Diversity and Distributions, (Diversity Distrib.) (2006) **12**, 475–482

BIODIVERSITY RESEARCH

Challenging Wallacean and Linnean shortfalls: knowledge gradients and conservation planning in a biodiversity hotspot

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ABSTRACT

Knowledge about biodiversity remains inadequate because most species living on Earth were still not formally described (the Linnean shortfall) and because geographical distributions of most species are poorly understood and usually contain many gaps (the Wallacean shortfall). In this paper, we developed models to infer the size and placement of geographical ranges of hypothetical non-described species, based on the range size frequency distribution of anurans recently described in the Cerrado Biome, on the level of knowledge (number of inventories) and on surrogates for habitat suitability. The rationale for these models is as follow: (1) the range size frequency distribution of these species should be similar to the range-restricted species, which have been most recently described in the Cerrado Biome; (2) the probability of new discoveries will increase in areas with low biodiversity knowledge, mainly in suitable areas, and (3) assuming range continuity, new species should occupy adjacent cells only if the level of knowledge is low enough to allow the existence of undiscovered species. We ran a model based on the number of inventories only, and two models combining effects of number of inventories and two different estimates of habitat suitability, for a total of 100 replicates each. Finally, we performed a complementary analysis using simulated annealing to solve the set-covering problem for each simulation (i.e. finding the smallest number of cells so that all species are represented at least once), using extents of occurrence of 160 species (131 real anuran species plus 29 new simulated species). The revised reserve system that included information about unknown or poorly sampled taxa significantly shifted northwards, when compared to a system based on currently known species. This main result can be explained by the paucity of biodiversity data in this part of the biome, associated with its relatively high habitat suitability. As a precautionary measure, weighted by the inferred distribution data, the prioritization of a system of reserves in the north part of the biome appears to be defensible.

Keywords

Anurans, Cerrado, biodiversity knowledge, conservation planning

INTRODUCTION

Knowledge about biodiversity remains inadequate and plagued by the so-called Linnean and Wallacean shortfalls (Lomolino, 2004; Whittaker *et al*., 2005; see also Brown & Lomolino, 1998). The first refers to the fact that most species living on Earth were still not formally described, whereas the second is defined by the fact that, for the majority of taxa, geographical distributions are also poorly understood and contain many gaps. As recently pointed out by Whittaker *et al.* (2005), these two shortfalls are scale dependent, both on evolutionary and on ecological dimensions. Although work done since the 18th century allows us to make general predictions of broad-scale diversity gradients based on current climate effects (see Hawkins, 2004 and references therein), we are far from a predictive theory capable of predicting species diversity based on complex environmental and historical factors acting at different scales in time and space.

DOI: 10.1111/j.1366-9516.2006.00286.x
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This scale dependence is important because most practical decisions about how to conserve biodiversity are taken at regional and even local scales. Indeed, the lack of knowledge about species richness, abundance and distribution has always been considered an obvious problem for reserve design (Polasky *et al.*, 2000; Gaston & Rodrigues, 2003; Brooks *et al.*, 2004a,b; Meir *et al.*, 2004; Fagan *et al.*, 2005; Laurance, 2005; Peres, 2005) and is the main justification for funding extensive research programs in ecology and systematics with the basic purpose of mapping species distributions (IUCN/SSC *et al.*, 2004).

Also, the effects of these shortfalls in systematic conservation planning may be more serious for poorly known, developing regions of the world, characterized by recent and highly urbanized human occupation and, often, by very high biodiversity. The Cerrado region of central Brazil has all these characteristics and was indeed recently considered one of the world's biodiversity hotspots (Myers *et al.*, 2000). It is located in the centre of Brazil and is the second larger biome of the country (the first is Amazon rainforest), encompassing a great amount of the environmental heterogeneity and different vegetation types, dominated by savannas (Ratter & Dargie, 1992; Ratter *et al.*, 1996; Bridgewater *et al.*, 2004; Silva *et al.*, 2006).

Recent analyses have shown that geographical patterns of description dates for anurans in Brazilian Cerrado are spatially correlated with total human population and biodiversity knowledge, as indicated by the number of inventories in this region (Diniz-Filho *et al.*, 2005). This suggests that new species discoveries are dependent on human occupation, which is expected since dense human occupation and the establishment of research programs in Cerrado region are relatively recent processes, mainly associated with modern and technological agricultural expansion in the late 20th century (Klink & Moreira, 2002). Thus, defining optimum strategies for broad-scale conservation planning in Cerrado based on these organisms must be viewed with caution and should consider the correlations between richness, endemism and biodiversity knowledge.

In this paper, we used simulation procedures (Rangel & Diniz-Filho, 2005) to generate geographical ranges for hypothetical undescribed species (HUS hereafter) under the assumption that these ranges will be restricted and will occur in areas that are currently less well sampled. This way, we were able to use patterns of biodiversity knowledge and environmental suitability to 'predict' where these species are most likely to be found in the future. These HUS may be not real in a biological sense. However, it is expected that their geographical structure, generated using coherent rules, can help to evaluate robustness of current networks to represent Cerrado biodiversity and give insights for future research and practical conservation actions, in a context of pattern-orientated modelling (Grimm *et al.*, 2005). Although there have been studies about the efficiency of conservation strategies in a world with dynamic landscapes and global climatic changes causing distributional shifts (e.g. Sala *et al.*, 2000; Araújo *et al.*, 2004; Meir *et al.*, 2004), as far we know the lack of knowledge about a group has never been explicitly incorporated into reserve design models.

METHODS

Data

The model used here to simulate the geographical range size and mid-point of the HUS was calibrated by the range size frequency distributions (RSFD) of the anurans species described after 1980. To determine this RSFD, we mapped the geographical range of the 131 species of anurans found in Brazilian Cerrado in a grid of 181 cells with a spatial resolution of 1° each, and evaluated the RSFD of those species described after 1980 (see Diniz-Filho *et al.*, 2005, 2006a, b for details and a map showing the cells). The relationship between description date and range size previously described was nonlinear and we observed a stabilization of small range sizes (median equal to four cells) after 1980, suggesting that species to be described in the future will have very small ranges (see Diniz-Filho *et al.*, 2005).

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 assumed that the number of inventories per cell represents a surrogate for biodiversity knowledge in the region. It is certain that these inventories have different qualities and reflect different sampling efforts, and thus only counting inventories to model biodiversity knowledge could be biased by this variation. Unfortunately, this more detailed information on effort and data quality is not available. More importantly, multiple inventories within a cell (even with variable quality and sampling effort) can be more informative about regional components of species diversity, although this may stay as an assumption of our modelling process.

Simulating the range size and position of the non-described species

The modelling procedures developed by Rangel & Diniz-Filho (2005) were used here to simulate geographical ranges for 29 HUS. This number of HUS was estimated following the predictions of asymptotic stabilization of overall richness in Brazilian Cerrado based on description dates on 160 species around 2050 (see Diniz-Filho *et al.*, 2005). We based this estimate on rates of species description since the 18th century, fitting a logistic model to accumulated species richness through time. This apparently high description date is not unexpected for amphibians, especially in the Neotropics (see Young *et al.*, 2000; Stuart *et al.*, 2004; Kohler *et al.*, 2005; Silvano & Sagallo, 2005). However, although we cannot be certain of this number, it is important to note that our results are qualitatively not affected by total richness values higher than this (results not shown), because the number of cells necessary to represent all described species and simulated HUS tend to stabilize due to 'saturation' of possible solutions at the coarse grain size used here.

The simulation procedures used here were described in detail by Rangel & Diniz-Filho (2005), and were adapted to meet our aims, as follows. First, the number of biological inventories in each cell (biodiversity knowledge) was considered a factor that imposes restrictions on the discovery of new species in a cell. Thus, a cell with a high number of inventories would have a small probability of new discoveries and this probability would increase linearly with the paucity of inventories. When starting the simulation of a HUS, a cell is randomly chosen and if it is considered to be occupied by the species being simulated (probabilistically, based on the level of knowledge), this cell is then initially defined as the species' initial cell. After assuming range continuity (see Araújo & Williams, 2000 for similar reasoning), this HUS will occupy all the adjacent cells only if the level of knowledge in these cells (i.e. number of inventories) is within a given range of values, based on a randomly taken standard deviation (SD_k) of variation around the knowledge level in the species' centre. The knowledge gradient over the Cerrado Biome was linearly transformed and constrained between two values, the K_{min} and K_{max}, indicating cells with minimum and maximum levels of lack of knowledge (i.e. high chances of finding a HUS), respectively. Once K_{min} and K_{max} are fixed, a desired RSFD can be obtained by varying SD_k only. A schematic presentation of these procedures is illustrated in Fig. 1.

Clearly, the discovery of a new species in a given cell depends on many factors beyond human knowledge (Blackburn & Gaston, 1995; Gaston *et al.*, 1995; Cabrero-Sañudo & Lobo, 2003), among them is habitat suitability. To take this into account, the annual mean temperature and actual annual evapotranspiration (AET) were used as surrogates of habitat suitability and incorporated in the simulation models as an interaction term (the product of standardized temperature or AET and knowledge level, in a cell). Both water and energy have been repeatedly found to be of crucial importance for broad-scale diversity patterns (Hawkins *et al.*, 2003; Currie *et al.*, 2004), and specifically for ectotherms, temperature seems to be a key variable (see Allen *et al.*, 2002; Brown *et al.*, 2004). Similar to the procedure previously described, the effects of knowledge and the two measures of environmental suitability were linearly combined and constrained between two values, K_{min} and K_{max}, indicating cells with minimum and maximum chances of finding a HUS, respectively. Thus, suitable cells (i.e. those hot or with high AET values) with small number of inventories (higher lack of knowledge) will have a higher probability of containing a non-described species. A symmetrical deviation from the optimal value for the species being simulated was randomly chosen from a normal distribution with a standard deviation (SD_s) as a surrogate measure of the HUS variation around centroid of species' environmental tolerance and lack of knowledge.

It is important to note that, in the original simulations by Rangel & Diniz-Filho (2005), the parameters of the model (SD_s and the extremes of the gradients, K_{min} and K_{max}) were used to understand the relative roles of deterministic environmental effects in relation to stochastic processes associated with geometric constraints as drivers of species richness, and they were free to vary. However, in this paper the idea is to generate simulated geographical ranges according to a set of rules (i.e. the effects of knowledge and habitat suitability), but conditioned to a real understanding of species richness in a given group of organisms. Geographical range characteristics (i.e. size, shape and placement) are then an emergent consequence of the spatial pattern of the environmental gradient, of the knowledge gradient, of the environmental condition of the initial cell, and finally, of the stochastic environmental tolerance for the species (see Grimm *et al.*, 2005). Thus, we explored the parameter space up to the final range size frequency distribution of the HUS matched as close as possible the observed RSFD of the anuran species in Cerrado described after 1980 (see Diniz-Filho *et al.*, 2005). This is important because, for example, if simulated ranges of HUS were too large, this would not affect current reserve systems because they would be distributed across all Cerrado. So, we assumed that range of the new species will be small and similar to those observed for recently described species.

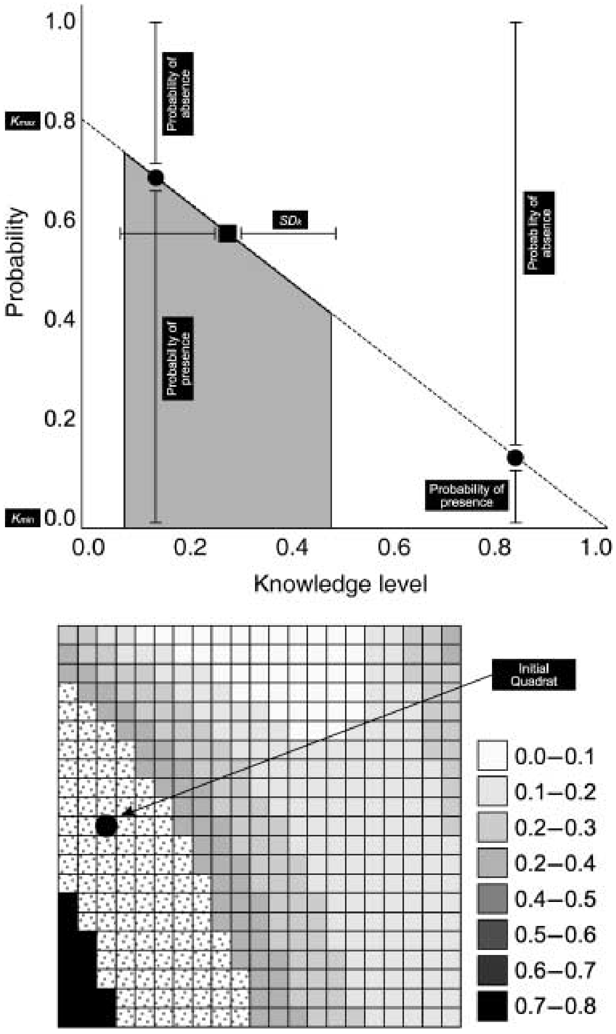

Figure 1 The modelling strategy used in this study. The probability of discovering a new species decreases linearly with the increase of knowledge level (i.e. standardized number of inventories in each cell). According to this probability, an initial cell is randomly chosen from the domain. Then, according to a Gaussian distribution, a deviation value is also stochastically defined, such that species will spread its geographical range to occupy continuously across the space all surrounding cells with knowledge level within the knowledge level of the initial cell and the deviation value (SD_k).

Simulations were performed 100 times for all 29 species, for different sets of variables constraining the occupation of geographical space by HUS. Three sets of simulations were performed. In the first, simulation of HUS was based on the knowledge gradient only (hereafter the *K* model), with $SD_k = 0.09$. In the second set, the effect of habitat suitability was taken into account in addition to knowledge (hereafter the *KT* model), and the SD_t was set to 0.08. In the third set, we replaced temperature by AET as a measure of environmental suitability (the *KA* model), and the SD_t parameter was set 0.025. In all cases, $K_{min} = 0.01$ and $K_{max} = 0.8$. Thus, if we set that probability of finding a species in a maximum sampled area is 0 and that the probability of finding a species in the maximum unknown area is 80%, the RSFD observed for recently described species, with very restricted ranges (a median of 4 cells) can be obtained by setting SD_k to very low values. So, if the HUS appear in a cell with 0.5 in the knowledge/habitat suitability gradient and the SD_k is set to 0.08, it will be able to occupy only adjacent cells but with values in the gradient ranging from 0.34 to 0.66, that is, 2 SD away from the HUS centre. Changing maximum and minimum of the gradients will necessarily change the SD_k in order to get the same RSFD.

Reserve design and analyses

We used simulated annealing algorithm on SSM routine of SITES software (Possingham *et al.*, 2000; see also Andelman *et al.*, 1999) to choose a subset of cells (the reserve network) that represent all anuran species at least once, based on the complementarity concept (Church *et al.*, 1996; Pressey *et al.*, 1997; Margules & Pressey, 2000; see also Cabeza & Moilanen, 2001; Williams *et al.*, 2004). One hundred runs and 10,000,000 iterations for each run were performed.

These procedures were performed for the actual data set (containing 131 species; see Diniz *et al.*, 2005) and for the 100 simulated data sets that were created under a scenario of likely discovery of new species constrained by the level of knowledge and habitat suitability (131 known species plus the 29 HUS). In both cases, we calculated the percentage of cells selected by SSM (in relation to the total number of cells in the network), which were localized in latitudes higher than the latitudinal mid-point of the Cerrado Biome (*c.* 15° S). A Kruskal–Wallis analysis of variance (Sokal & Rohlf, 1995) was used to test the significance of the northward shift in the geographical position of the reserves due to the description of new species in this part of the biome, as could be expected by the lack of inventories. Thus, four groups were compared. The first was formed by the 100 near-optimum solutions provided by SSM with the actual data set (see Diniz-Filho *et al.*, 2006a). The others comprised the best-solutions found by SSM for each of the 100 simulations for each data set, that is, based on the knowledge influence alone and on the joint influence of habitat suitability and knowledge, based on the two different climatic variables.

Finally, we also performed a gap analysis to evaluate the effectiveness of the current reserve network (i.e. selected using the 131 known species of anurans) in representing the total set of potential species, combining current known species and the 29 HUS.

RESULTS

The first step in the simulations is to check if the range size frequency distribution of the HUS matches observed ones. The intercepts of the linear regression equations, estimated by regressing observed ranges on average simulated ranges (see Sokal & Rohlf, 1995), were not significantly different from zero ($a = 0.038$; $t = 0.024$; $P = 0.981$, for the *K* model; $a = -0.033$; $t = 0.023$; $P = 0.981$ for the *KT* model, and $a = -0.695$; $t = 0.663$; $P = 0.513$ for the *KA* model) and the slopes did not differ from 1.0 ($b = 0.979$; $t = 0.151$; $P = 0.882$ for the *K* model; and $b = 0.909$; $t = 0.186$; $P = 0.854$, for the *KT* model, and $b = 1.18$; $t = 1.93$; $P = 0.064$). Thus, the parameters used in our simulations were adequate to reproduce the range size frequency distribution of the species described between 1980 and 2002 (Fig. 2).

As expected, the simulations for both *K* and *KT* models revealed that most of the HUS were concentrated in the north-eastern part of the biome (Fig. 3a,b), in which few inventories were already performed and, simultaneously, in which highly suitable environmental conditions (i.e. higher temperatures) are found. The *KA* model also generated a similar pattern, but also with a concentration of HUS in the south-western part of the biome, close to the Pantanal wet area (Fig. 3c). This is expected because AET is capturing effects of both water and energy on richness (see Hawkins *et al.*, 2003).

Using the known species' distributions, reserve systems are usually composed by cells mainly located in the southern part of the biome (Fig. 4), as shown by frequency of cells in 100 networks with 17 cells each (Meir *et al.*, 2004; see also Ferrier *et al.*, 2000). Indeed, only two cells with maximum irreplaceability (i.e. occurring in all alternative reserve networks) were found in latitudes lower than 15° S (i.e. in the northern part of the biome), and even so they were located near the established latitudinal mid-point. Also, combining the 100 alternative reserve networks that would be necessary to solve the set-covering problem, on average, only a small fraction of these cells with maximum irreplaceability (11.7%) would be localized in latitudes lower than 15° S.

On average, after updating the data with the 29 HUS, the number of reserves in the networks necessary to represent each species at least once under the two simulated scenarios increased from 17 to and average of 29 ± 2.19 SD (*K* model), 30 ± 2.19 SD (*KT* model) and 30 ± 1.97 (*KA* model). However, although this increase is expected because more species with restricted ranges were added to the system, a clear northward shift in the spatial localization of reserves also occurred (Fig. 5). This is expected by looking at the maps of Fig. 3. For example, the mean percentage of cells that should be localized in the northern part of the biome increased from 26% in the current data to 35% under the *K* model. Under the *KT* and *KA* models, the proportion of cells in the networks that should be localized in the northern part of the biome increased even more (38% and 36%, respectively; Kruskal–Wallis ANOVA, $P < 0.001$; Fig. 5).

The efficiency attained by one of the possible networks (specifically, the one with minimum human population size; see Diniz-Filho *et al.*, 2006a) with 17 cells based on the actual data

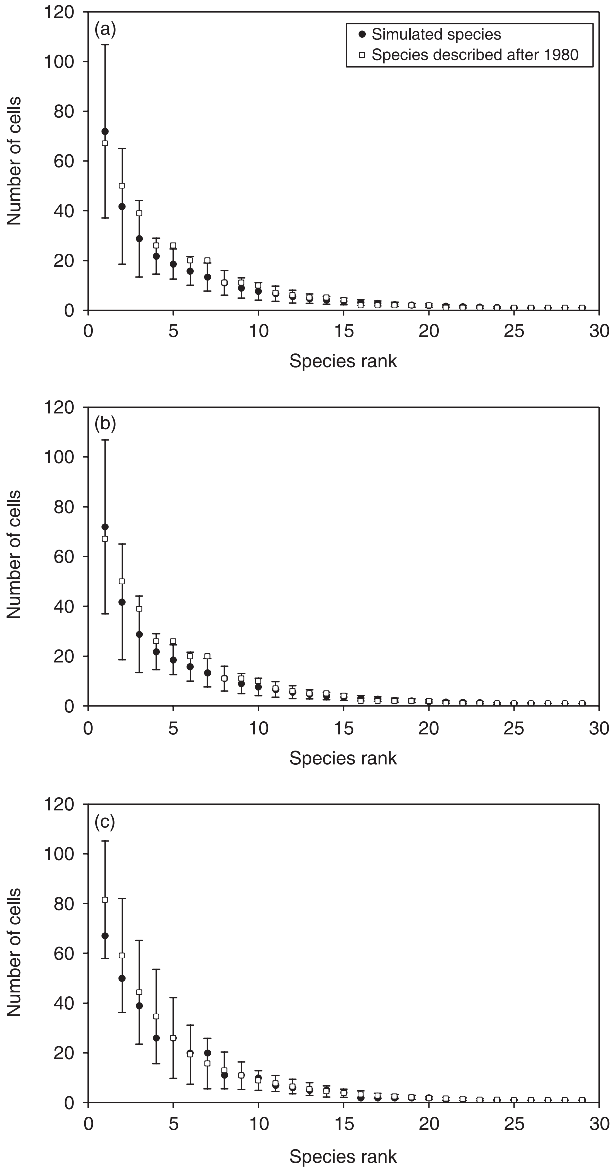

Figure 2 Ranked range sizes of 29 species recently described in the Cerrado Biome and average range (± standard deviation) sizes of 29 HUS (species that probably will be described in the further), based on (a) the level of biodiversity knowledge (the *K* model) and the combined effect of biodiversity knowledge and habitat suitability, for *KT* (b) and *KA* (c) models. See text for further details.

set, in representing the simulated species ranged from approximately 10% to 48.3% in the *K* model, from 10.3% to 55% in the *KT* model, and from 11.2% to 59.3% in the *KA* model.

DISCUSSION

Recently described anuran species in the Cerrado Biome were, in general, small bodied and range restricted (Diniz-Filho *et al.*, 2005), and maximum diversity for the group is found in the central and south-eastern parts of the biome (Diniz-Filho *et al.*, 2004, 2006b). Thus, not surprisingly, the network size increased after the inclusion of simulated species in the regional pool, which are range restricted. The northward shift in the localization of the cells was, however, a specific result of the paucity of faunal inventories in the northern part of the biome and relatively high habitat suitability, which were both allowed in our models. New faunal inventories in the northern part of the Cerrado Biome would also increase the number of records of old-described species, expanding their distributions towards north. Therefore, reserves in this part of the biome, due to the probable presence of HUS, would increase the persistence of old-described species. Although this last possibility was not explicitly included in our simulations, our results are conservative in respect to this additional complication. On the other hand, as a net result, the importance of northern cells would also increase even more due to the reduction of the complementarity value of the cells located in the south.

Surely, the best way to circumvent both Wallacean and Linnean shortfalls is to invest in biodiversity inventories (Balmford & Gaston, 1999). The paucity of data in a large area such as the Cerrado Biome, however, will be not solved in the near future (Kier *et al.*, 2005). Allied to this, the 'forgotten ecosystem' (see Marris, 2005) is under a continuous process of habitat conversion caused by high-tech agriculture and cattle ranching activities. The agricultural front is rapidly expanding towards the north (Klink & Moreira, 2002; Klink & Machado, 2005). Thus, due to these threats, establishment of conservation actions cannot wait, indefinitely, for the availability of reliable and comprehensive data sets on biodiversity. The use of biodiversity surrogates, for instance, could be a way to select priorities areas for conservation when data on species distributions are lacking.

Our proposal to establish reserves in the northern part of the biome may be viewed as a simple application of the precautionary principle (see Cooney, 2004; Prato, 2005 and references therein). For example, according to Laurance (2005), the lack of biogeographical knowledge can be considered the main justification for the need of large reserves in the Amazon. More accurately, in the original article by Peres (2005) (summarized by Laurance, 2005), the need for higher-order biodiversity surrogates (e.g. vegetation typology) for deciding the geographical location of Amazonian reserves was recognized.

Here, we suggest that the level of biodiversity knowledge (or, more precisely, the lack of knowledge) and potential habitat suitability can be used, together or in isolation, to 'predict' the size and placement of geographical ranges of undescribed species. In a second step, simulated ranges of HUS could be added to the actual data set on species distributions to design a reserve network that takes into account the uncertainty generated by unknown species. Although this it is not enough to permit detailed, fine-scale, systematic conservation planning, it may furnish initial guidelines for implementations and improvements in the current prioritization system.

The model developed here can be viewed in the context of pattern-orientated modelling (see Grimm *et al.*, 2005), since HUS are not 'real' in a systematic sense, although we expect that their geographical properties (i.e. their RSFD) will match real ones, allowing Wallacean and Linnean shortfalls to be taken into

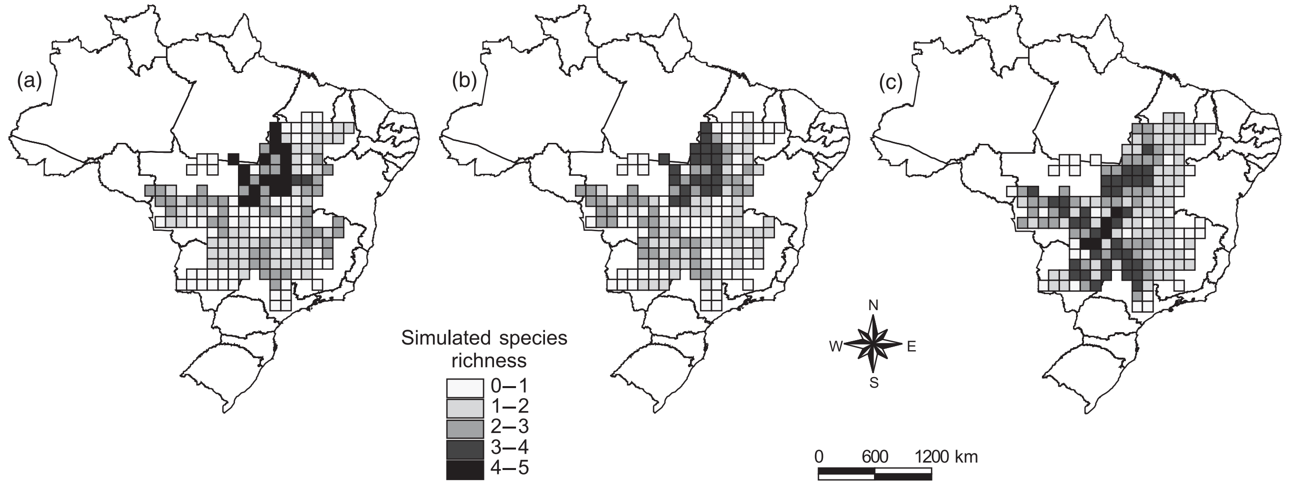

Figure 3 Average species richness, generated by 100 simulations, across the 181 cells covering the Cerrado Biome, based on biodiversity knowledge only (*K* model, a), and on biodiversity knowledge and habitat suitability (*KT* model, b, and *KA* model, c).

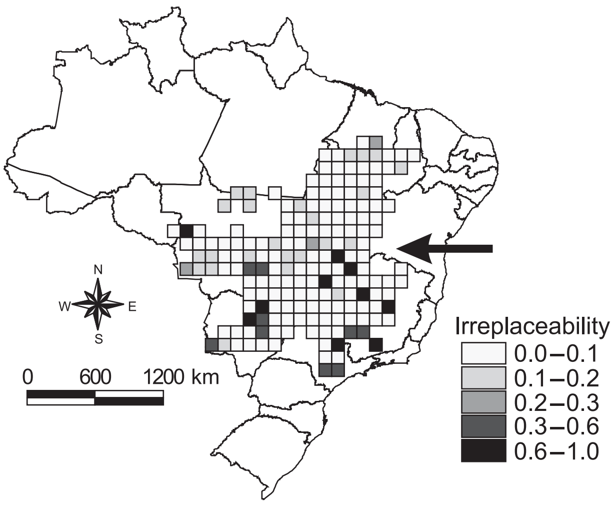

Figure 4 Spatial patterns in the irreplaceability estimated by the frequency of cells in the 100 optimal solutions obtained with the 131 species of anurans that can be found in Brazilian Cerrado (modified from Diniz-Filho *et al.*, 2006a). The arrow shows the line of 15° of latitude south, used here to separate the biome into north and south parts (see Fig. 5).

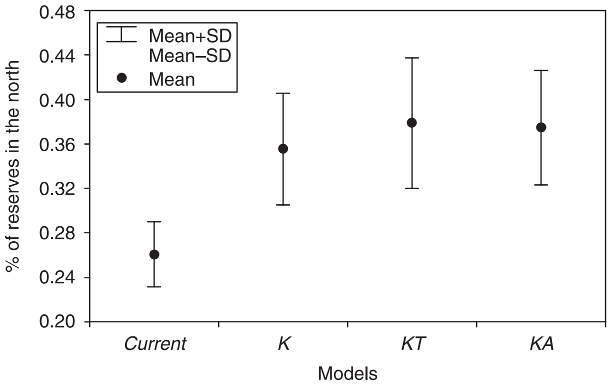

Figure 5 Percentage of reserves located in latitudes lower than 15° (the northern part of the Cerrado Biome), as estimated by the complementarity analyses. Current, *K*, *KT* and *KA* indicate, respectively, the results obtained with the actual data on anurans distribution (± standard deviation, based on 97 near-optimal solutions); with the *K* model (allowing for the influence of knowledge level alone) with the *KT* model (allowing for the influence of both knowledge level and habitat suitability, as measured by annual mean temperature) and with the *KA* model (allowing for the influence of both knowledge level and habitat suitability, as measured by actual annual evapotranspiration). Error bars for both *K* and *KT* models represent the estimated standard deviations based on 100 simulations.

account in reserve design. The main output of the model is that a northward shift in reserve location is expected due to new discoveries in a near future (see Diniz-Filho *et al.*, 2005). Our modelling approach cannot be 'tested' in a formal sense until new species are described for the region, especially after inventories in the northern part of the biome.

One way to check the validity of our modelling strategy would be a retrospective approach, in which newly described species (say, those described after 1980) are deleted from the data set and simulated to verify if final patterns of richness and endemism match current ones. However, this would require also a temporal dimension for the inventories (i.e. the number of inventories that existed before the 1980s), and these data are not available. Also, we know that, unfortunately, recent inventories were still concentrated in the southern part of Cerrado, close to large research centres and universities.

Thus, our analyses provide a first insight towards using broad-scale simulations to take into account uncertainty in biodiversity knowledge in a tropical hotspot. Due to the current overall lack of knowledge for most taxa, this may be a major source of error in current systematic conservation planning in hyperdiverse developing countries. Even within nations, some regions demand more knowledge than others. We believe that, although predictions are not possible in a taxonomic sense, they are probably realistic in terms of distribution and endemism patterns. As a final recommendation, the clear message of our model is that a northward shift in Cerrado reserves must be expected. To take into account other societal demands, new reserves in the northern part of the Cerrado Biome should be in the form of less restrictive categories of conservation units, until more detailed data for species distribution of target taxa become widely available.

ACKNOWLEDGEMENTS

We thank Brad Hawkins, Miguel A. Olalla-Tarraga, Hugh Possingham and two anonymous reviewers for many comments that improved previous versions of the manuscript. Financial support for this study came from a PRONEX program of CNPq and SECTEC-GO (proc. 23234156). Work by JAFDF, LMB and RPB were also partially supported by other CNPq projects (grants: 300762/94-1, 302707/2004-2; 400381-97.4, respectively). Our research program in macroecology and biodiversity has also been continuously supported by CAPES and FUNAPE-UFG. We thank M.B. Araújo for the discussions on simulating species distributions and B.A. Hawkins for reading and commenting on earlier drafts of this paper. This paper is dedicated to the memory of Antonio Bini, who dedicated all his life to protect the environment.

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