



# Global patterns of plant diversity and floristic knowledge

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## ABSTRACT

**Aims** We present the first global map of vascular plant species richness by ecoregion and compare these results with the published literature on global priorities for plant conservation. In so doing, we assess the state of floristic knowledge across ecoregions as described in floras, checklists, and other published documents and pinpoint geographical gaps in our understanding of the global vascular plant flora. Finally, we explore the relationships between plant species richness by ecoregion and our knowledge of the flora, and between plant richness and the human footprint – a spatially explicit measure of the loss and degradation of natural habitats and ecosystems as a result of human activities.

**Location** Global.

**Methods** Richness estimates for the 867 terrestrial ecoregions of the world were derived from published richness data of *c.* 1800 geographical units. We applied one of four methods to assess richness, depending on data quality. These included collation and interpretation of published data, use of species–area curves to extrapolate richness, use of taxon-based data, and estimates derived from other ecoregions within the same biome.

**Results** The highest estimate of plant species richness is in the Borneo lowlands ecoregion (10,000 species) followed by nine ecoregions located in Central and South America with  $\geq 8000$  species; all are found within the Tropical and Subtropical Moist Broadleaf Forests biome. Among the 51 ecoregions with  $\geq 5000$  species, only five are located in temperate regions. For 43% of the 867 ecoregions, data quality was considered good or moderate. Among biomes, adequate data are especially lacking for flooded grasslands and flooded savannas. We found a significant correlation between species richness and data quality for only a few biomes, and, in all of these cases, our results indicated that species-rich ecoregions are better studied than those poor in vascular plants. Similarly, only in a few biomes did we find significant correlations between species richness and the human footprint, all of which were positive.

**Main conclusions** The work presented here sets the stage for comparisons of degree of concordance of plant species richness with plant endemism and vertebrate species richness: important analyses for a comprehensive global biodiversity strategy. We suggest: (1) that current global plant conservation strategies be reviewed to check if they cover the most outstanding examples of regions from each of the world's major biomes, even if these examples are species-poor compared with other biomes; (2) that flooded grasslands and flooded savannas should become a global priority in collecting and compiling richness data for vascular plants; and (3) that future studies which rely upon species–area

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calculations do not use a uniform parameter value but instead use values derived separately for subregions.

### Keywords

Conservation, data quality, ecoregions, human footprint, representation, species richness, vascular plants,  $z$  values.

## INTRODUCTION

Studies of global patterns of plant species richness are few in number and those published to date have not been made within an explicit geographical framework (Malyshev, 1975; Barthlott *et al.*, 1996, 1999, in press; Mutke & Barthlott, 2005). This limits the use of these maps to set rigorous global biodiversity priorities. Plants represent 10 times as many species as all terrestrial vertebrates combined (Groombridge & Jenkins, 2002). They also play a dominant role in determining the life histories of millions of invertebrate species, serve as the foundation of most foodwebs (Huston, 1994), and play a vital role in human welfare and economic development. Despite their importance and numerical abundance, however, vascular plants are often given less consideration in evaluating global networks of protected areas and in guiding efforts to improve those networks than are vertebrates (De Klerk *et al.*, 2004; Fjeldså *et al.*, 2004; Burgess *et al.*, in press, but see Myers *et al.*, 2000). To address this shortcoming, comprehensive studies of vascular plant diversity are essential.

One approach of priority-setting applies area-selection methods to grid-based data, serving the aim of maximizing the number of species or other measures of biodiversity within a set of areas (Williams *et al.*, 1996; Faith, 2002). However, this requires data sets of grid-based distribution maps which, on the global scale, are still lacking and will presumably continue to be out of reach in the near future for vascular plants and practically all other large groups of organisms. As an alternative strategy, Olson & Dinerstein (1998) proposed the selection of a set of ecoregions from all major biomes and biogeographical realms. However, that study was mainly based on animal data, lacking the important group of vascular plants. One major aim of the present paper is to fill this gap by providing a global data set of vascular plant species richness on the scale of ecoregions.

Ecoregions are relatively large units of land delineated to reflect the boundaries of natural communities of animal and plant species in their natural state. Several studies (Dinerstein *et al.*, 1995; Olson & Dinerstein, 1998; Ricketts *et al.*, 1999; Olson *et al.*, 2001; Wikramanayake *et al.*, 2001; Burgess *et al.*, 2004) used this framework because of the advantages that a system following natural boundaries has compared with political borders or grid cells. Other global studies of biodiversity priorities have now adopted the global ecoregions map as a basemap to compare distributions of biodiversity. For

example, The Nature Conservancy has adopted ecoregions as a framework to guide their conservation work worldwide (Hoekstra *et al.*, 2005), and the biodiversity hotspots adopted by Conservation International (Myers *et al.*, 2000) are now adjusted to coincide with ecoregion boundaries (T. Brooks, pers. comm.).

A comprehensive global map of plant diversity will powerfully inform biogeographical and conservation work in many ways, three of which we highlight in this paper. First, it will help to evaluate previous priority-setting efforts. Several conservation assessments (e.g. Davis *et al.*, 1994, 1995, 1997; Myers *et al.*, 2000) target those areas with extremely rich plant biotas and thus remain limited mostly to tropical moist forests and Mediterranean systems. In contrast, other global priority-setting efforts (Olson & Dinerstein, 1998) advocate a representation approach to setting priorities, such that the most outstanding examples within each biome are included. Biomes are very coarse classifications of ecosystem types, based largely on dominant vegetation (e.g. temperate grasslands and savannas); each biome contains distinct species assemblages and ecological processes and each therefore requires effective conservation (Olson *et al.*, 2001). The necessary data sets for such global representation analyses exist for vertebrates, with richness and endemism data now available for more than 30,000 species of birds, mammals, reptiles and amphibians (WWF, 2005; J. Lamoreux, pers. comm.). A comparable global map of plant richness would offer more comprehensive analyses of biodiversity patterns worldwide.

Secondly, a global data set of plant richness will help to prioritize efforts for future surveys and data collection. Frodin (2001) made a major contribution to this aim by identifying 'areas that most need floras'. However, with the information provided by that study it is difficult to answer two sorts of questions: Which are the most understudied biomes and which are the areas where richness data on the ecoregional scale are missing? We therefore put a special focus on a systematic assessment of data quality that points to knowledge gaps and can also guide the further processing and interpretation of the richness data presented here.

Finally, this data set can be used for a wide set of analyses relating biodiversity patterns to anthropogenic threats or to abiotic drivers of species richness. We provide an example of this type of analysis by comparing plant diversity, knowledge status and human footprint (Sanderson *et al.*, 2002) for each terrestrial ecoregion.

## METHODS

### Species richness

All 867 terrestrial ecoregions (Olson *et al.*, 2001; WWF, 2001) were subject to an individual assessment, and estimates of species numbers were derived from published and unpublished richness data and from a variety of additional information (for a full bibliography see Appendix S1). For each ecoregion, we chose the most appropriate from four different methods. In cases where a single method was suspect, we employed more than one method to compare results and derive a final estimate of species richness.

The assessment is mainly based on a compilation of species richness data for more than 1800 selected geographical units (hereafter referred to as OGUs, operational geographical units) derived from the literature. This data set includes both administrative units, such as countries or protected areas, and natural units, such as mountain ranges or vegetation units. It is a subset of a larger data set of which many OGUs were eliminated because they were rated unsuitable for this approach (e.g. due to large differences in area compared with the size of the ecoregion). This data set was also used by Mutke & Barthlott (2005) and Barthlott *et al.* (in press). A previous, considerably smaller version of it formed the basis for the global plant diversity maps produced by Barthlott *et al.* (1996, 1999). We applied the following four methods.

#### *Direct use of published data*

For many ecoregions, published species numbers were available, especially for islands and for 110 ecoregions covered in the assessment of North American ecoregions by Ricketts *et al.* (1999). We adopted most of them without any change (this applied to *c.* 18% of the 867 ecoregions). Other figures (for an additional *c.* 17% of ecoregions) were checked thoroughly on the basis of the other three methods and corrected, if deemed necessary. This was the case for the expert estimates for 140 ecoregions in the Indo-Pacific published by Wikramanayake *et al.* (2001) and for a few other ecoregions.

#### *Extrapolation of richness data with species–area curves*

Richness values of OGUs overlapping with an ecoregion were extrapolated up, or in some cases down, to the size of the ecoregion using the power model of the species–area relationship:

$$S_e = S_u \left( \frac{A_e}{A_u} \right)^z$$

where  $S_e$  is the estimated number of species in the ecoregion,  $S_u$  the species number of the OGU,  $A_e$  the area of the ecoregion,  $A_u$  the area of the OGU and  $z$  a parameter the value of which was empirically determined by regression analysis using the OGUs for each biome (see Olson *et al.*, 2001; WWF,

2001 for delineation of biomes). The latter was made for the global extent of each biome because apart from the biome ‘Tropical and Subtropical Moist Broadleaf Forests’, the data set for each biome was too small to be split up into subregions still yielding significant results for all subregions.

When more than one OGU overlapped with an ecoregion, the results of the extrapolation were weighted according to the suitability of OGUs, such as difference in size and degree of overlap. Both a high area of overlap and a small difference in total area size are factors that increase the accuracy of richness extrapolations and hence the weight that underlying data were assigned when considering more than one OGU for the richness estimate of an ecoregion. Further criteria were the degree to which overlapping OGUs were rated to be representative for the ecoregion with regard to factors relevant for the richness estimate such as vegetation type, topographic structure and climate.

Depending on how we rated the suitability of the overlapping OGUs and their richness figures to be used for this extrapolation, individual corrections to the extrapolated species numbers were often made taking into account further qualitative and quantitative information, such as vegetation, geodiversity, precipitation and state of floristic research in the area. Especially in cases when the difference in area between OGU and ecoregion was higher than one decimal order of magnitude, we treated the resulting extrapolated figures with special care and made rather conservative estimates of species richness based on them. This was made with respect to the uncertainty about the real slope of the species–area curve in that area and the tendency of the power model to overestimate richness when extrapolating to areas that are much larger than the OGU (Palmer, 1990). This method was applied to *c.* 53% of ecoregions.

#### *Use of taxon-based data*

Krupnick & Kress (2003) conducted a study on 84 Indo-Pacific ecoregions. For this study area, they compiled distribution data of all species of the seven families Bignoniaceae, Dipterocarpaceae, Ericaceae, Euphorbiaceae, Fagaceae, Legumes and Rosaceae from literature sources. The families were chosen with the aim of using the combined data as an indicator for the richness of all vascular plants. We derived estimates of total species richness by extrapolating the species numbers of the underlying data set (G. Krupnick, unpubl. data) up to the total flora of each ecoregion, using a factor which reflects the ratio between total vascular plant richness and richness in the indicator families from known literature data. For example, there were 629 ‘indicator species’ in the Philippines according to that data set, 178 of which (= 28.3%) occur in the Mindoro rain forests, one of the Philippine ecoregions. According to Davis *et al.* (1986), the total number of plant species in the Philippines is 8900. Hence, we predicted 2519 species (=  $8900 \times 28.3\%$ ) for the Mindoro rain forests. This method was applied to the 84 ecoregions mentioned above, i.e. *c.* 10% of all ecoregions.

### *Estimates based on other ecoregions*

When no data were available for an ecoregion, we made estimates based on the richness of OGU's located elsewhere in the same biome, on richness estimates for similar ecoregions and on all further relevant information available as mentioned above. For *c.* 19% of ecoregions, i.e. for all ecoregions rated 'very poor' in the data quality assessment described below, this was the sole method applied, and it was used as a complementary method for *c.* 30% of ecoregions.

In all cases, in making our richness assessments, we tried to estimate as closely as possible, the total number of vascular plant species naturally occurring in each terrestrial ecoregion before industrial-age human interference. However, it was often difficult to judge the degree to which richness figures were reflecting an anthropogenically altered state of vegetation or the degree to which they included introduced species and species that followed human alteration.

Because so many different qualitative and quantitative criteria were considered, estimating richness of ecoregions using the four above methods included a certain degree of subjective decision-making in many cases. Of course, using a strict algorithm throughout the process would have increased the repeatability of the method. However, the design of the algorithm would also have required subjective decisions. Furthermore, transforming qualitative and semi-quantitative into quantitative data would have produced an unmanageable workload for an undertaking that covers 867 ecoregions. Being confronted with the decision of either (1) using a strict algorithm and thus excluding a wide array of available data or (2) using all available quantitative, semi-quantitative, and qualitative data and thus somewhat reducing the repeatability of the method, we chose the latter option. The reader is given two sorts of information by which to judge the quality of each richness estimate: first, the index reflecting the suitability and quality of underlying data explained below and secondly, the full bibliography (Appendix S1).

### **Biodiversity information availability**

The suitability and quality of data available for estimating species richness (hereafter referred to as data quality) was rated on a scale ranging from 1 to 4 for each ecoregion in the following way. Whenever we found a richness estimate in the literature for an OGU identical or practically identical to the ecoregion boundary, the index value 1 (= good) was assigned. When OGU's overlapped with the ecoregion, we either assigned a value of 2 (= moderate) or 3 (= poor), depending on the extent of the overlap and the difference in area between OGU's and the targeted ecoregion. Both a low area of overlap and a large difference in total area size are factors which reduce the accuracy of richness estimates and hence of the data quality rating. Further criteria were the degree to which overlapping OGU's were rated to be representative for the ecoregion with regard to vegetation type and other factors relevant for the richness estimate. When no

OGU's overlapped with an ecoregion or when the overlapping OGU's were too different in size or overall ecological composition to derive a richness estimate, we assigned an index value of 4 (= very poor). After assigning index scores as outlined above, we changed some of them when the probability was rated high that richness data were heavily influenced by one of the following factors which have a negative effect on data quality: first, when species numbers included an unidentified but presumably large number of aliens or subspecies; secondly, when the species numbers presumably reflected a situation heavily altered by human impact; and thirdly, when we had reason to assume that the reliability of the source was poor. However, it remains a source of uncertainty that in most cases richness figures were not accompanied in the literature consulted by comments on the state of floristic research in the study area. Hence, even when we rated the quality of underlying data to be good for an ecoregion, the richness assessment may include some error.

### **Regression analyses between species richness, human footprint and data quality**

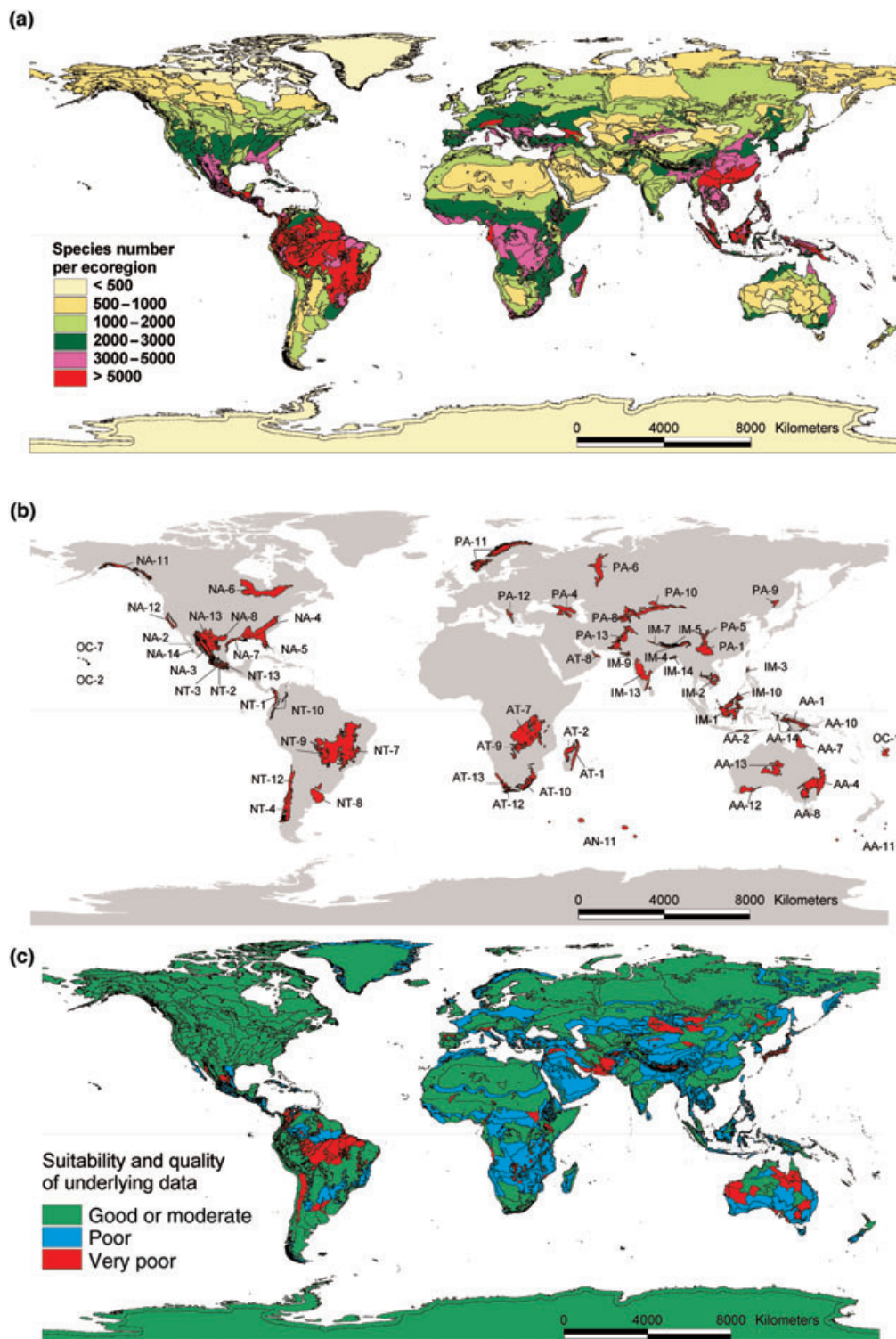
We conducted regression analyses between the three indicators: richness, data quality and mean human footprint (Sanderson *et al.*, 2002) per ecoregion. The human footprint is an additive, aggregate index of human activity, combining data on human population, land transformation, and the density of electric power and transport infrastructure. For these purposes, species richness values were calculated for a standard area using the *z* values derived from the regression analysis in order to eliminate the effect of area.

## **RESULTS**

### **Species richness**

The map of plant richness reflects the well-known latitudinal diversity gradient (Fig. 1a). The Borneo lowlands contain more vascular plant species than any other ecoregion on earth, with 10,000 species, followed by nine ecoregions with  $\geq 8000$  species each in Central and South America. Of the 51 ecoregions with  $\geq 5000$  species, all but five are located in the Tropical and Subtropical Moist Broadleaf Forests biome, which is unequalled in the mean species richness of its ecoregions (Table 1). The notable exceptions are five temperate forest ecoregions: two forest ecoregions in SW China (Qionglai-Minshan Conifer Forests and Yunnan Plateau Subtropical Evergreen Forests), the Montane Fynbos and Renosterveld (Southern Africa), the Alps conifer and mixed forests (Europe), and the Caucasus mixed forests (located between Europe and Asia) (see Appendix S2 for a complete list of vascular plant richness by ecoregion).

By classifying ecoregions in a hierarchical fashion, we can also display for the first time the most species-rich ecoregions within each biome and within each of the eight biogeographical realms as delineated by Olson *et al.* (2001) and WWF (2001)



**Figure 1** Results of the assessment of vascular plant species richness and data quality. Projection: Geographic. (a) Vascular plant species per ecoregion. (b) Ecoregions highest in species richness in each biome within each biogeographical realm. Realms: AA, Australasia; AN, Antarctic; AT, Afrotropics; IM, IndoMalay; NA, Nearctic; NT, Neotropics; OC, Oceania; PA, Palearctic. Biomes: 1 – tropical and subtropical moist broadleaf forests; 2 – tropical and subtropical dry broadleaf forests; 3 – tropical and subtropical coniferous forests; 4 – temperate broadleaf and mixed forests; 5 – temperate conifer forests; 6 – boreal forests/taiga; 7 – tropical and subtropical grasslands, savannas and shrublands; 8 – temperate grasslands, savannas and shrublands; 9 – flooded grasslands and savannas; 10 – montane grasslands and shrublands; 11 – tundra; 12 – mediterranean forests, woodlands and scrub; 13 – deserts and xeric shrublands; 14 – mangroves. (c) Suitability and quality of underlying plant data at the scale of ecoregions.

No.	Biome	<i>z</i>	Mean plant species richness	Mean of data quality index
1	Tropical and subtropical moist broadleaf forests	0.24–0.33*	3161	2.6
2	Tropical and subtropical dry broadleaf forests	0.21	1440	2.8
3	Tropical and subtropical coniferous forests	0.19	2225	2.9
4	Temperate broadleaf and mixed forests	0.17	1909	2.3
5	Temperate coniferous forests	0.14	1570	1.9
6	Boreal forests/taiga	0.16	822	1.5
7	Tropical and subtropical grasslands, savannas and shrublands	0.18	1731	2.6
8	Temperate grasslands, savannas and shrublands	0.12	1372	2.1
9	Flooded grasslands and savannas	0.12	767	3.5
10	Montane grasslands and shrublands	0.17	1397	2.9
11	Tundra	0.13	438	1.6
12	Mediterranean forests, woodlands and scrub	0.20	2294	2.7
13	Deserts and xeric shrublands	0.11	1078	2.7
14	Mangroves	†	205	3.9

\*In this biome, the underlying data set was large enough to be split up into four subregions, yielding the following *z* values: Asia 0.26, Central America 0.33, South America 0.32, Australia and Africa 0.24.

†No figure given due to poor data situation.

(Fig. 1b). In the few cases where two or three ecoregions shared the highest rank in a given biome, we selected the ecoregion highest in data quality and smallest in area (see Appendix S3 for a complete list of richest ecoregions by biome).

Calculated *z* values used to estimate plant richness differed widely among biomes, ranging from 0.11 (deserts and xeric shrublands) to 0.33 (Central American tropical moist forests) (Table 1).

### Analysis of data quality

The suitability and quality of underlying data was rated to be good for 18% of the ecoregions, moderate for 25%, poor for 38% and very poor for 19% (Fig. 1c). Large regions lacking virtually any suitable data on vascular plant richness included the southern section of the Amazon basin, northern Colombia, some parts of Northern China, most of Japan, several ecoregions in arid Australia and large parts of the area covered by the three neighbouring countries of Iran, Afghanistan and Pakistan. Boreal forests, taiga and tundra were characterized by high quality data, while mangroves and flooded grasslands and savannas were deemed generally data-poor (Table 1) (see Appendix S2 for more detailed information on data quality).

The regression analysis between richness per standard area and the data quality index yielded significant results for four biomes: the tropical and subtropical moist broadleaf forests, the tropical and subtropical grasslands, savannas and shrublands, the montane grasslands and shrublands, and the deserts

**Table 1** *z* values as derived from linear regressions of the log–log transformed raw data (all correlations were significant at  $P < 0.05$ ), mean plant species richness per ecoregion and data quality and suitability index (ranging from 1 = good to 4 = very poor). Note that ecoregions differ in size, which limits the comparability of mean plant species richness per ecoregion

and xeric shrublands. All of these cases pointed to the tendency of better data quality being found in ecoregions with higher species richness. In all other biomes we found no significant relationship (Table 2).

### Human footprint

Worldwide, richness standardized for area and human footprint were positively related, i.e. a higher human footprint can be found in ecoregions with higher species richness (Table 2). Within biomes, however, this positive relationship only holds for five biomes: the boreal forests and taiga, the temperate grasslands, savannas and shrublands, the montane grasslands and shrublands, the tundra and the deserts and xeric shrublands.

### DISCUSSION

The general trends of plant species richness (Fig. 1a) are concordant with previous studies (Malyshev, 1975; Barthlott *et al.*, 1996, 1999, in press; Mutke & Barthlott, 2005). These previous maps present species density values for standard area sizes throughout the world. However, due to a lack of data on species turnover, their richness figures cannot be easily transferred to an explicit geographical framework of planning units, which is a prerequisite for their use in conservation strategies and other analyses.

The data presented here refer to the now widely used ecoregions scheme (see Introduction) and thus have a greater

**Table 2** Results of regression analysis between richness per standard area, data quality and mean human footprint. All significant correlations between richness and human footprint were positive. All significant correlations between richness and the data quality index were negative, actually indicating a positive correlation between data quality and richness due to the fact that higher index values denote a lower data quality. No analysis was made for mangroves because of the poor data situation

	$r^2$ of data quality vs. richness	$r^2$ of footprint vs. richness
Global	n.s.	0.09***
Tropical and subtropical moist broadleaf forests	0.06**	n.s.
Tropical and subtropical dry broadleaf forests	n.s.	n.s.
Tropical and subtropical coniferous forests	n.s.	n.s.
Temperate broadleaf and mixed forests	n.s.	n.s.
Temperate coniferous forests	n.s.	n.s.
Boreal forests/taiga	n.s.	0.18*
Tropical and subtropical grasslands, savannas and shrublands	0.21**	n.s.
Temperate grasslands, savannas and shrublands	n.s.	0.14*
Flooded grasslands and savannas	n.s.	n.s.
Montane grasslands and shrublands	0.10*	0.25***
Tundra	n.s.	0.14*
Mediterranean forests, woodlands and scrub	n.s.	n.s.
Deserts and xeric shrublands	0.06*	0.09**

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; n.s., not significant.

potential to serve as the starting point for further conservation or biogeographical studies based on this framework. These include correlation analyses with other data sets, such as plant endemism or the richness of other taxa. Furthermore, an evaluation of current priority sets based on our selection of 63 ecoregions could be performed. We suggest that current global plant conservation strategies are reviewed to check if they cover the most outstanding examples of regions from each of the major biomes of the world, even if these examples might be rather species-poor compared with other biomes.

We regard it as a major methodological asset of the richness data presented here that they do not rely on a uniform parameter value of the species–area curve but on  $z$  values differentiated by biome. Another aspect of the data set that increases its value for further analyses is the data quality index associated with each richness figure. We also used this index to identify gaps in the knowledge on plant diversity that can guide future priorities in data collection and compilation, both by regional location and by biome.

### Global priority setting for conservation

The set of 63 ecoregions richest in their respective combination of biome and biogeographical realm (Fig. 1b) overlaps highly

with various priority sets that have been proposed, but marked differences can also be found. Among the 63 ecoregions, 12 are not part of a Global 200 region (Olson & Dinerstein, 1998) and hence might be missed in that strategy from the point of view of plant conservation. A more detailed assessment, including levels of endemism and further criteria, could clarify whether they deserve to be included in the Global 200 selection.

Our set includes several ecoregions that are not high in richness when compared with ecoregions in other biomes, but are some of the most outstanding examples of biomes underrepresented in either the 25 hotspots delimited by Myers *et al.* (2000) or the 234 Centres of Plant Diversity (Davis *et al.*, 1994, 1995, 1997), or both. Examples include the Sundarbans mangroves (India and Bangladesh) and the Baluchistan xeric woodlands (Pakistan and Afghanistan).

Given the different approaches of the sets of regions mentioned above, it is not surprising that they only partly overlap. However, these differences show where future priority setting could be improved. The Global 200 were mainly based on animal data, a shortcoming that can now be addressed with the data presented here. The Centres of Plant Diversity Project (Davis *et al.*, 1994, 1995, 1997) was a major undertaking of data compilation for global plant conservation strategies but did not give any explicit definition of rules for an area to be included in the selection of priority sites. The hotspots approach locates a set of regions that represent many endemic species in a small total area, including level of threat and loss of primary vegetation as further criteria. However, there are further important aspects of biodiversity, such as maximized floristic complementarity (Küper *et al.*, 2004) or the diversity of biomes, lacking in that approach. We regard it as essential that a selection of the most valuable areas covers all major ecosystems.

### Gaps in floristic knowledge

Data quality and its spatial variation can be interpreted both from the broad geographical perspective across all biomes and within each biome separately. Among the areas with very poor underlying data (Fig. 1c), the southern section of the Amazon basin and northern Colombia are especially remarkable because they are presumably the most species-rich of all data gaps. They are also the only two areas we identified that overlap with the ‘areas that most need floras’ (Frodin, 2001). However, due to the different approach, it is unsurprising that the overlap is so small. In this study we only focused on species richness data, which can also be taken from extrapolations and expert estimates if better sources, such as floras, are not available, whereas Frodin (2001) was pointing out the lack of floras and thus of much more comprehensive information in the regions identified as research priorities. Furthermore, we did not restrict the identification of data gaps to the very species-rich regions and in many regions we performed our analysis at a narrower spatial scale.

The poor data quality in some parts of arid Australia might be an artefact of our limited access to data. Access to floristic

literature from Northern China and Japan was also difficult but our impression was that this actually reflected a lack of plant species richness data at the ecoregional scale in these regions. As far as most other data gaps identified here are concerned, we are rather sure that they reflect an absence of documented, reliable information on plant species richness at the ecoregion scale.

When examining data quality by biome, the flooded grasslands and flooded savannas are poorly known (Table 1). The relatively low species richness and the inhospitable working conditions make this biome unattractive for fieldwork, which might be the main reason for the low knowledge status. Data quality is only worse for mangroves. However, they have to be treated differently because their species richness is more determined by untypical species, which can be regarded as less important for conservation in this biome than the typical mangrove species, for which data availability is much better.

Our result that, at least within those biomes where significant results were obtained, species-rich ecoregions are better studied than species-poor ones (Table 2), can be explained by the assumption that species richness is a factor which attracts floristic work. However, many examples of species-rich ecoregions with very poor data, such as large parts of the Amazon and northern Colombia, illustrate that this correlation finds its limit when poor infrastructure or the poor regional, social and economic conditions restrict access to biodiverse areas. Some of the areas with high biodiversity but difficult accessibility might have a particularly high potential for conservation. Therefore, the further identification of such areas and subsequent biodiversity inventory is an urgent priority.

### Human footprint

For most biomes, no significant correlation was found between species richness and human footprint. However, for some biomes, significant results were obtained and in these cases, the regression analysis shows the tendency that at the spatial scale studied here, the results differ between two groups of biomes.

The first group is of biomes such as deserts, tundra and taiga, where limits to plant growth can be observed due to constraints such as low water availability or short vegetation period. Here, a significant positive correlation between richness and human footprint was found (Table 2). Obviously, within these biomes, people tend to live in those areas where conditions for plant growth and thus for cultivation of crops are better, which, in such biomes, often correlates with areas of high species richness. In contrast, within the second group of biomes, where plants can grow almost anywhere, humans do not seem to settle depending on conditions for plant growth and hence no significant correlation was found.

Previous work, such as the studies by Balmford *et al.* (2001) for subsaharan Africa, and by Chown *et al.* (2003) for Southern Africa, also found a positive correlation between richness and measures of human impact. However, they performed their analyses on a narrower spatial scale and resolution and did not differentiate between biomes.

As far as the reverse perspective is concerned, i.e. the influence of human footprint on biodiversity, our data set only offers very limited possibilities for interpretation. This is mainly due to the structure of available data on the global scale, which we presume are closer to the natural state of biodiversity than to the current situation at the beginning of the twenty-first century. The data are certainly influenced by human interference of the previous centuries but, in large parts of the world, the diverse degradation processes of the past few decades are not adequately reflected by available floristic studies.

### Methodological issues of richness assessment

So far, broad-scale biodiversity mapping projects based on species–area calculations have almost invariably used a uniform parameter value for the species–area curve (recent examples include Brooks *et al.*, 2002; Zurlini *et al.*, 2002; Thomas *et al.*, 2004). However, as demonstrated by previous work (e.g. Malyshev, 1975) and reinforced by the present study, the shape of the species–area curve varies considerably between biomes. This is unsurprising given that the mechanisms and conditions that determine the range sizes of species are different in, e.g. deserts vs. grasslands or tropical forests. We therefore suggest that future studies that rely upon species–area calculations do not use a uniform parameter value but instead use values derived separately for subregions such as biomes. Cowling *et al.* (1996) have demonstrated that, while species richness per standard area varies between the mediterranean-climate regions of the world, the  $z$  values are homogeneous. However, within other biomes a variation of  $z$  values can be expected, as demonstrated for the tropical and subtropical moist broadleaf forests (Table 1). The degree to which the calculation of parameter values can be made for subregions with significant results will ultimately depend on the size of the data set at hand.

When interpreting the richness values presented here, it should be noted that to some degree, larger ecoregions tend to have more species than smaller ones. However, as conservation planning within an ecoregion should aim to protect all species, or at least as many as possible, we mainly focused on the total species number per ecoregion rather than species numbers standardized by area.

### The road ahead

Many promising areas of research are now possible with this new data set to enhance creation of a comprehensive global biodiversity strategy for the terrestrial realm. In particular, two types of analyses shall be mentioned here. First, it should become a research priority to test the correlation between vascular plant richness and plant endemism. Such tests can be conducted at regional and eventually global scales. Various studies have demonstrated a fairly good correlation between species richness and range-size rarity or endemism (Crisp *et al.*, 2001; Kier & Barthlott, 2001; Linder, 2001; Ricketts, 2001; Taplin & Lovett, 2003). One might assume that the general patterns would not



change fundamentally in continental regions but might differ considerably or even be inversely related in some island ecoregions. However, this remains to be verified and even if the general patterns were similar, the important differences could point more accurately to gaps in our present global plant conservation network. A second type of analysis is to test for correlations between plant species richness and terrestrial vertebrate richness by ecoregion. A new data base featuring richness and endemism values for birds, mammals, reptiles and amphibians (WWF, 2005) will facilitate both regional and global comparisons in a fundamental test of species concordance.

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## SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JBI/JBI1272/JBI1272sm.htm>

**Appendix S1** Full bibliography (list of c. 300 literature references).

**Appendix S2** Table with quantitative results for each ecoregion: working figure of species richness, minimum and maximum species richness, quality and suitability of underlying data.

**Appendix S3** Ecoregions highest in species richness in each biome within each biogeographical realm.

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