BIODIVERSITY RESEARCH

The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia

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ABSTRACT

The distribution of tropical plant and animal diversity is still poorly documented, especially at spatial resolutions of practical use for conservation. In the present study, we evaluated the level to which geographical incomplete data availability of species occurrence affects the perception of biodiversity patterns (species richness and endemism) among pteridophytes in Bolivia. We used a data base of Bolivian pteridophytes (27,501 records), divided it into three time periods (1900–70, up to 1990 and up to 2006), and created grid-files at 15′-resolution for species richness and endemism. For each of these biodiversity properties we estimated the species richness (Chao 2) and the index of sampling completeness (C index) per grid, and then all these variables at both species richness and endemism were correlated. Patterns of richness were fairly consistent along all periods; the richest areas were placed along the humid-montane forest, even though they were strongly influenced by collecting intensity. Endemism had a lower degree of correlation with collecting intensity, but varied much more strongly through time than species richness. According to the C index, which gives the ratio between estimated (by Chao 2) and recorded values of species richness and endemism, both biodiversity properties tended to be undersampled in the richest grid cells. Inter-temporal correlations showed sharper differences of correlations for endemism than species richness. Consequently, already in 1970, botanists had a correct idea of the spatial distribution of pteridophyte richness in Bolivia (even though the magnitude was grossly underestimated). In contrast, patterns of endemism, which are of high conservation importance, may not even today be reliably known.

Keywords

Bolivia, collecting activity, conservation, pattern of endemism, pattern of species richness, Pteridophyta.

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INTRODUCTION

The tropics are well-known to harbour a high proportion of global biodiversity. This contrasts with the still imperfect knowledge of the taxonomy and distribution of many tropical taxa. Large regions of the tropics have never been inventoried in detail for many plant and animal groups (Frodin, 2001; Kier *et al.*, 2005), and thousands of species continue to be described each year (Sayer & Whitmore, 1991; Reed, 1996; Nichols *et al.*, 1998; Midgley *et al.*, 2002). Reliable data on the distribution of tropical biodiversity is of crucial importance both for ecologists seeking to understand how this diversity has evolved and is maintained, and for conservationists struggling to optimize the use of their limited resources. In the last two decades, a number of global prioritization schemes have been proposed, such as the biodiversity hotspots of Myers *et al.* (2000) or the Global 200 approach of WWF (Olson *et al.*, 2001). These schemes attempt to quantify the spatial distribution of biodiversity, among other factors (Reid, 1998; Stattersfield *et al.*, 1998; Myers *et al.*, 2000). As useful as these approaches are, their spatial resolution is very low, for example, the tropical Andes recognized as a single, high priority region by Myers *et al.* (2000). While the general assessment of the tropical Andes as a biodiversity hotspot in need of conservation action is certainly correct, actual conservation actions usually have to take place at a much finer scale, for example, involving individual protected areas and it is at this scale that biological baseline data in the tropics is often inadequate.
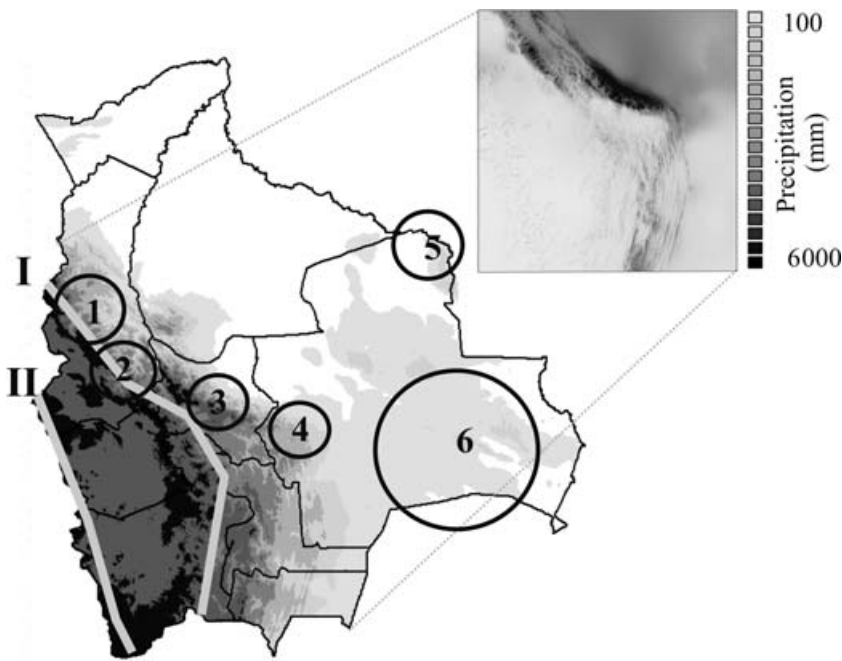
Figure 1 Digital altitudinal model of Bolivia (Hijmans *et al.*, 2005b) showing geographical features mentioned in the text: I, eastern Andean range; II, western Andean range; 1, central La Paz; 2, south-central La Paz; 3, central Cochabamba; 4, Andean Elbow; 5, Noel Kempff Mercado National Park; and 6, Cerrado and Dry Chaco. Upper right, the annual rain model developed by Dr J. Böhner, Goettingen University, Germany (projection: Lambert equal-area azimuthal).

The use of large biodiversity data bases drawing information from a wide range of sources, such as museum collections and published records, is potentially critical in assessing biodiversity patterns due to the risk of assuming, overlooking or misunderstanding information, and due to biases in the geographical configuration of data (Kodric-Brown & Brown, 1993; Freitag *et al.*, 1998). Possibly the most important source of spatial bias is the ad hoc spatial arrangement of the samples, that is, with most of the collected data coming from easy-access localities (Ponder *et al.*, 2001; Reddy & Dávalos, 2003; Grand *et al.*, 2007). Some authors have shown that the unevenness in collecting activity affects the locally recorded species richness (Freitag *et al.*, 1998), the perception of centres of endemism (Ponder *et al.*, 2001), the selection of priority areas for conservation (Reddy & Dávalos, 2003; Grand *et al.*, 2007) and even compromise the geographical placement of the postulated Amazonian refuges during the dry periods of the Pleistocene (Nelson *et al.*, 1990).

The aim of the present study was to assess the degree to which the spatial arrangement of collecting intensity and the resulting imperfect knowledge of the distribution of biodiversity in the tropical Andes affects the perception of biodiversity patterns, and resulting potential conservation actions. Using the example of pteridophytes (ferns and fern-like plants), we analysed two different aspects of biodiversity, namely species richness and endemism. Although both overall richness and levels of endemism tend to be higher in the tropics than in temperate regions, these two aspects tend to show only limited correlation at the spatial level relevant for conservation actions (e.g. Jetz & Rahbek, 2002; Jetz *et al.*, 2004). Our approach was to map the temporal development of the knowledge of the distribution of pteridophyte richness and endemism in Bolivia using three time periods (up to 1970, up to 1990 and up to 2006). We used pteridophytes as a model group because they have been the focus of taxonomic and

ecological research by one of us (Kessler) since 1995 (e.g. Kessler, 2000; Kessler *et al.*, 2001a,b) and are now possibly the best-known major plant group in Bolivia. Pteridophytes contribute considerably to plant diversity in humid tropical forests, especially in montane regions, where they represent up to 19% of the local plant diversity (Young & Leon, 1990). The total known species richness of Bolivian pteridophytes is 1165 species (M. Kessler & A. R. Smith unpubl. data), *c.* 10% (123 species) of which have been proposed as threatened (www.fernsofbolivia. uni-goettingen.de).

METHODS

Study area

Bolivia (1.1 million km²) can be broadly divided into Andean and lowland areas. The Andes are divided in two ranges: the eastern and the western. This configuration causes a contrasting distribution of climatic and ecological conditions. The eastern (outer) slopes of the eastern Andean range are extremely humid, reaching *c.* 6000 mm of rainfall per year in central Cochabamba. However, south of the 'Andean elbow' humidity decreases considerably (Fig. 1). The main natural vegetation in this area is humid montane forest. Contrastingly this high mountain range produces a rain-shadow effect to the west, giving rise to principally drought-adapted vegetation in the inter-Andean valleys and slopes, and westwards across the dry grasslands of the high-Andean plateau (3800–4000 m).

The lowlands are not homogeneous either. Northern Bolivia is dominated by rain forest whose distribution extends narrowly along the lower eastern Andes to the 'Andean elbow', and in eastern Bolivia to the protected area – Noel Kempff Mercado (Fig. 1). The area between these two narrow spits of rain forest is mainly

dominated by seasonally flooded savannas with gallery forest along the rivers. Tropical dry forests dominate the southern landscapes (e.g. dry Chaco, Cerrado, etc; Fig. 1) apart from a limited section of the Pantanal wetlands that occurs in south-easternmost Bolivia (Ibisch & Mérida, 2003).

Data

We used a data base of Bolivian pteridophyte compiled by M. Kessler and A. R. Smith in the scope of work on a forthcoming field guide to the ferns of Bolivia (www.fernsofbolivia.uni-goettingen.de). This data base contains records from all major herbaria and relevant collections of Bolivian ferns up to December 2006. It contains 27,501 accounting for > 95% of all pteridophyte collections made in Bolivia until 2006. Well over 60% of these records are based on determinations made by M. Kessler, A. R. Smith and researchers collaborating with them on the flora project, ensuring a high quality of species determinations. Prior to the actual analysis we undertook a 'data-cleaning' process according to the following criteria: (1) scientific names were standardized according to M. Kessler and A. R. Smith, (2) records not determined up to species level were removed, and (3) only records with reliable geographical references in the data base were taken into account, in this way controlling for all possible sources of error detailed by Chapman (2005). After this process, the databank was reduced to 23,221 records with a mean and median of 20 and 10 records per species, respectively. We treated these species as endemics that are restricted to Bolivia. Although this definition of endemism may be problematic in some biogeographical analyses (Gaston, 1994), it is useful in the context of conservation planning and in the case of Bolivia is unproblematic because the low collection density in bordering regions of the neighbouring countries implies that only two range-restricted species occur in Bolivia, and just outside of it in Peru; all other shared species are much more widespread. Ultimately, because our aim was to compare spatial patterns of total and endemic species richness over time, and not to, for example, to conduct biogeographical analyses as such, the actual definition of endemism is not crucial for the scope of this paper.

Analysis

Three time periods were defined for the temporal approach. The first period ranged up to 1970, covering a period of limited collecting activity. During this period, most of the collecting activity was carried out by foreign botanists who deposited their collections in herbaria in Europe and US prior to the establishment of the National Herbarium of Bolivia in La Paz. The second period extends to 1990, that is, includes the phase during which the National Herbarium was established, while the third period reaches to the end of 2006, that is, covers the phase of intensive research on Bolivian ferns by Kessler and coworkers (since 1995). For all periods, we used the current species determinations of the records because the data base does not include information on the names used for the respective specimens in the past.

For the spatial analysis we used Diva GIS 5.4, a free geographical information system developed by Hijmans et al. (2005a). We mapped species richness, number of endemic species, sampling intensity (defined as the number of collections per grid) and subsequent estimates (Chao 2 and completeness index), at a grid resolution of $15' \times 15'$ for each time period (c. 735 km^2). This resolution result represents a compromise between sampling unevenness and the finest possible resolution that reflect biodiversity patterns (Fjeldså et al., 1999). A parallel analysis analysing the same data at a resolution of $1° \times 1°$ resulted in very similar patterns (R. W. Soria & M. Kessler, unpubl. data), suggesting a limited influence of spatial resolution. In order to maintain a constant area between grids, we used the Lambert equal-area projection. Chao 2 was calculated using the available application of diva of 'point to grid' in the menu 'analysis'. Since this estimator bases its calculation on the incidence of species per sample (not as a synonym of a record, but a set of records from an area), diva divides every grid into several subgrids (being every subgrid a sample unit), and applies the following formula: $S_{Chao2} = S_{obs} + (Q_1^2/2Q_2)$, where S_{Chao2} is the estimated species richness, S_{obs} is the recorded species richness throughout all samples, Q_1 is the number of species occurring in one sample and Q_2 is the number of species occurring in two samples (Colwell & Coddington, 1994; Magurran, 2004; Hijmans et al., 2005a). We chose this estimator because it outperforms other estimators in a wide range of data (Herzog et al., 2002; Walther & Moore, 2005) and because it makes our study comparable to others (e.g. Soberón et al., 2007). The degree of completeness in the recorded species richness and endemism of every cell were calculated by dividing the recorded values (of species richness and endemism, respectively) by the predicted ones (Chao 2). This proportion is known as the index of completeness or C index (Soberón et al., 2007). Finally, in order to assess the degree of congruence in perceived patterns between time periods, we performed analyses of correlation between all variables (species richness, endemism, effort, Chao 2 and C), within and between all periods. Because our data did not fulfil the normal parametric requirements (normal distribution), nonparametric spearman correlations were used.

RESULTS

Our data set contained 23,221 reliably determined and georeferenced records of pteridophytes from Bolivia, collected between 1900 and 2006. In the first period (1900–70) the mean number of collections per year was 12.5, increasing to 166.3 (per year) for the period 1971–90, and to 959.2 for the period 1991–2006. Up to 1970, the total number of pteridophyte collections from Bolivia was 881, corresponding to 404 species. In 1990, there were 4207 records representing 743 species. Finally, in 2006 the total number of species was 1165 species (23,221 records), including 123 endemic species.

Considering the spatial distribution of collections, the most intensely collected area in all periods was the eastern slopes of the Andes; actually, more than the 95% of the collections during the first period came from this region. At this time, the cell with the
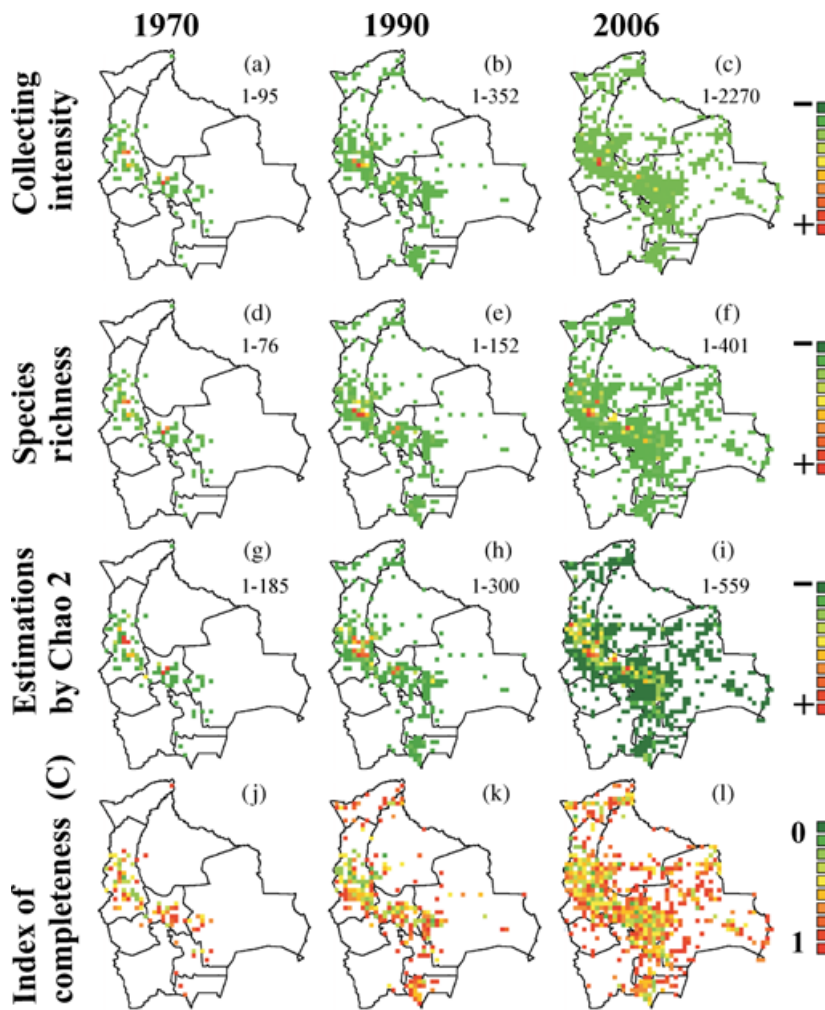
Figure 2 Spatial analysis of species richness. Maps of intensity of collection, recorded species richness, estimated species richness (Chao 2) and completeness for all periods (scale increment in equal intervals). Pixel size is $15' \times 15'$ (*c*. 27×27 km^2), using a Lambert equal-area azimuthal projection.

highest species richness had 76 species and was placed on the eastern humid Andes in central Cochabamba (Fig. 2d). A second centre of species richness was identified for the lower humid montane forest in south-central La Paz (59 spp.; Fig. 2d). The extent of collecting activity increased up to 1990, especially southwards along the Andean range and scatteredly in the northern and eastern lowlands. The highest species richness was found in several cells in humid montane forest of south-central La Paz (152, 129 and 127 spp.) and central Cochabamba became the secondary centre of species richness, with two cells holding 104 and 103 spp. (Fig. 2e). Finally, up to 2006 about 95% of the cells on the eastern Andean slopes had been surveyed for ferns (Fig. 2c). At this time, the highest species richness was recorded in central Cochabamba (401 spp.), with the second-richest cell in central La Paz (393 spp.; Fig. 2f).

Although the location of richest cells shifted between central Cochabamba and south-central La Paz between periods, the general pattern of species richness was relatively constant, showing high richness in the humid montane forest (including transition zones) and lower values in the lowlands and the highlands. These geographical patterns were highly correlated with the intensity of collection for all time periods (Table 1, Fig. 2a–f).

A (partial) correction of the influence of collection intensity by the Chao 2 estimator resulted in patterns consistent with those previously depicted by the crude data but with spatially more even patterns (Fig. 2d–i). Although these patterns were also correlated with the intensity of collection in all periods, the resulting correlation values were lower than for raw species richness (Table 1).

The C index reported on average the lowest correlation with other variables for all periods (Table 1). As a matter of fact, there was a tendency towards lower sampling completeness in cells with high recorded and estimated richness (Fig. 2j–l).

The geographical patterns of endemism did not coincide closely with the species-richness patterns. The cell with highest endemism up to 1970 (4 spp.) was found in central La Paz, and several other records north-east and east from this cell, whereas in central Cochabamba just two cells held endemic species (Fig. 3d). The quantity of cells holding endemic species up to 1990 increased, and almost all of them were placed in the humid Andean forest south to the 'Andean elbow' (Fig. 3e). At this time, the highest endemism coincided with the richest cell (Figs 2e and 3e). Finally, up to 2006 there were two clearly defined centres of high endemism, the highest coincided with the one identified up
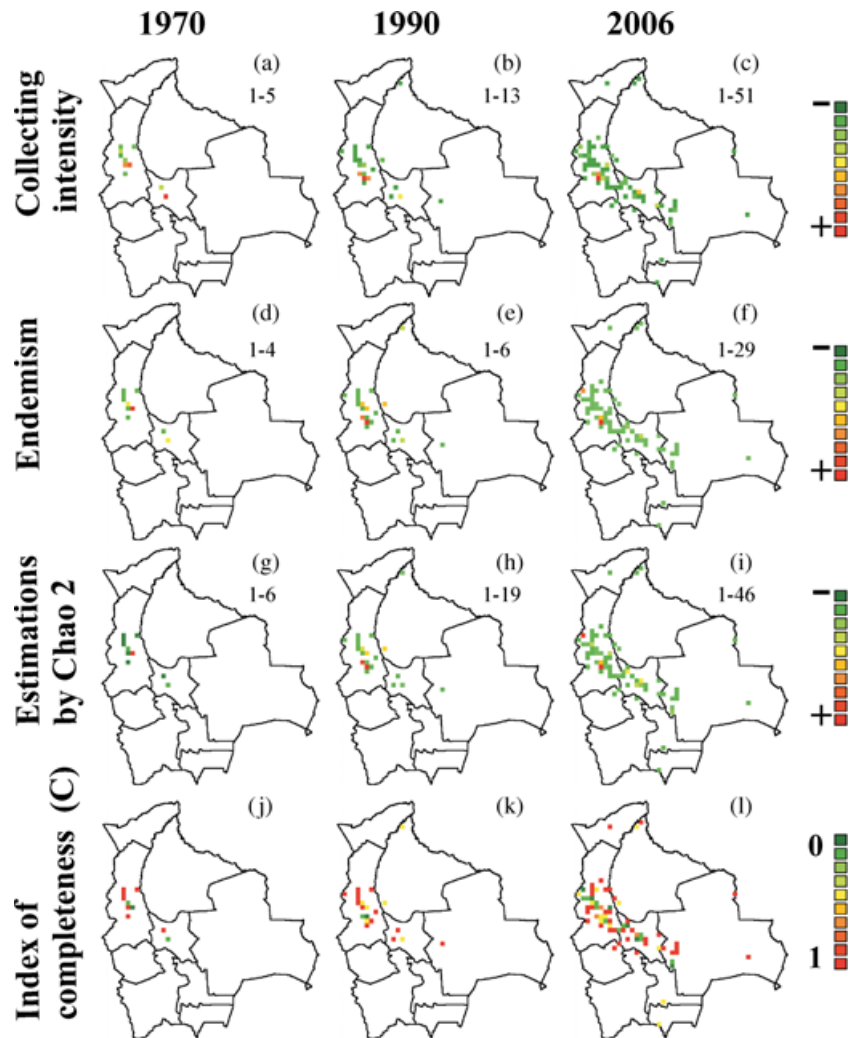
Figure 3 Spatial analysis of species endemism. Maps of intensity of collection of endemic species, recorded endemism, estimated endemism (Chao 2) and completeness for all periods (scale increment in equal intervals). Pixel size is 15′ × 15′ (*c*. 27 × 27 km²), using a Lambert equal-area azimuthal projection.

Table 1 Correlation matrix for species richness

	Up to 1970 (*n* = 84 cells)				Up to 1990 (*n* = 230 cells)				Up to 2006 (*n* = 550 cells)			
	Spp.	IC	Chao 2	C	Spp.	IC	Chao 2	C	Spp.	IC	Chao 2	C
Spp.	1	–	–	–	1	–	–	–	1	–	–	–
IC	0.997	1	–	–	0.995	1	–	–	0.991	1	–	–
Chao 2	0.904	0.908	1	–	0.903	0.902	1	–	0.910	0.905	1	–
C	−0.828	−0.807	−0.851	1	−0.765	−0.736	−0.881	1	−0.704	−0.704	−0.801	1

Significant correlations with *P* < 0.05 are in bold. Spp., species richness; IC, intensity of collection; Chao 2, estimations by Chao 2; and C, index of completeness (see text for further explanations).

to 1990, but at this time the amount of endemic species in this cell reached 29; the second most important cell was placed north-western La Paz (19 spp.).

Although to a lower degree compared with species richness patterns, endemism patterns correlated positively with the intensity of collection for the last two periods (Table 2), and it

also correlated closely to the estimated endemism by the Chao 2 (Fig. 3, Table 2).

Finally, considering 2006 scenarios as the most probable estimation of the real patterns of species richness and endemism, between-periods correlations within variables were more stable and higher for species richness than for endemism (Fig. 4), and

Table 2 Correlation matrix for endemism

	Up to 1970 (n = 11 cells)				Up to 1990 (n = 22 cells)				Up to 2006 (n = 68 cells)			
	End	IC	Chao 2	C	End	IC	Chao 2	C	End	IC	Chao 2	C
End	1	–	–	–	1	–	–	–	1	–	–	–
IC	0.584	1	–	–	**0.476**	1	–	–	**0.597**	1	–	–
Chao 2	**0.930**	0.584	1	–	**0.917**	**0.577**	1	–	**0.975**	**0.563**	1	–
C	**−0.906**	**−0.640**	**−0.911**	1	**−0.790**	**−0.538**	**−0.954**	1	**−0.791**	**−0.472**	**−0.869**	1

Significant correlations with $P < 0.05$ are in bold. End, number of endemic species (endemism); IC, intensity of collection; Chao 2, estimations by Chao 2; and C, index of completeness (see text for further explanations).
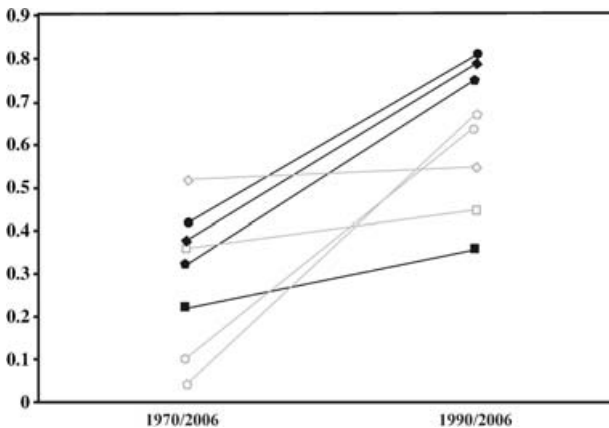

Figure 4 Inter-period correlations of collecting intensity (pentagons), observed species numbers (diamonds), estimated species numbers through the Chao 2 index (circles), and the C index (squares) for species richness (dark lines, closed symbols) and endemism (grey lines, open symbols) of pteridophytes in Bolivia.

in all cases, patterns in 1990 correlated more closely to patterns in 2006 than patterns in 1970.

DISCUSSION

The aim of this study was to assess the degree to which the history and intensity of field sampling influence the perception of patterns of species richness and endemism in the tropics. Regarding the overall pattern of species richness of ferns in Bolivia (Fig. 2d–f), the areas with highest species richness was quite consistent across time, with the humid eastern slopes showing the highest values. However, the detailed patterns correlated with the geographically uneven collection intensity (Figs 2a–c and 4) and the specific distribution of the cells with the highest recorded richness changed markedly over time as a result of shifts in the geographical distribution of botanical collections. As in many previous studies on this subject (e.g. Freitag *et al.*, 1998; Reddy & Dávalos, 2003), we found a strong positive association between sampling intensity and recorded species richness. However, this does not imply that the cells with the highest recorded richness have such high values only because they are well collected. After all, cells with few species will have a

low number of collections simply because botanists find few ferns to collect. As any field botanist knows, botanists tend to concentrate their efforts in more diverse (and hence 'interesting') areas, avoiding poor species-richness areas.

Therefore, the challenge at hand is to quantify the degree to which the high number of records (and hence species) in some cells are a result of the highly diverse fern flora or of high sampling intensity. This assessment depends on having fairly complete samples for at least some cells. However, our calculations of expected total species numbers with the Chao 2 estimator and of the C index of sampling completeness revealed that sampling in Bolivia is still far from complete. Indeed, there was a tendency towards less complete sampling in cells with high richness and high number of collections, suggesting that despite the extra effort spent by botanists in species-rich habitats, these are still less completely sampled than many of the species-poor cells.

An alternative approach to assess the reliability of the detected richness patterns is to compare our analysis with field data from local surveys. Bolivia has been subject to intensive studies of fern diversity using over 1000 standardized plots of 400 m² (Kessler, 2000, 2001; Kessler *et al.*, 2001a,b). While the spatial scale of the two approaches differs by over six orders of magnitude and hence precludes a meaningful quantitative statistical comparison of the spatial patterns of species richness, there is an overall agreement between both approaches. Both our study and the field data document highest fern richness at mid-elevations in the northern Andes, and a general decline of richness from north to south. These patterns suggest a strong dependence of fern diversity with humidity and are in accordance with patterns found elsewhere (e.g. Rey Benayas & Scheiner, 2002; Guo *et al.*, 2003; Aldasoro *et al.*, 2004; Bhattarai *et al.*, 2004; Karst *et al.*, 2005; Bickford & Laffan, 2006; Kluge & Kessler, 2006).

Thus, by 1970 biologists already had a correct, even if rough, idea of the overall spatial distribution of fern richness in Bolivia. The magnitude of the richness, however, was strongly underestimated. The richest cell had only 76 recorded species and while the application of the Chao 2 estimator corrected this value to 185, this is still far less than the highest cell-count of 401 known today. Clearly, and as also shown in previous studies (e.g. Herzog *et al.*, 2002; Walther & Moore, 2005) the Chao 2 estimator can only partly correct for incomplete sampling. Soberón *et al.* (2007) have recently shown that estimators do not work accurately on

'degenerated cells' with low sampling intensity. Several authors (Colwell & Coddington, 1994; Colwell *et al.*, 2004; Colwell, 2005) have recommended estimating the error of the estimated values, but this cannot be applied to Chao 2. We selected the Chao 2 estimator because it is considered to outperform other estimators (Walther & Moore, 2005) and because it has been used in similar studies (e.g. Soberón *et al.*, 2007), allowing direct comparison. Other estimators suffer from the same general limitations (Herzog & Kessler, 2002; Walther & Moore, 2005). Thus, the use of estimators clearly has limitations and it may be more realistic to use them to assess the degree of sampling completeness than to try to calculate 'true' species numbers.

Turning towards patterns of endemism, patterns changed more strongly with time than patterns of species richness (Fig. 4). Importantly, patterns of endemism were less influenced by collection intensity (Tables 1 and 2). Although the highest numbers of endemic ferns in Bolivia are also found on the humid eastern Andean slope, their distribution within this region is much more irregular than that of species richness. Again, this is confirmed by field surveys. For example, 514 collections made in a cell in northern La Paz, close to the Peruvian border, since 2002 have revealed no less than 19 endemic species (M. Kessler *et al.* unpubl. data). In contrast, a collection of 303 ferns made by M. Kessler and coworkers on the Cordillera Mosetenes in northern Cochabamba in 2004 recorded a single endemic species, despite specific searches for unusual ferns. The spatially uneven and less predictable distribution of endemic species compared to overall species richness has previously been documented, for example, for birds in Africa (Jetz & Rahbek, 2002; Jetz *et al.*, 2004) and palms in the Neotropics (Kreft *et al.*, 2006). Recently, Küper *et al.* (2006) scanned for data-deficiency for vascular plants at a sub continental scale in Africa, finding that geographical patterns of data-deficiency show a reduced geographical overlap when range size of species is incorporated (compare fig. 2a–c in Küper *et al.*, 2006). This outcome also supports our findings, and presumably reflects the stronger influence of historical factors in determining the evolution and distribution of species with restricted ranges.

Several general conclusions can be drawn from this study. First, general patterns of species richness can be deduced from fairly incomplete data. However, and second, despite ferns being one of the better-known major plant groups in Bolivia, the absolute number of species per cell and the distribution of endemics are still very incompletely known. If we consider that the sampling intensity of many plant taxa in Bolivia today is roughly comparable to that of ferns in 1990, we can conclude that for these taxa any conclusions about total species numbers and levels of endemism have to be drawn with extreme care. For example, quantitative analyses of the distribution of the diversity and endemism of orchids in Bolivia have been carried by Vásquez and Ibisch (2004) based on a mean of 3.58 collections per species, which is still less than the 5.7 fern collections per species in 1990. Clearly, conservation and research based on such incomplete data can potentially be misleading. Indeed, one of the problems in understanding patterns of endemism in tropical taxa may be our limited knowledge of the distribution of endemic taxa. Since endemism is an important characteristic of

biodiversity, and the fact that ferns are one of the best-known plant groups of Bolivia, we must encourage the increase of field data, especially in those places poorly explored. This will offer a better support to those governmental and non-governmental offices in charge of conservation initiatives.

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