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RESEARCH PAPER

Macroecological correlates and spatial patterns of anuran description dates in the Brazilian Cerrado

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ABSTRACT

Aim To quantify the relationship between the description dates of anuran species in the Brazilian Cerrado and some macroecological traits, and to verify the spatial patterns of average description dates and their correlation with human occupation and biodiversity knowledge.

Location Brazilian Cerrado (South America).

Methods The average date of description of 131 species of anurans found in 181 cells overlaying the Brazilian Cerrado was recorded. Description date was regressed across species on body size and geographical range size. Phylogenetic effects that could bias the significance tests of the multiple regression model of description dates on macroecological traits were taken into account using a phylogenetic subtraction method in which families and genera were classificatory factors in a nested two-way analysis of variance (ANOVA) model. We also conducted a spatial analysis of the average description date that was estimated for each cell. This cell-based metric was regressed on human population size, the year of foundation of the municipalities and the number of inventories undertaken in each cell. The influence of spatial autocorrelation patterns was taken into account by using the geographically effective number of degrees of freedom.

Results The number of new species being discovered in the Brazilian Cerrado has been increasing, especially over the last 50 years. Cross-species analyses indicated that description dates were negatively correlated with body size and geographical range size, taking phylogenetic effects into account. Even after controlling for the spatial structures in all variables, average description date was positively correlated with human population in geographical space, but because of multicolinearity structure in the data, it was not possible to quantify the independent influence of human population and number of inventories on description date.

Conclusions As found in previous papers, large-bodied and widely distributed species are likely to be described first. Species yet to be discovered are probably small-bodied and with narrow distributions, more restricted to the Cerrado biome. Also, the explicit spatial approach showed that the average description date is spatially correlated with total human population and biodiversity knowledge in the Cerrado region. Our findings suggest that incorporating human population density into the reserve design algorithms, which has usually been done to avoid or minimize conservation conflicts, may also produce good results because this will preserve many places where most of the non-described species will probably be found in the future.

Keywords

Anurans, Cerrado, description dates, knowledge gradients, macroecology, spatial autocorrelation, species richness.

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INTRODUCTION

A reliable knowledge of spatial patterns in biodiversity is essential for understanding ecological and evolutionary processes and for establishing effective regional conservation planning (Gaston & Rodrigues, 2003). In principle, at local spatial scales, detailed and systematic sampling efforts can deal with the problem of absence of detailed data of species abundance and overall species richness. However, at broad spatial scales, uncertainty in species diversity estimates can be serious due to the paucity of systematic sampling across large areas (entire biomes or continents, in which knowledge is usually biased towards more populated areas or to areas more attractive to researchers), or due to disagreements in taxonomy affecting species lists (Silva & Medellín, 2001; Isaac *et al*., 2004). At the same time, at these broad regional scales, dealing with this uncertainty may be critical since the time to perform faunal and floral assessments to define conservation actions is always limited. Higher-taxon approaches (Williams & Gaston, 1994; Grelle, 2002) and rapid faunal assessment programmes have been proposed exactly in this context.

The magnitude of knowledge about biodiversity has been discussed since the middle of the 1950s (May, 1988). However, more recently, many analyses evaluating the cumulative number of species described across time have shown that many species remain to be discovered (Gaston *et al*., 1995; Dolphin & Quicke, 2001; Cabrero-Sañudo & Lobo, 2003). Also, macroecological traits of species already described, such as body size and geographical range size, can be used as predictors of description dates. In general, large-bodied and widely distributed species are expected to be described earlier, although there is taxonomic and geographical variation in these patterns (see Blackburn & Gaston, 1995; Reed & Boback, 2002; Collen *et al*., 2004). So, it may be possible to forecast the general characteristics of species that will be described in the future. This information, when associated with analyses of spatial patterns in description dates, can guide the search for new species or, alternatively, would help define the uncertainty component to be included in statistical and mathematical models for regional conservation planning.

Here, we evaluate the patterns of description date in anurans from the Cerrado region of central Brazil, showing relatively high correlations between description dates and two macroecological traits (i.e. body size and geographical range size). We also evaluate how average description dates are distributed in geographical space and how spatial correlations of these description dates can be matched with prospective scenarios for discovering new species as long as human occupation expands towards the northern part of the biome. This is important for conservation purposes as the Cerrado region of central Brazil was recently considered as one of the world's 'hotspots' for biodiversity conservation (Myers *et al*., 2000) because of its high endemism of plants and its high rates of habitat conversion and biodiversity loss as a result of recent human occupation and agricultural expansion (Klink & Moreira, 2002). Also, anurans are an important group to be evaluated because they are relatively less studied than other vertebrate groups and many species were described in the 1990s (Colli *et al*., 2002), they have the highest rates of endemism in the Cerrado (Myers *et al*., 2000), and because there is a growing concern about the decline in amphibian populations worldwide (see Collins & Storfer, 2003 and Stuart *et al*., 2004 for recent reviews).

MATERIALS AND METHODS

Data

We obtained from the literature the year of description (i.e. the year when the species was formally described for the first time and considered as an independent taxonomic unit) of 131 species of anurans found in the Brazilian Cerrado (Colli *et al*., 2002) [a detailed species list and references are available from the authors upon request — see also Diniz-Filho *et al*. (2004a,b) for preliminary data sets and species lists].

For each species, we also obtained geographical range size and body size (rostrum to anal body length, in millimetres). Geographical ranges were defined as the total extents of occurrence based on minimum convex polygons (MCP) and were mapped using a spatial resolution of 1° grid cells. Although MCP tends to overestimate the extents of occurrence of species (see Gaston, 2003), it is a useful and a conservative measurement of geographical ranges for Cerrado fauna (see Discussion), for which a few records, concentrated in the southern part of the biome, are usually available for most groups of organisms. For the Cerrado region, which was covered with a total of 181 cells (Fig. 1), a binary matrix was constructed by recording the species whose geographical ranges overlap each cell, and the species richness was calculated by summing the species present in these cells.

We also obtained data expressing the pattern of human occupation in the Cerrado from the year 2000 census conducted 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 populations from 1054 municipalities whose geopolitical limits are within the Cerrado border. We also obtained the average year of municipality foundation for each cell. The number of faunal inventories in each cell was derived from the maps provided by a workshop on conservation priorities in Cerrado and Pantanal (see Cavalcanti & Joly, 2002), and we assume that the number of inventories per cell represents a surrogate for biodiversity knowledge in the region.

When necessary, variables were log-transformed prior to the analysis to normalize distributions.

Statistical analyses

Dates of species description were analysed in two ways: across species and across geographical space. For cross-species analysis, dates of description were regressed against body size and geographical range size. However, when dealing with cross-species studies, it is important to control for phylogenetic structure in data that can bias statistical analyses because of non-independence of taxa (Harvey & Pagel, 1991; Freckleton *et al*., 2002; Martins *et al*., 2002). Unfortunately, no detailed phylogeny is available for Neotropical anurans and the lack of a reliable phylogenetic

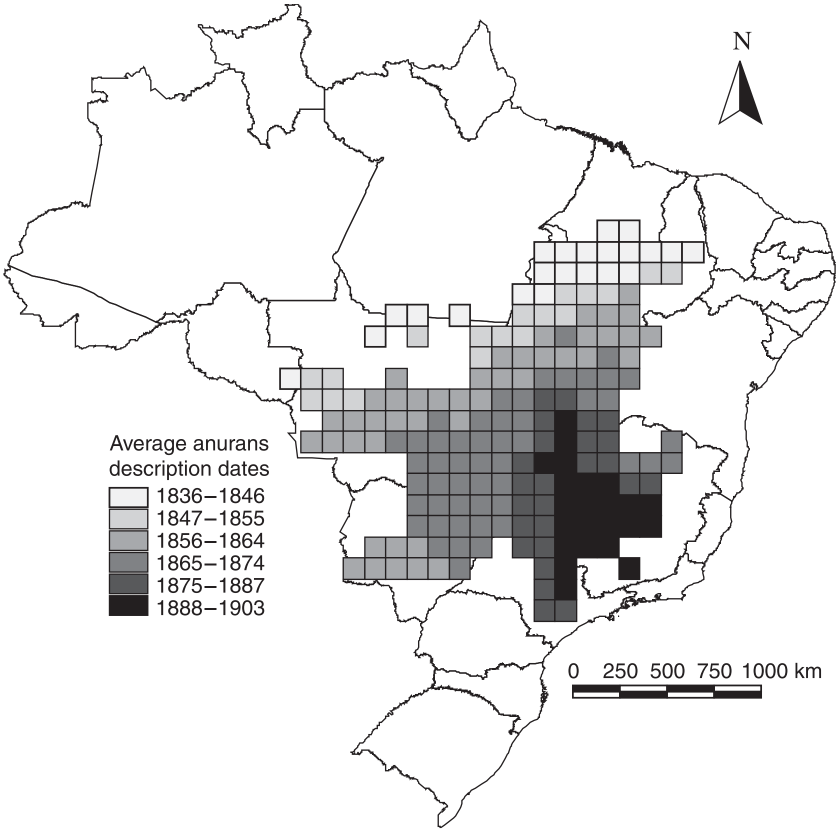

Figure 1 Average description dates of 131 anuran species found in the Cerrado region in 181 cells covering the biome.

hypothesis prevents the use of more powerful phylogenetic comparative methods (Martins *et al.*, 2002). Even so, we evaluated the historical effects among species using Stearns' (1983) phylogenetic subtraction method, in which the taxonomic structure (species allocation into families and genera) is used as a proxy for phylogenetic effects (see also Harvey & Pagel, 1991).

Body size and geographical range size of species were used as response variables in a nested two-way analysis of variance (ANOVA) model in which classification variables were families and genera within families. Stearns' (1983) method, as in more complex statistical methods [see Martins *et al.* (2002) for a recent comparison], is used to partition the variance of a trait into a phylogenetic (or taxonomic) component, which contains the shared variance among species due to phylogenetic structure, and a specific component that expresses the variation among species independently of this structure. The residuals of the nested ANOVA model in Stearns' method approximate the specific component, and thus, tests of correlation among residuals of different traits are not biased by the phylogenetic structure.

We used the average dates of description for the species occurring in each cell of the Cerrado region to evaluate the geographical patterns in this variable. These average description dates were regressed across cells on total human population size, average year of municipality foundation and biodiversity knowledge. In this analysis, the problem of non-independence defined previously may also occur due to spatial autocorrelation in the data (Legendre & Legendre, 1998; Lichstein *et al.*, 2002; Diniz-Filho *et al.*, 2003). Spatial autocorrelation patterns in these variables were then evaluated by means of spatial correlograms constructed using Moran's *I* coefficients obtained for 10 distance classes (see Legendre & Legendre, 1998; for details).

Since significant spatial autocorrelation was found (see Results), the geographically effective number of d.f. (ν^*) for significance tests for correlation coefficients was calculated using Dutilleul's (1993) method (see also Legendre *et al.*, 2002). We also added a quadratic term (second order) of geographical coordinates (latitude and longitude of the centres of each cell) into the multiple regression model of average description dates against human occupation to evaluate how the slopes of these predictors were affected by including broad-scale spatial patterns into the model.

RESULTS

The cumulative increase in the number of anuran species described from the Cerrado region from 1758 to 2003 is shown in Fig. 2. Approximately half of the species were described after 1927, and 20 were described in the 1990s. The cumulative increase in species richness is best fitted using a linear model ($R^2 = 0.949$), although a good fit was also obtained using a logistic model, with maximum richness projected to stabilize at about 160 species described by the year 2050 ($R^2 = 0.922$).

The combined effects of body size and geographical range size explained around 64.8% of the variance in description dates across species ($F = 72.97$, $P < 0.001$), with significant slopes for all predictors. A quadratic term was added to the regression model, accounting for the curvilinear relationship between geographical range size and year of description. Slopes for body size and geographical range size were negative, indicating that recently

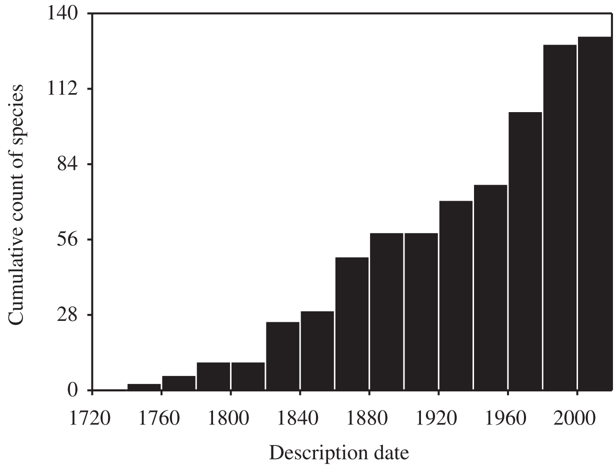

Figure 2 Cumulative frequency of species description dates for anurans from the Brazilian Cerrado. The increase in species richness is best fitted by a linear model ($R^2 = 0.949$) or by a logistic model, with maximum richness projected to stabilize at about 160 species described by the year 2050 ($R^2 = 0.922$).

Table 1 Results of Stearns' (1983) phylogenetic subtraction method applied to three macroecological traits, including the R^2 of nested ANOVA model and F-values for family and genera, used as classificatory variables. The r refers to the correlation between body size and geographical range size with description dates, after taking hierarchical structure into account (using ANOVA residuals)

		F-values		
Traits	R^2	Family	Genera	r
Geographic range size	13.8	1.24	0.69	−0.754**
Body size	31.3	5.05**	1.63	−0.387**
Description date	19.1	2.55*	0.53	

*$P < 0.05$; **$P < 0.01$.

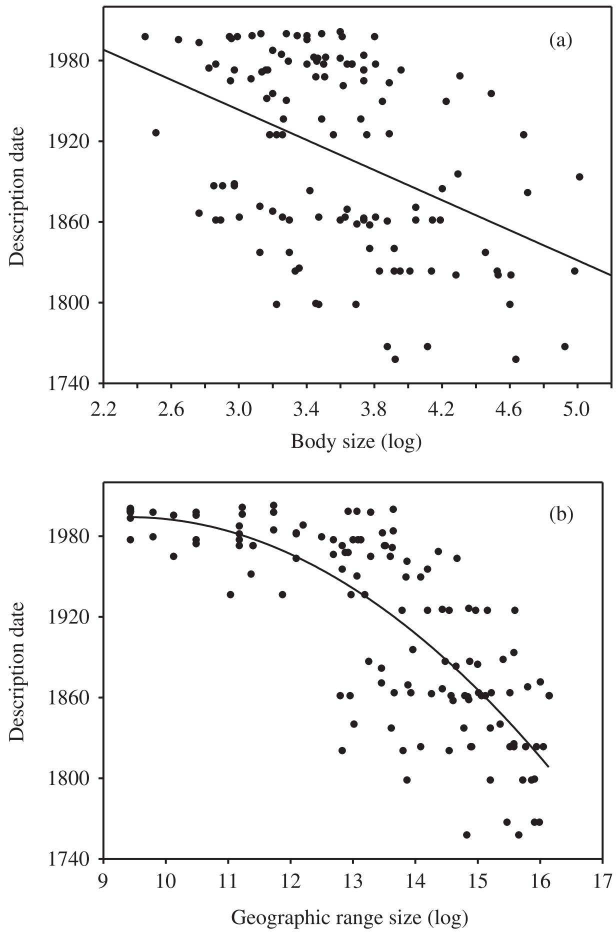

Figure 3 Relationship between description dates across 131 species of anurans from the Brazilian Cerrado and (a) body size and (b) geographical range size. Relationships shown are based on original data, but phylogenetically corrected relationship using Stearns' (1983) method showed the same overall patterns (see text for detail).

described species tend to be small-bodied and geographically restricted (Fig. 3).

These results for the cross-species analyses were not qualitatively affected by taxonomic structure in the data, evaluated using Stearns' (1983) method. Significant taxonomic structures were found in nested ANOVAs for description date ($P < 0.05$) and body size ($P < 0.01$) at the family level, but not for geographical range size (see Diniz-Filho & Tôrres, 2002; Freckleton *et al.*, 2002). When using nested ANOVA residuals, correlations of description date with body size and geographical range size remained significant at $P < 0.01$, and were both negative (Table 1). The relationship between description date and geographical range becomes linear when based on ANOVA residuals, and 61.3% of the variance in ANOVA residuals of description dates was explained by ANOVA residuals of both predictors ($F = 95.29$, $P < 0.001$).

Average description dates were later in the southeastern part of the Cerrado region, decreasing towards the northwest (Fig. 1), and had a strong spatial pattern as indicated by the spatial autocorrelation analysis (Fig. 4). Human population, year of foundation of municipalities and biodiversity knowledge also possess spatial autocorrelation patterns, with varying magnitudes and shapes, and the combined effects of these spatial structures clearly bias the statistical prediction of description dates by these indicators of human occupation in the Cerrado.

Average description dates were significantly correlated with human population size ($r = 0.512$; $P = 0.043$; $v^* = 14$) and biodiversity knowledge ($r = 0.226$; $P = 0.039$; $v^* = 81$), and only marginally with the average year of municipality foundation ($r = -0.419$; $P = 0.082$; $v^* = 16$). A multiple regression model indicated that these three variables explained together *c.* 30% of variation in average year of description. However, after including second-order geographical trends into the multiple regression model, only the effect of human population remained significant ($t = 2.36$; $P = 0.019$) (Fig. 5a) and the overall R^2 increased to 0.90. This confirmed the strong spatial component of description dates previously found in the autocorrelation analyses. It is important to note that there is a multicolinearity problem in this model, mainly due to a correlation between biodiversity knowledge and human population ($r = 0.41$; $P = 0.001$; $v^* = 116$). Indeed, when human

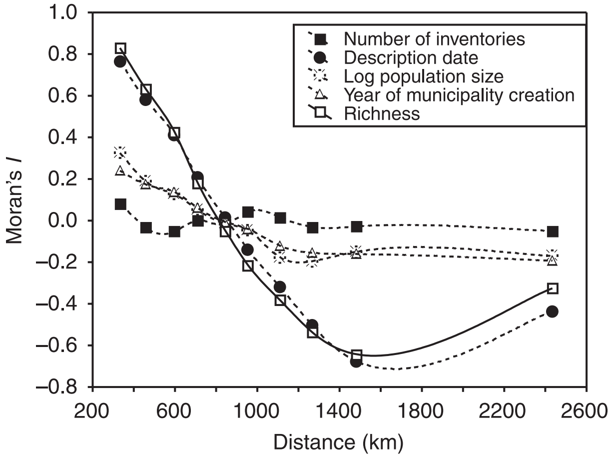

Figure 4 Spatial correlograms using Moran's I coefficients for the variables analysed in this study.

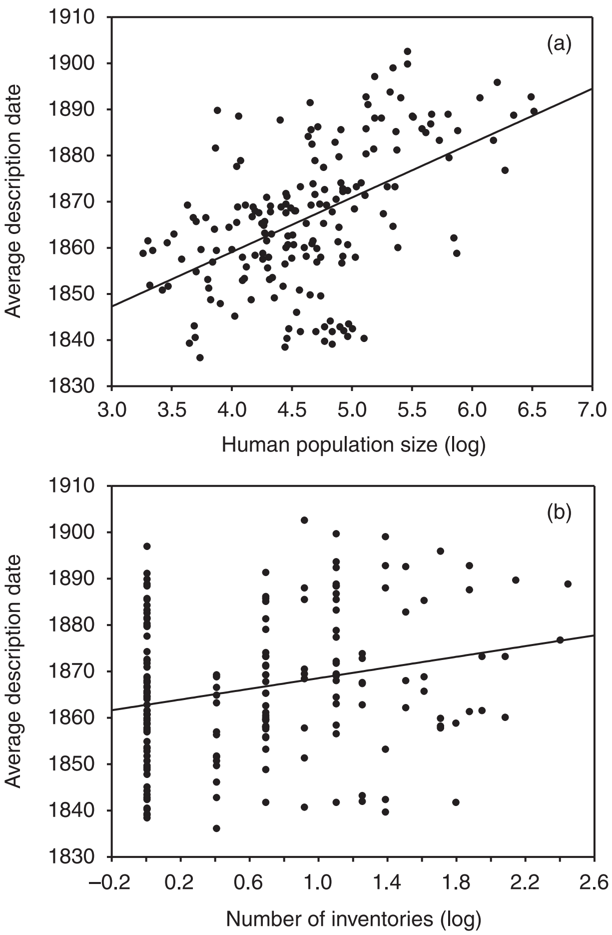

Figure 5 Spatial relationship between average description date in cells with (a) human population size and (b) biodiversity knowledge.

population is removed from the multiple regression, biodiversity knowledge became significant ($t = 2.471$; $P = 0.014$) (Fig. 5b).

Also, as average description dates may be intrinsically correlated with species richness (see Brett, 2004), we confirmed the patterns described above by mapping species richness in the Cerrado for species with distinct description dates. The richness of species described before 1927 was relatively high across the entire part of the Cerrado region, as expected if they have larger ranges, although this richness component decreases towards the north (Fig. 6a). On the other hand, species described after 1927 are much more concentrated in the southeast (Fig. 6b).

DISCUSSION

Many recent studies have shown that macroecological predictors may be correlated with the description date of species (Collen *et al.*, 2004 and references therein). These correlations may allow us to understand why some species were described earlier than others and, simultaneously, may furnish empirical guidelines for discovering new species, predicting their attributes and eventually, helping to define conservation priorities (Medellín & Soberón, 1999).

For Cerrado anurans, the discovery of new species continues to the present and considering the poor knowledge of biodiversity in the Cerrado (see Young *et al.*, 2000), this cannot be attributed to a taxonomic inflation process (i.e. an increase in species number as a result of a change in the species concept, rather than of new discoveries; Isaac *et al.*, 2004). However, irrespective of the processes originating new species' descriptions, the shape of the curve strongly suggests that many species remain to be dis-covered or described. Finding macroecological correlates across species and geography may help to predict the species' traits and where these species are likely to be found.

As has been found in previous papers, description dates for Cerrado anurans are negatively correlated with body size and geographical range size (see Blackburn & Gaston, 1995; Reed & Boback, 2002; Collen *et al.*, 2004). Although these correlations may vary between groups and regions of the world (e.g. Gaston *et al.*, 1995; Dolphin & Quicke, 2001), for Cerrado anurans, large-bodied and widely distributed species are likely to be described earlier and, simultaneously, species yet to be discovered are probably small-bodied and with narrow distributions.

Further, geographical patterns of average description dates may suggest where new species are likely to be found. Although some papers have evaluated variation among patterns of species descriptions among biogeographical regions (Gaston *et al.*, 1995; Dolphin & Quicke, 2001), in this study we used an explicit spatial approach to show that the average description date is spatially correlated with total human population and biodiversity knowledge in the Cerrado region. So, discoveries occurred more recently in more densely populated cells, which also are the regions best surveyed for overall biodiversity. Initially, the opposite pattern would occur, because the earlier a region is occupied and colonized, accumulating higher human population sizes, the greater the chances of describing the species. On the other hand, newly occupied areas should have only the newly described species, such that a negative correlation between human population size and average description date should be expected. However, it is important to consider the spatial patterns of human colonization in the Cerrado and how ranges of species are estimated.

The positive correlation makes sense by considering the recent process of human occupation of the Brazilian Cerrado, which is

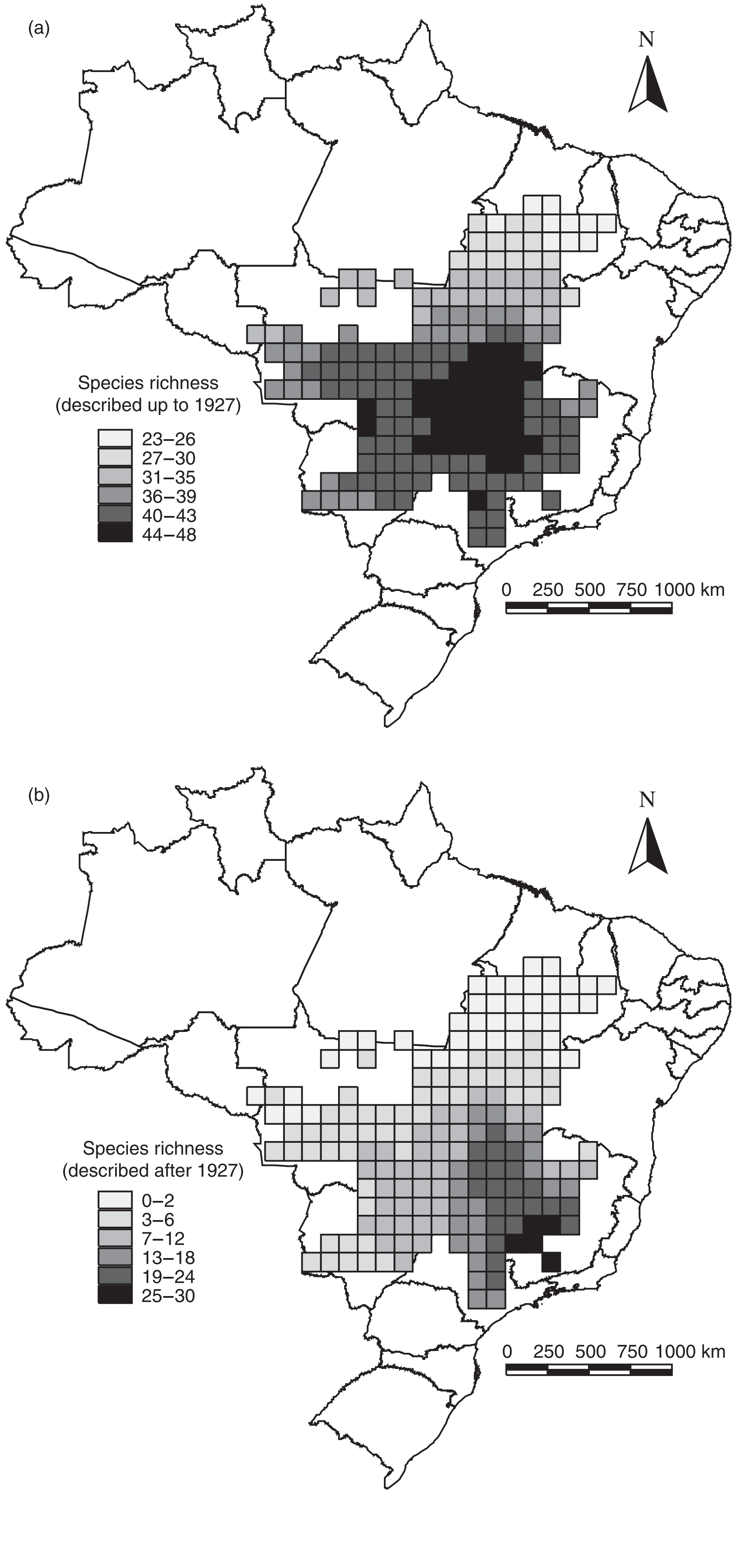

Figure 6 Spatial patterns of species richness for species described before (a) and after 1927 (b).

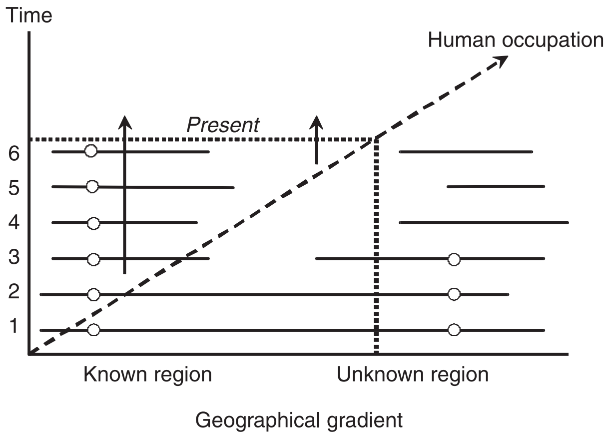

Figure 7 Graphical model of the mechanism involved in the positive relationship between average description date and current human population size and knowledge of biodiversity found by this study. Geographical ranges of hypothetical species are displayed as horizontal bars, and are 'distributed' in the time axis for visualization purposes. Gradients are generated by the space–time correlated process of human population in a region (dashed arrow), which separates the geographical area in known (occupied at a given time, say time 6 to present) and unknown (not occupied at a given time) regions (dashed lines). Because widely distributed species are described earlier, they are also recorded (open circles) for unknown regions because of range estimates using MCP, but narrow ranged species have to wait for human colonization to be described. In known regions, there is more time for occupation, increasing human population size and knowledge of biodiversity (vertical arrows) and, consequently, both widely and narrowly distributed species are described. Thus, average description dates vary between the two regions (3.3 units for known region against 2.0 for unknown region) and are positively correlated with human population size and knowledge of biodiversity, even if richness is constant throughout geographical space.

characterized by successive wave fronts of colonization coming from the south and southeastern parts of the country since the 18th century (see Klink & Moreira, 2002). Less populated cells in the northern Cerrado, on the other hand, have average old description dates because they are now occupied by widely distributed species that were described earlier, usually elsewhere in the country or in South America. Finding undescribed endemic species in these regions would require better and more localized sampling strategies and this would then increase the average description dates of these regions in the future (see Fig. 7). However, to predict where new discoveries are likely to occur, more complex scenarios should also be considered. It would be necessary to consider different assumptions about biodiversity patterns in anurans, about how the knowledge of these patterns arose in recent years and how human populations occupied the Cerrado region. This matches recent claims (Gaston, 2004) to incorporate human occupation patterns into macroecological research programmes.

Regions with more recent average description dates are also those more recently occupied by humans, suggesting that new discoveries are dependent on human occupation (see Fig. 7). This is expected because dense human occupation in Cerrado is a relatively recent process, mainly associated with modern and technological agricultural expansion in the 20th century (Klink & Moreira, 2002). The correlation between human population density and biodiversity knowledge supports this pattern. But the maintenance of the observed spatial pattern in description dates will depend on the 'true' (and presumably unknown at the present time) spatial pattern of species richness. Although work done since the 18th century allows us to make general predictions of broad-scale diversity gradients by current climate effects (Hawkins, 2004), we are far from a predictive theory capable of predicting species richness based on complex environmental and historical factors acting at different scales in time and space, especially for a restricted group of organisms (anurans) living in a poorly studied region (Cerrado). Thus, it may be best to generate alternative scenarios for biodiversity patterns to predict spatial patterns in discoveries.

Assuming that species richness is approximately constant across the entire Cerrado region and that the wave of human occupation will continue in the same direction, this leads to the prediction that average description dates will also increase in the north. On other hand, the true species richness may be higher in the northern region of the biome (mainly in the northwest), especially when considering that both productivity (actual and potential evapotranspiration) and average temperature increase towards these regions and that species richness usually tracks these environmental factors (see Allen *et al.*, 2002; Hawkins *et al.*, 2003). Thus, we expect that if human occupation continues northwards or if more inventories are conducted in this region, a large number of new species will be discovered there, completely changing the shape of the average description dates in the map we presented here. It is important to note that evaluating species' ranges using minimum convex polygons (MCV), despite possible overestimation, nevertheless provides a conservative way to deal with spatial variation in description dates. Because the widely distributed species are usually found in most cells, increases in average description dates as a consequence of increasing knowledge on biodiversity patterns in the north will more likely occur because of the addition of new species, not because species that are previously known from the southern region will have their geographical ranges 'expanded' towards the north. But, of course, some of these old described species in the north may be closely related species to those already described, and this will also increase the rate of species description. It is also important to consider that this future interactive process of knowledge gain and human occupation may also increase species losses and create many uncertainties in both the future spatial pattern of richness and species' description dates, or at least cause species' range contractions towards different regions, in an ecologically version of the well-known Heisenberg's uncertainty principle of physics. If biodiversity knowledge depends on human occupation, it will be almost impossible to know biodiversity and conserve it simultaneously without effective regional planning.

Finally, our findings suggest that initial attempts to define optimum strategies for broad-scale conservation planning in Cerrado based on these organisms (see Diniz-Filho *et al.*, 2004b) must be viewed with caution, as they did not take into account the correlations between richness and biodiversity knowledge we detected here. Clearly, new research efforts should be concentrated in the northern Cerrado, and the discovery of new species in this region could change the spatial configuration of reserve systems optimally designed to conserve biodiversity. Our lack of knowledge about species richness or abundance estimates has always been considered an obvious problem for reserve design (Rodrigues & Gaston, 2002; Gaston & Rodrigues, 2003), and is a part of the current justification for expensive research programmes in ecology and systematics with the purpose of mapping species distributions and documenting their ecological attributes (see Brooks *et al*., 2004 for a recent discussion). At the same time, the incorporation of human population density into reserve design algorithms (e.g. Balmford *et al*., 2001; Chown *et al*., 2003) has been usually done to avoid or minimize conservation conflicts and increase the probability of the long-term persistence of species and other conservation targets, allocating conservation units outside regions widely used by human activities.

Our analyses for anurans in the Cerrado region suggest a unique solution to deal with lack of knowledge on biodiversity and, simultaneously, minimize potential human development–conservation conflicts. If species richness and endemism follow the expected trends in both temperature and productivity and, in fact, they increase towards the north of the Cerrado, the strategy of minimizing conflicts currently adopted by some researchers (see Balmford *et al*., 2001) may produce good results not simply because it avoid conflicts between human development and conservation, but also because reserve networks will include many units in regions where most of the non-described species will probably be found in the future. This may be particularly important for anurans as there is a growing concern about the decline in their populations worldwide (Young *et al*., 2000; Stuart *et al*., 2004), creating demands for urgent strategies to maximize conservation efforts, especially in regions in which few detailed data on diversity, abundance and distribution are available.

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BIOSKETCHES

José Alexandre F. Diniz-Filho is interested in statistical methods applied to macroecology and evolutionary biology. Current projects involve the application of spatial autocorrelation analysis and phylogenetic comparative methods to understand ecological processes associated with gradients in species richness, and the application of spatial statistics to define operational units for conservation and to establish conservation priorities.

Rogério Pereira Bastos is interested in anuran biology and ecology. His current studies have focused on distributional patterns of anuran species in Central Brazil and their implications for conservation, and anuran behavioural ecology.

Luis Mauricio Bini is interested in statistical methods applied to biodiversity analyses and limnology. Current projects involve the analysis of spatial population synchrony of aquatic assemblages in reservoirs and floodplains. He is also interested in how population dynamics are linked with more general biodiversity patterns, mainly the relationship between species diversity and ecosystem stability.

Thiago Fernando Lopes Valle de Britto Rangel is interested in statistical and computational methods applied to macroecology and conservation biology. Current projects involve the development and implementation of software to simulate evolutionary dynamics of macroecological patterns.

Priscilla Carvalho's current work involves the application of quantitative methods in macroecology and limnology, including the use of endangered species lists to understand macroecological patterns and processes. Current projects also involve scientometric analysis and the application of comparative methods in biology.

Rodrigo J. Silva's current projects involve the fusion, at a macroecological scale, between ecological and socio-economic data, to establish conservation priority in the Brazilian Cerrado.