generated networks suggests a relatively high flexibility in optimal complementarity sets for reserve selection. Our results indicated that correlation between richness and human population does not necessarily result in conflicts, given the opportunities for conciliating conservation and development. However, the analyses performed here are initial explorations within the framework of conservation biogeography, so more detailed studies are necessary to establish conservation planning at regional and local scales.

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1. Introduction

Many recent papers have found broad-scale correlations between species richness and human population density (Balmford et al., 2001; Araújo, 2003; Chown et al., 2003; Luck et al., 2004; Gaston and Evans, 2004). These correlations have been interpreted such that processes driving species richness, mainly related to high ecological productivity and occupation of more suitable habitats, also drive human populations, under the 'more-individuals' energy hypothesis (Balmford et al., 2001; Chown et al., 2003; Gaston and Evans, 2004; Currie et al., 2004; Evans and Gaston, 2005). Also, this

correlation could suggest a potential conflict between biodiversity conservation and human development, both because of direct impacts on the environment (i.e. habitat conversion) or because of higher land prices and increase in other associated costs to conserve biodiversity (Luck et al., 2004; but see Faith, 2001a, 2001b; Huston, 2001).

However, Faith (2001a) argued, in a response to Balmford et al. (2001), that coincidence between species-rich and development-opportunity areas does not necessarily imply any conflict between biodiversity conservation and development. This occurs because conservation planning is usually based on complementarity procedures, in which even species-poor areas can have high complementarity values, and many of these areas together may provide an effective protection at regional scale. So, even though correlations between species richness

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and human occupation may arise due to multiple complex ecological processes, it may be possible to find alternative solutions that conserve all species by using complementarity-based strategies and, eventually, by incorporating economic constraints in the optimization models (see [Faith et al., 2003](#)).

This debate could be solved if determines the extent to which the complementary values of an area are a function of the overall species richness. If richness is determined by overlap of small-ranged, endemic species, concentrated into a few rich areas, also harboring large-ranged species, in a perfectly nested system (see [Fischer and Lindenmayer, 2005](#)), then a high correlation between richness and complementarity value will arise. This occurs because species with small ranges are attractors of complementarity solutions, and consequently the selected units will also occur in rich areas. Under this scenario, a potential conflict between biodiversity conservation and human development is likely to arise. On the other hand, if these small-ranged species are disperse in geographic space, in an imperfectly nested system, then there may be more opportunities for conservation outside the richest areas, and so [Faith's \(2001a\)](#) argument gain force.

In this paper, we analyzed the broad-scale relationships between species richness, complementarity and human population size in Brazilian Cerrado, showing how the relationship between these variables may be useful to indicate potential conservation conflicts. The Cerrado region of Central Brazil was recently considered one of the world 'hotspots' for biodiversity conservation ([Myers et al., 2000](#)) because of its high endemism (mainly of plants) and its high rates of biodiversity loss due to recent human occupation and agriculture expansion ([Klink and Moreira, 2002](#)). This way, optimum strategies that provide quick answers about biodiversity conservation are urgently required for this biome. At the same time, anurans are an important group to study in this situation, since there is a growing concern about the decline in amphibian populations worldwide (see [Alford and Richards, 1999](#); [Collins and Storfer, 2003](#); [Stuart et al., 2004](#)). These declines are increasingly creating demands for effective strategies to maximize conservation efforts for amphibian populations, especially in regions in which few detailed data on diversity, abundance and distribution are available, such as in the Cerrado of Central Brazil ([Young et al., 2001](#)).

2. Material and methods

2.1. Data

Extents of occurrence (based on minimum convex polygons) of the 131 species of anurans that can be found in Brazilian Cerrado ([Colli et al., 2002](#)) were mapped with a spatial resolution of 1° grid cell, with a total of 181 cells covering the Cerrado Biome ([Fig. 1](#)) (a detailed species list and references are available from the authors upon request—see also [Diniz-Filho et al., 2004a, 2004b](#), for a preliminary dataset). A binary matrix was constructed by recording the species

whose geographic ranges overlap each cell, and species richness was calculated by summing the species present in cells. Although macro-scale approaches are usually coarse (see [Blackburn and Gaston, 1998](#)), they can provide overall guidelines for conservation and define the focus for more local and effective conservation efforts in poorly known biomes in the Neotropical region, such as Cerrado (see [Diniz-Filho et al., 2004a](#); [Diniz-Filho et al., 2005a, 2005b](#)).

Human population data are part of the official census of Brazilian population for the year 2000, by the Brazilian Agency of Geography and Statistics (IBGE). For the 181 cells covering the Cerrado biome, human population was obtained by summing urban or rural population from 1054 municipalities whose geopolitical limits are within the Cerrado border. Human population data were log-transformed prior to the analysis to normalize distribution.

2.2. Analysis

Species richness for each cell was correlated with log-transformed human population data. Since significant spatial autocorrelation is usually found for this kind of data, biasing Type I error estimates due to inflation of degrees of freedom (see [Legendre et al., 2002](#); [Diniz-Filho et al., 2003](#)), geographically effective number of degrees of freedom (v^*) for significance tests can be calculated using [Dutilleul's \(1993\)](#) method, implemented in MODTTEST software (P. Legendre, available at <http://www.fas.umontreal.ca/biol/legendre/>).



Fig. 1. The grid system with 181 cells of 1° of latitude and longitude overlaying the Brazilian Cerrado.

Based on the presence–absence matrix of species in grid cells, optimization routines using simulated annealing (see Possingham et al., 2000; Cabeza and Moilanen, 2001) were used to solve the set-covering problem, i.e. to conserve at least one ‘population’ (cell) of each species with a minimum total number of cells (the reserve network). Simulated annealing algorithm begins with a random set of reserves and, for each iteration, it swaps sites in and out of that set, measuring the change in cost according to the following function:

$$\text{Cost} = \sum \text{Cost for site } i + \sum \text{Penalty cost for species } j; \quad (1)$$

where $i = 181$ cells and $j = 131$ species. The optimization procedure was repeated 100 times, with species’ penalties equal to 2 (i.e. larger than 1.0), ensuring that all species tend to be conserved in most solutions. Final networks were obtained after 1000,000 iterations, implemented in the SSM routine of SITES (see Andelman et al., 1999). The frequency of each cell in the various optimized networks indicates its relative importance for complementarity solutions, and consists in a simple way to estimate the irreplaceability of that cell (Meir et al., 2004; see also Ferrier et al., 2000 for a more complex approach).

Finally, after establishing the optimal reserve networks we applied the randomization procedure recently proposed by Araújo et al. (2002) and Chown et al. (2003) to evaluate the flexibility of complementarity solutions to deal with potential conservation conflicts. The human population in the optimal networks was summed over all cells belonging to each network. These values were then compared with 10,000 values of summed human population and species richness obtained by randomly generating reserve networks across the Cerrado region with the same minimum number of cells defined by the SSM. Randomization was performed in Random Reserve Selection (RRS) software written by one of us (T.F.L.B.V.R.) in Delphi language for IBM-PC compatibles and available from the authors upon request. In a flexible scenario, it would be possible to find out different networks (groups of 17 cells) that possess, by chance alone, a combination of low total human population and high species richness. On the other, if richness is driven by locally restricted species, which in turn overlap areas of high human population, a constraint in the relationship will appear and this combination of low total human population and high species richness rarely appear by chance alone.

Under this randomization approach, interpreting positive deviations of total observed human population within network from those values obtained by chance alone is straightforward, i.e. there is a coincidence between sites chosen by optimization strategies and peaks of human population, which in turn suggests that there may be low flexibility to find solutions with high overall species richness and relatively low human population, at least using this minimum number of cells. Alternatively, if total human population in the observed network is a typical value obtained in the simulations, it indicates that optimization strategy adopted does not incorporate more or less total human population than equivalent systems

with the same number of cells. This suggests a lot of flexibility to minimize human populations in final networks (Chown et al., 2003), without any change in the number of cells of the system.

However, the comparison between observed and simulated values of total human population within networks should not be interpreted in absolute terms, because even if total human population is a random value from the simulations, its absolute value within the network can be very high and suggests potential conservation conflicts at local or regional scales. Also, it is important to stress that, in the 10,000 simulated networks, maximum efficient will not be achieved (since these random networks barely cover all species), and so a comparison between efficiency (proportion of species cov-

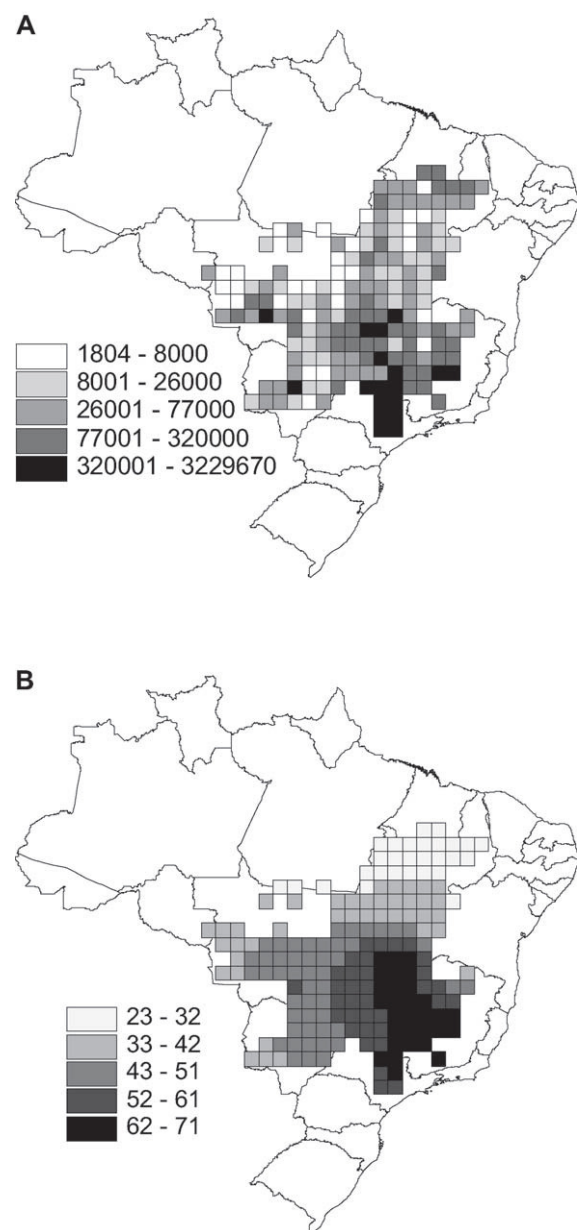


Fig. 2. Spatial patterns of (A) human population size at log-scale and (B) anuran species richness across Brazilian Cerrado.

ered) and cost (total human population) may be useful to interpret the deviations between observed and simulated data.

3. Results

A positive correlation between human population size (Fig. 2a) and anuran species richness (Fig. 2b) in Cerrado was observed ($r = 0.46$; $P = 0.033$ with 19.5 geographically effective degrees of freedom, ν^*) (Fig. 3a). This correlation is indeed supported by a visual inspection of maps showing the spatial patterns of these two variables across the region.

According to the simulated annealing algorithm, 17 is the minimum number of cells containing all species at least once, and 97 solutions, with a relatively high level of spatial coincidence, were found (Fig. 4a). These 17 cells in the optimal reserve network contain a total human population ranging from 2942,195 to 4319,845 people (average of $3565,924 \pm 545,695$ [standard deviation] people), representing in average 11.8% of the human population in the entire Cerrado grid. The solution with smaller summed human population is shown in Fig. 4b, with a total human population of 2942,195, and summing the area of the 17 cells (about 12,300 km²), this is equivalent to around 17 people per km², a relatively low human population density. The irreplaceability, as estimated by the relative frequency of cells in these 97 networks, is

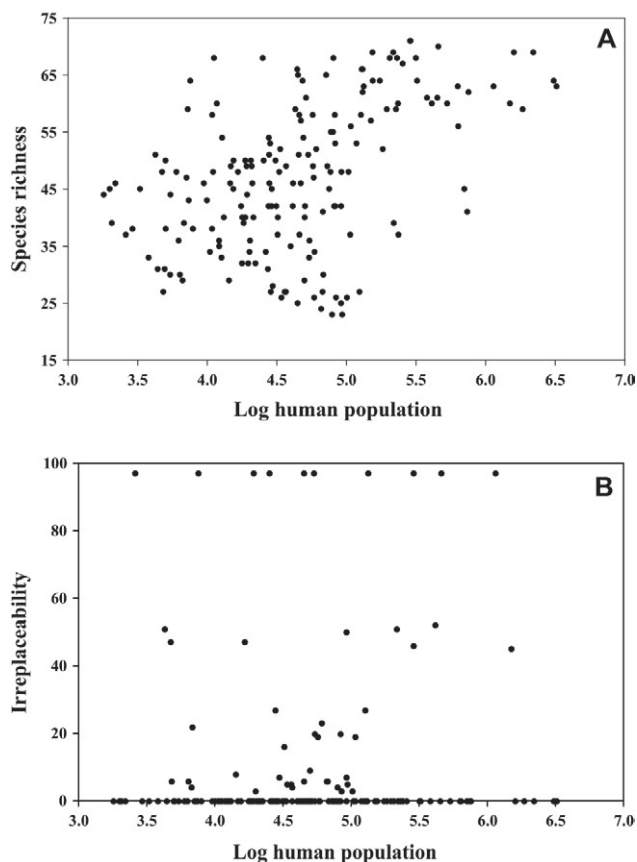


Fig. 3. Relationships between anuran species richness and human population size (a) and between anuran species richness and irreplaceability (b).

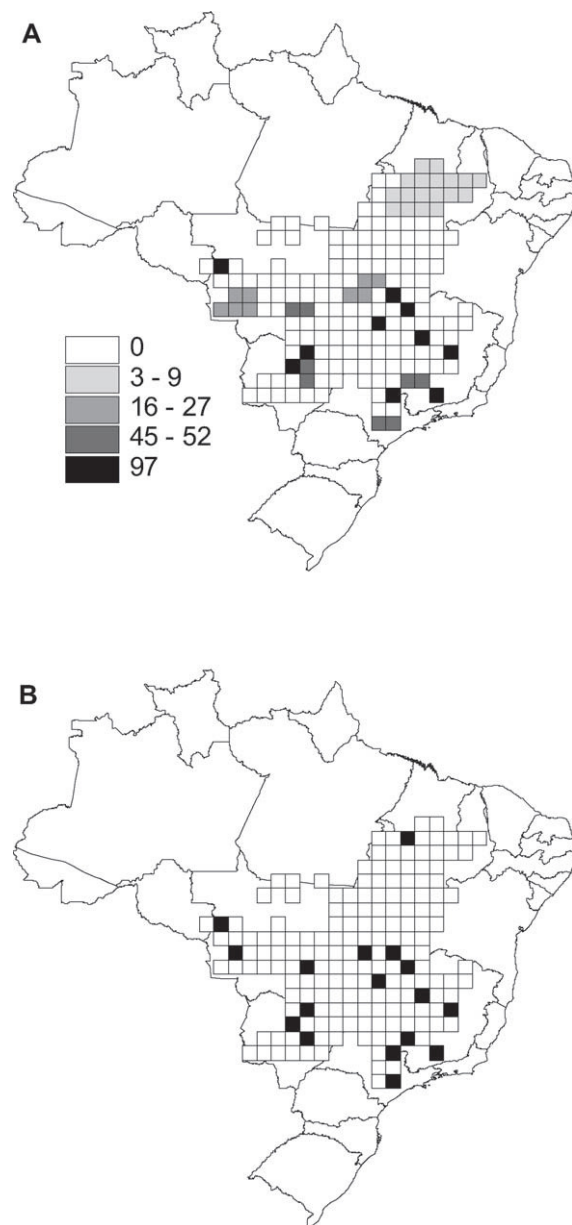


Fig. 4. a) Spatial patterns in the irreplaceability estimated by the frequency of cells in the 97 optimal solutions and; b) SSM solution with lowest total human population.

poorly correlated with human population size ($r = 0.075$; $P = 0.323$; $\nu^* = 173.9$; Fig. 3b). There is a small, albeit significant, correlation between irreplaceability and species richness ($r = 0.268$, $P = 0.017$; $\nu^* = 76.9$).

Comparing the mean total human population density (as estimated from the 97 solutions with 17 cells each) with the 10,000 values obtained from randomly generated networks with 17 cells suggests that the optimum reserve networks defined by simulated annealing do not contain significantly more humans than expected by chance alone (Fig. 5a), indicating a relatively high flexibility in optimal complementarity sets for the selection of reserve networks. The human population in the randomly generated networks range from about 300,000 to more than 11 million, but the randomly generated

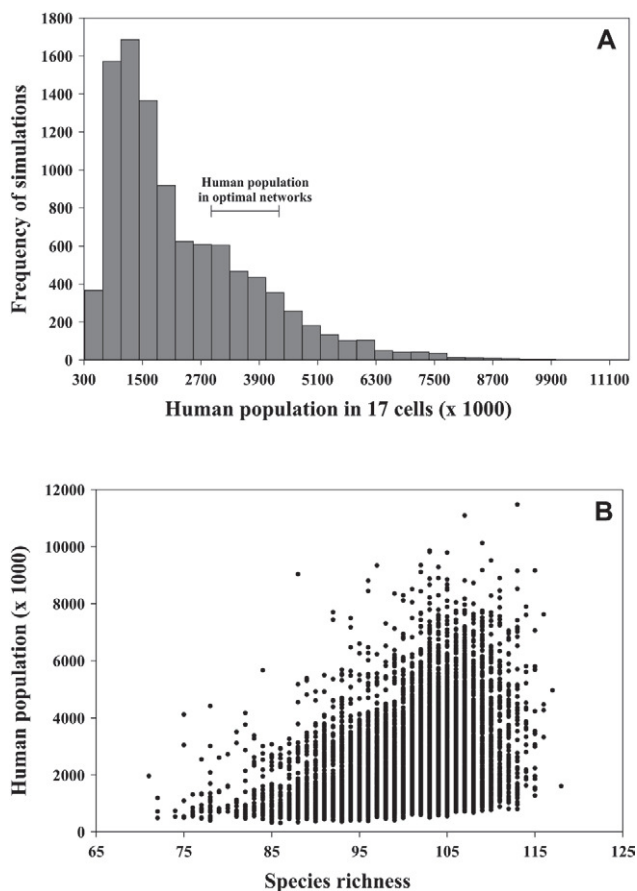


Fig. 5. a) Frequency distribution of total human population size in 17 cells randomly selected from the grid overlaying the biome Cerrado. The horizontal bar indicates the range of human population sizes in the 97 solutions with 17 cells obtained by the simulated annealing algorithm. b) Relationship between species richness and total human population in the 10,000 randomly generated networks with 17 cells.

systems with 17 cells and low human populations tend to conserve only a relatively small fraction (i.e. about 55%) of the overall species pool in the region (Fig. 5b). Sub-optimum networks (which preserve, say, 90% of all species), may include large variance in human population sizes, so that a solution with very low relative total human population size may be found.

4. Discussion

Our analyses revealed that regions with high species richness are coincident with populous regions, as found elsewhere (Balmford et al., 2001; Araújo, 2003; Chown et al., 2003; Luck et al., 2004; Gaston and Evans, 2004; Evans and Gaston, 2005). According to Balmford et al. (2001), this coincidence may imply potential conservation-human development conflicts. However, as pointed out by Faith (2001a,b), this inference must be done carefully because complementarity values of the areas were not taken into account (but see Moore et al., 2001, for a reply). Indeed, in this paper we found a low correlation between estimates of relative importance of each cell (irreplaceability) and human population in Cerrado.

Under strong pressures from human development, most conservation biologists now agree that efforts must be done to minimize conservation costs with maximal efficiency. In our analyses with Cerrado anurans, highly important cells to complementarity systems are not coincident with areas with high human population, suggesting that richness is not mainly explained by small ranged-species and, consequently, that there are many opportunities for conservation outside the richer areas. This is confirmed by randomization test based on complementarity patterns (reserve network), which showed that total human populations within the 97 optimal networks highly overlap the values generated by chance alone. Chown et al. (2003) obtained a different result for reserve networks designed to conserve bird diversity at a more regional scale, in South Africa, with human populations significantly larger than those in randomly selected networks with the same size. Our simulations also revealed a huge variance of human population size within randomly generated networks with 17 cells, which in turn could conserve relatively large fractions of the overall species richness by chance alone. All these results showed that there is a high flexibility for biodiversity conservation in Cerrado, at least in respect to human population sizes, despite the relatively high spatial correlation between this variable and anuran species richness (Faith, 2001a,b).

It is important to note that the correlation between richness and human population reported here might be due to variations in the degree of knowledge about anuran fauna in Cerrado region (see Diniz-Filho et al., 2005b). This may occur because species in the northern part of the biome are those with larger geographic ranges and that were described earlier, usually elsewhere in the country or South America. Otherwise, species found in regions of high overlap with highly human populated areas, in southern part of the biome, were described more recently and usually have restricted geographic ranges, probably due to absence of recent surveys. Hence, results presented here, mainly those reporting a low correlation between human population and complementarity value (and, consequently, low conservation conflict), are probably conservative in respect to this 'knowledge effect', once expansion of known geographic ranges and future description of new species in the northern part of the biome will tend to reduce irreplaceability values in the southern and increase them in the northern (i.e. in the regions of low human population). Probably, this also will reduce even more the current overlaps between richness, irreplaceability and human population.

Thus, our results indicated that potential conservation conflicts at broad-scales in Brazilian Cerrado might be not difficult to solve. Of course, the analyses performed here are only initial explorations of conservation problems at broad scales, within a framework of 'conservation biogeography' (Whittaker et al., 2005). So, although 3000,000 people living within a network is a high absolute number, it is important to consider that our large grain size (about 12,300 km²) leads to a relative low human population density around 17 people km⁻² (see Cohen, 1997; Cincotta et al., 2000). It is important to

stress, however, that human population is not necessarily the best indicator of conservation-development conflicts (Faith, 2001a; Luck et al., 2004). This may be especially valid for Brazilian Cerrado, a region in which human population is relatively aggregated and for which intensive and highly technological agricultural activities are developed, mainly for soybean and rice crops (Fearnside, 2001; Klink and Moreira, 2002). Future investigations must deal with this specific issue in Brazilian Cerrado. Also, more detailed studies are necessary to establish conservation planning at regional and local scales, and in this case even regions with high population densities, or any other form of human occupation, could provide opportunities for conciliating conservation and development.

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