



Relative need for conservation assessments of vascular plant species among ecoregions

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ABSTRACT

Aim (1) To determine the relative need for conservation assessments of vascular plant species among the world's ecoregions given under-assessed species distributions; (2) to evaluate the challenge posed by the lack of financial resources on species assessment efforts; and (3) to demonstrate the utility of nonlinear mixed-effects models with both homoscedastic and heteroscedastic error structures in the identification of species-rich ecoregions.

Location Global.

Methods We identified the world's ecoregions that contain the highest vascular plant species richness after controlling for area using species–area relationship (SAR) models built within a mixed-effects multi-model framework. Using quantitative thresholds, ecoregions with the highest plant species richness, historical habitat loss and projected increase in human population density were deemed to be most in need of conservation assessments of plant species. We used generalized linear models to test if countries that overlap with highly important ecoregions are poorer compared with others.

Results We classed ecoregions into nine categories based on the relative need for conservation assessments of vascular plant species. Ecoregions of highest relative need are found mostly in the tropics, particularly Southeast Asia, Central America, Tropical Andes and the Cerrado of South America, and the East African montane region and its surrounding areas. Countries overlapping with ecoregions deemed important for conservation assessments are poorer as measured by their capita gross national income than the other countries. The nonlinear mixed modelling framework was effective in reducing residual spatial autocorrelation compared with nonlinear models comprised of only fixed effects. In contrasting multiple SAR models to identify species-rich ecoregions, there was not one SAR model that fitted best across all biomes. Not all SAR models displayed homoscedastic errors; therefore it is important to consider models with both homoscedastic and heteroscedastic error structures.

Main conclusions We propose that conservation assessments should be conducted first in ecoregions with the greatest predicted species richness, historical habitat loss and future human population increase. As ecoregions deemed to be important for conservation assessments are located in the poorest countries, we urge international aid agencies and botanic gardens to cooperate with both local and international scientists to fund and implement conservation assessment programmes there.

Keywords

Biodiversity, conservation assessment, conservation biogeography, habitat loss, human population, IUCN, plant species, policy, species–area relationship.

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INTRODUCTION

As autotrophs, plants are the fundamental components of the Earth's ecosystems. They support non-plant taxa by serving as the foundation of most food webs (Huston, 1994; Primack & Corlett, 2005), and are involved in many ecological processes necessary for the maintenance of life on Earth (Hamilton & Hamilton, 2006). For example, plants play an essential role in releasing the oxygen needed by animals, fungi and aerobic bacteria to survive. Plants also have utility value for humans. They form the fundamental part of recreational landscapes, protect against floods and avalanches, regulate water supply, and provide food and materials. However, terrestrial plant species and the biodiversity they support are increasingly threatened with extinction by habitat losses resulting mainly from anthropogenic land-use changes (Millennium Ecosystem Assessment, 2005; Bradshaw *et al.*, 2009a). In the tropics, there is clear evidence of rapid deforestation in recent decades (Bradshaw *et al.*, 2009a), with an annual mean loss of c. 10 million ha from 1990 to 1997 (Hansen & DeFries, 2004). Temperate grasslands, temperate broadleaf forests and Mediterranean forests have all experienced at least 35% conversion to cropland (Millennium Ecosystem Assessment, 2005), and even the boreal forest zone has become fragmented (Bradshaw *et al.*, 2009b; Hansen *et al.*, 2010). With high expected rates of continued habitat loss, many plant species are likely to face extinction, thereby compromising ecosystem services that sustain the quality of life for people (Daily, 1997; Ehrlich & Pringle, 2008) and the rest of Earth's biota.

It is important to acquire knowledge on the population numbers and geographical range of species and their rates of change so that conservation managers can focus on those at greatest risk. One of the key strategies outlined by the Convention on Biological Diversity (CBD; <http://www.cbd.int>) is to conduct preliminary assessments of the conservation status of all plant species on Earth by the year 2010. This patently was an impossible target because only about 12,000 vascular plants out of an estimated total global flora of 223,300–422,000 species (Prance *et al.*, 2000; Govaerts, 2001; Bramwell, 2002; Scotland & Wortley, 2003) have currently been assessed by the International Union for Conservation of Nature (IUCN). Furthermore, of these 12,000 species, about 7800 have not been assessed in the past 10 years and therefore require an updated species assessment. Although one could argue that most of the vascular plant species assessed are those thought to be threatened (Lughadha *et al.*, 2005), the proportion of assessed plant species is still lower than that of other taxonomic groups, such as amphibians, birds and mammals. Assuming that the true proportion of threatened plants is comparable with that of the other fully assessed taxa, many plant species might be driven to extinction even before scientists estimate population sizes and ranges, so it is critical to expedite the assessment process to avoid possible extinctions. However, resources available for conservation are limited, especially in

the developing world (Sodhi *et al.*, 2007; Wilson *et al.*, 2009), so determining the areas of greatest predicted species diversity has become a centrepiece for maximizing the efficiency of resource allocation. The question is: where should we focus our efforts on species assessments? Although existing global conservation templates that rank areas based on species diversity, such as biodiversity hotspots (BH; Myers *et al.*, 2000) and the Global 200 (G200; Olson & Dinerstein, 2002) templates can be adapted to prioritize species assessments, they are based largely on expert opinion (Brooks *et al.*, 2006). While expert opinion can be reasonably accurate (Krupnick & Kress, 2003), it also means that the results of the analyses cannot be replicated, raising questions regarding the transparency of these approaches (Brooks *et al.*, 2006). Moreover, the G200 template does not focus specifically on the conservation of plant species, while the BH approach ignores future human population increase (and therefore latent threat), and does not explicitly consider species–area relationships (SAR) to control for the varying patch size of each conservation unit.

Here we provide a new template to guide the conservation assessment of native vascular plant species using the World Wildlife Fund (WWF) ecoregions framework (Olson *et al.*, 2001). Ecoregions are defined as terrestrial areas harbouring a distinct assemblage of natural communities and species prior to major land-use change (Olson *et al.*, 2001). Our template relies on the premise that the greatest number of declining species will be found in ecoregions with the highest species richness, and at the same time the highest degree of habitat loss and future human population pressure. Our premise is supported by many studies showing a link between habitat loss and species endangerment. For example, Wilcove *et al.* (1998) found habitat loss to be the single greatest threat to biodiversity in the USA, and Brooks *et al.* (1999) showed that the degree of deforestation predicts the proportion of threatened bird and mammal species across island groups in Southeast Asia. We incorporated projected human population pressure, given its direct association with land conversion and habitat degradation (Cincotta *et al.*, 2000; Jha & Bawa, 2006), as a surrogate for future rates of habitat loss and therefore species endangerment. We chose not to include present human population density because it stems from historical population growth and is therefore strongly linked to one of our existing criteria – historical habitat loss (Spearman rank-order correlation: $\rho = 0.72$, $P < 0.001$, $n = 747$). Moreover, historical habitat loss is a more direct indication of the historical and present threat compared with present population density. Although ideally we should use endemic plant species richness because species assessments are most important for areas with a large number of irreplaceable endemic species, the lack of global data on the ecoregion scale precluded its use. However, vascular plant species richness is correlated with endemism on both subcontinental (Kerr, 1997; Linder, 2001) and global (Hobohm, 2003) scales; thus conservation assessments in the most species-rich ecoregions will cover a large number of globally

range-restricted (and hence extinction-prone; Bradshaw *et al.*, 2008) plant species. The number of existing plant assessments could directly influence the relative assessment need among ecoregions. For instance, an ecoregion with a high proportion of its flora already assessed will be less important than an equally species-rich but less well-assessed ecoregion. However, we did not consider the distribution of existing plant assessments because the number of valid assessments (*c.* 4000) is a small proportion (*c.* 1%) of the total flora in the world, and these assessments do not appear to be concentrated in a particular region according to the IUCN Red List (<http://www.iucnredlist.org>). We therefore argue that plant species richness is likely to be a reasonable metric to use, given the low and relatively unvarying number of assessed flora across the ecoregions.

Existing studies have discussed the shortfall of financial resources in establishing protected areas (Bruner *et al.*, 2004) and field-based conservation programmes (Balmford *et al.*, 2003) in developing countries. Bruner *et al.* (2004) found that at least US\$4 billion is required to establish and manage an expanded protected-area system in the developing world over this decade. Balmford *et al.* (2003) underlined the need for greater investment in field conservation projects in developing countries. Lee & Jetz (2008) also found that the per capita income of countries decreases with present-day conservation value (surrogated by vertebrate species richness). However, no study has explored the association between the need for conservation assessments among ecoregions and financial resources. Here, we offer a preliminary assessment of the challenge posed by the lack of financial resources in ecoregions of high importance, which can impede studies that contribute to the conservation assessment of species. We follow existing studies (Balmford *et al.*, 2003; Lee & Jetz, 2008) in using per capita income as a surrogate for locally available conservation funding, and test the hypothesis that countries overlapping with ecoregions of high assessment importance have lower available conservation funding.

Our study is the first to assess the relative need for conservation assessments among ecoregions for vascular plant species by taking into account spatial autocorrelation, uncertainty in the form, and error structure of SAR models, as well as current and future endangerment by introducing historical habitat loss and predicted human population pressure. Unlike recent studies that selected areas for reserve land acquisition (Underwood *et al.*, 2008) or specific threat-guided conservation responses (Wilson *et al.*, 2007), we do not consider estimated economic cost in assigning relative levels of need, because there are few published data on the cost of plant species assessment projects over a range of countries (Siebert & Smith, 2005), and the cost-effectiveness of species assessment programmes can be improved by employing volunteers and removing non-essential aims (Siebert & Smith, 2005). We hope that our new global conservation assessment template will stimulate species assessments to inform conservation priorities better in the world's most species-rich and threatened ecoregions.

MATERIALS AND METHODS

Ranking ecoregions based on plant species richness

Building nonlinear mixed-effects species–area relationship models

We collated the number of vascular plant species in each ecoregion from Kier *et al.* (2005), derived from published richness data of *c.* 1800 operational geographical units via collation and interpretation of published data, taxon-based data, estimation derived from ecoregions in the same biome, and extrapolation of richness values from overlapping geographical units using the power SAR. Following Lamoreux *et al.* (2006) and Guilhaumon *et al.* (2008), we excluded mangrove ecoregions and large, uninhabited ecoregions of Greenland and Antarctica because of few reliable data, leaving a total of 797 terrestrial ecoregions for species–area analysis. We recognize that the species richness of *c.* 53% of the ecoregions in our base dataset was derived by extrapolating the species richness from one or more overlapping operational geographical units using the power law (Kier *et al.*, 2005). This is unlikely to have confounded our results because the SAR was fitted using a different set of data at a different scale. SAR models were fitted at the ecoregion level to account for area differences in our analyses, while the power law SAR was fitted at the scale of the operational geographical units to derive ecoregion-level estimates. However, we do acknowledge that our results are influenced by the quality of the underlying data from which ecoregion-level estimates were derived.

Direct comparisons of the number of species cannot be made owing to size differences among ecoregions. For example, a larger ecoregion can have more vascular plant species, but may also require greater financial resources to complete the species assessments because of its size. Species richness scales with size in a nonlinear way, so using the simple species richness per unit area metric will bias the prioritization towards smaller ecoregions. Therefore ecoregions have previously been ranked according to their residuals in a linearized power-law regression:

$$\hat{S} = \log c + z \log A$$

where \hat{S} = estimated species richness, A = land area, and c and z are constants (e.g. Lamoreux *et al.*, 2006; Lee & Jetz, 2008), to measure the conservation value of an ecoregion by the number of species it has compared with the number of species expected for an ecoregion of its area. However, the common application of the log-linear power law as the only form of SAR could result in the biased selection of ecoregions. First, there is typically high variability among datasets in the choice of the top-ranked SAR (Fattorini, 2006; Guilhaumon *et al.*, 2008). Second, the log-linear power law is incorrect when the error term in the power law, $\hat{S} = cA^z$, is additive (Wright, 1981; Pattyn & van Huel, 1998; Fattorini, 2006).

To overcome these problems, Guilhaumon *et al.* (2008) fitted a suite of curvilinear SAR models to species–area data,

and ranked ecoregions with respect to their positions in the bootstrapped confidence interval of the model-averaged SAR. However, the curvilinear models they fitted by minimizing the residual sum of squares assumes normality and homoscedasticity for the maximum likelihood equivalence of parameter estimates (Rao, 1973). The information-theoretic index, Akaike's information criterion (AIC), used as a measure of model parsimony and to assign relative weights of evidence for model averaging, will be unbiased only when these assumptions are met (Anderson, 2008). For our data, we found that the residuals of many SAR models fitted by this method were not homoscedastic and have to be excluded in model-averaging, resulting in the loss of information. We also hypothesized that there might be positive spatial autocorrelation in the model residuals owing to ecoregions in each biogeographical realm sharing a similar evolutionary history and containing distinct species assemblages (Olson *et al.*, 2001; Millennium Ecosystem Assessment, 2005). Spatial autocorrelation might bias parameter estimates of models (Dormann *et al.*, 2007) and lead to incorrect conclusions about the importance ranking of ecoregions. However, previous studies (Fattorini, 2006; Guilhaumon *et al.*, 2008) did not consider the problem of spatial dependence in the identification of species-rich hotspots.

To account for the uncertainty in the species–area relationship, the non-homoscedastic error structure of the model, and potential spatial autocorrelation, we built a suite of nonlinear fixed-effects models and mixed-effects nonlinear models following four different SAR forms (power, exponential, negative exponential, and monod functions; reviewed in Tjørve, 2003; Table 1) within each biome. The variables \hat{S} and A were standardized by rescaling to improve convergence of the parameter estimation algorithm; each value was divided by the minimum across the ecoregions in each biome. Using the rescaled variables, we built a new set of nonlinear mixed-effect SAR models by maximizing the log-likelihood using the nlme function in the nlme package (Pinheiro & Bates, 2000) in R v. 2.10 (R Development Core Team, 2009). These models allow the parameter estimates to vary among biogeographical realm classes and therefore account for the variation of species richness among biogeographical realms; that is, ecoregions within each biogeographical realm will have species richness closer to one another because of their shared evolutionary history. We built the constant-variance mixed-effect models first and checked model residuals for heteroscedasticity using

residual plots. Heteroscedastic models were rebuilt by modelling the variance as a function of fitted values.

To assess the utility of nonlinear mixed-effect models in reducing spatial autocorrelation, we built nonlinear models consisting of only fixed effects where the model parameters were not allowed to vary across biogeographical realm classes, using the gnls function implemented in the nlme package (Pinheiro & Bates, 2000) in R v. 2.10. Similarly, the constant-variance models were built first, and their residuals inspected for heteroscedasticity. Heteroscedastic models were refitted using the same function with their variance modelled as a function of the fitted values. The resulting set of fixed-effects SAR models fit using this method hence took into account heteroscedasticity, but not potential spatial autocorrelation.

Assessment of spatial autocorrelation, model-averaging procedure and species richness rankings of ecoregions

We used the Mantel test to check for residual spatial autocorrelation in both nonlinear mixed-effects and fixed-effects models. The Mantel test assesses the correlation between two distance matrices (Legendre & Legendre, 1998). To perform the Mantel test, we assembled a matrix of pairwise great circle (accounting for the curvature of the Earth's surface) distances between ecoregion centroids. We then created a second matrix containing the pairwise Euclidean distances between the Pearson residuals for every ecoregion. If the model residuals show spatial autocorrelation (ecoregions nearer to one another tend to have residuals that are similar), this process would detect a positive correlation between the two pairwise distance matrices. We used a permutation test – function mantel implemented in package vegan in R v. 2.10 – to assess the residual spatial autocorrelation of the SAR models.

Aikaike's information criterion corrected for small sample sizes (AIC_c), a likelihood-based information-theoretic measure of model fit or adequacy, was used to compare the relative fit of models (Burnham & Anderson, 2002). To compute AIC weights ($wAIC_c$) for a model, we followed the information-theoretic calculations described in Burnham & Anderson (2002). The $wAIC_c$ of any particular candidate model can vary from 0 (no support) to 1 (complete support) relative to the entire model set. Three nonlinear mixed-effects SARs – one from the temperate coniferous forests biome, two from the boreal forests and taiga biome – were excluded from the model-averaging because of spatially autocorrelated residuals. We demonstrate the fitting and averaging of nonlinear mixed-effect SAR models for the tropical and subtropical moist broadleaf forests biome in Fig. 1. Species–area relationship models for the other 12 biomes are presented in Appendix S1 in the Supporting Information.

Finally, we ranked the species richness of ecoregions with respect to the size of their residuals in the model-averaged population-level SAR in each biome. Effectively, the size of the residuals allows us to compare the conservation value among ecoregions within the same biome, indicated by the number of

Table 1 Species–area relationship models investigated in this study.

Name	Equation
Power	$\hat{S} = cA^z$
Exponential	$\hat{S} = c + z \log A$
Negative exponential	$\hat{S} = c[1 - \exp(-\frac{A}{z})]$
Monod	$\hat{S} = \frac{cA}{z+A}$

\hat{S} , estimated species richness; A , land area; c and z are constants.

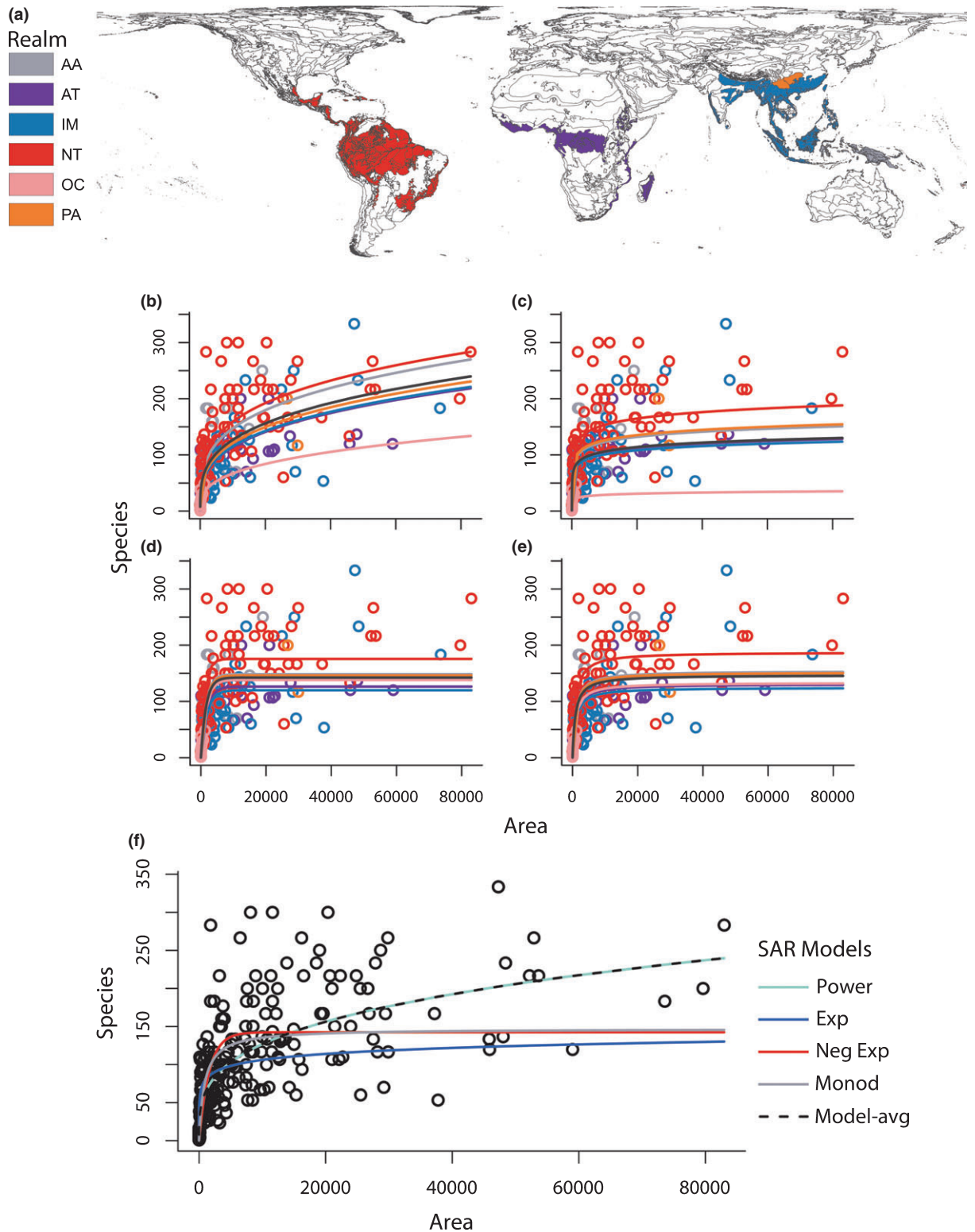


Figure 1 Nonlinear mixed-effects models applied to the tropical and subtropical moist broadleaf forests biome to control for area in ranking vascular plant species richness. (a) The model parameters are allowed to vary across biogeographical realms. Four candidate species–area relationship (SAR) models were fitted to the biome: (b) power law, (c) exponential, (d) negative exponential and (e) monod models. In each of these models, the population-level SAR (black line) is fitted based on the contributions from the estimated fixed effects and the estimated random effects across realm classes. Finally, we averaged the four SAR models using AIC_c weights ($wAIC_c$) to obtain the final fitted model (f; dotted line). Codes for biogeographical realm classes: AA, Australasia; AT, Afrotropical; IM, Indo-Malayan; NA, Nearctic; NT, Neotropical; OC, Oceania; PA, Palearctic.

species it has, with the number of species expected for an ecoregion of its area (Fattorini, 2006; Lamoreux *et al.*, 2006; Lee & Jetz, 2008).

Historical habitat loss

We overlaid a modified version of the Global Land Cover 2000 dataset (Hoekstra *et al.*, 2005) over a map of WWF ecoregions (Olson *et al.*, 2001). We calculated historical habitat loss by expressing the area of human-modified land-cover as a percentage of total terrestrial land area in each ecoregion. Our definition of human-modified land cover includes cultivated and managed land, cropland mosaics, and artificial surfaces and associated areas. We detected a weak negative correlation between historical habitat loss and ecoregion size (Spearman rank correlation: $\rho = -0.22$); however, additional bootstrapping analyses (Brett, 2004) suggested that the relationship might be spurious or weakly positive (Appendix S2).

Human population density projections (2005–15)

We used the Global Population of the World version 3 (GPWv3) dataset, a gridded human population density database at 2.5 arc-minute resolution, to incorporate predicted change in human population density from 2005 to 2015 (CIESIN & CIAT, 2005). This dataset is derived by extrapolating existing patterns in population increase (Balk *et al.*, 2005); therefore we expect it to take into account ongoing migration trends, but not novel migration patterns in the future. We derived the annual percentage change in human population density for each ecoregion as:

$$r = \left[\left(\frac{\text{POP}_{2015}}{\text{POP}_{2005}} \right)^{1/10} - 1 \right] \times 100$$

where: r = annual percentage change in human population density, pop_{2015} = projected population density in 2015, and pop_{2005} = population density in baseline year 2005. This equation computes the geometric rate of change – also known as the compound rate – which takes into account the population change of each subsequent year.

Analyses

Relative need for conservation assessments among ecoregions

After removing 41 ecoregions with missing data, and excluding nine ecoregions containing fewer than 50 pixels for either land-use or human population datasets to reduce the potential error arising from low pixel sample size in small ecoregions, there were 747 ecoregions remaining for analysis. As in previous studies (e.g. Myers *et al.*, 2000), we introduced quantitative thresholds to assess the relative need for conservation assessments among ecoregions. Future population growth, together with historical habitat loss and SAR-controlled vascular plant species richness, provide an indication of the relative level of

threat to the vascular plants in each ecoregion, and form the basis of our assessment of the relative assessment importance. To qualify as being important for conservation assessments, we first specified that an ecoregion must be ranked above the 20th percentile in plant species richness (among ecoregions within its biome), historical habitat loss, and projected increase in human population density. This initial threshold value was chosen because it yields a number of ecoregions ($n = 406$) comparable with that identified by the G200 ($n = 369$) and BH ($n = 451$) templates. When we used the 10th percentile threshold, 571 ecoregions were selected, whereas a 30th percentile threshold selected only 273 ecoregions. To identify the ecoregions with the greatest need for conservation assessments, and to assess the sensitivity of the results to different threshold values, we repeated the analyses at both lower and higher threshold values (10th, 30th, 40th, 50th, 60th, 70th and 80th percentiles, respectively).

This multiple-threshold method also enables us to assign ecoregions in nine categories of decreasing need for conducting conservation assessments of plant species. Ecoregions identified using the 80th percentile threshold were allocated the highest assessment need (category 9), followed by successive 10-percentile decrements (70th, 60th, etc.). Ecoregions placed in category 1 were not considered to be important at any of the eight thresholds (i.e. ecoregions not ranked >10th percentile in the three metrics).

Overlap with the biodiversity hotspots and G200 templates

Our framework to assign relative assessment need to ecoregions differs in many ways from the BH and G200 templates, so we expect that our template identifies important ecoregions previously not accounted for in the BH and G200. To test this hypothesis, we compared our sets of important ecoregions (identified at various thresholds) with the G200 and BH templates, and noted the ones that were not included in the two existing templates. We also determined the degree of overlap between our set of important ecoregions with those identified in the G200 template (Olson & Dinerstein, 2002) and the BH template (Myers *et al.*, 2000; as updated in Mittermeier *et al.*, 2004).

Testing the lack of financial resources in ecoregions with high relative importance

We adopted the average per capita gross national income adjusted for purchasing power parity (GNI-PPP) for 2003–07 as a surrogate of a country's financial resources (World Bank World Development Indicators, <http://www.worldbank.org/data>). To evaluate the challenge posed by the lack of local financial resources, we fitted generalized linear models (GLMs) to the data using the maximum likelihood estimation with the `glm` function of R v. 2.8 (R Development Core Team, 2009). We generated two GLMs that represented the hypothesized correlation between a country's GNI-PPP and its assessment need status (whether a country overlaps with one or more

ecoregions deemed important for conservation assessments). The GLM response was binomial with a logit-link function. We used AIC_c to assign relative strengths of evidence to the different competing models (Burnham & Anderson, 2002). To evaluate the relative likelihoods of candidate models, we calculated wAIC_c following Burnham & Anderson (2002). All calculations were performed in R v. 2.8.

RESULTS

Ecoregions with a high relative need for conservation assessments

Our analyses included 747 ecoregions in 13 biomes, located across all seven biogeographical realms on Earth. An overview of the characteristics of the ecoregions is presented in Table 2. Four hundred and six ecoregions had >20th percentile values of plant species richness, historical habitat loss and future human population growth (categories 3–9 in Fig. 2), covering a total area of 47,356,000 km² (total area of 747 ecore-

gions = 130,869,000 km², therefore 36% of these). Most of these ecoregions are tropical and subtropical moist broadleaf forests (143 ecoregions, 35%), followed by deserts and xeric shrublands (43, 11%), and tropical and subtropical dry broadleaf forests (39, 10%). In terms of coverage, the tropical and subtropical dry broadleaf forests biome was the highest (76% of all ecoregions in the biome), followed by tropical and subtropical coniferous forests (75%), and tropical and subtropical moist broadleaf forests (70%). The majority of the ecoregions with >20th percentile values of plant species richness, historical habitat loss and future human population growth are situated in the Neotropical (117, 29%) and Indo-Malayan (67, 16%) realms. In terms of biogeographical coverage, a greater proportion of ecoregions in the tropical biogeographical realms (74% of Neotropical ecoregions, 68% of Indo-Malayan ecoregions, 59% of Afrotropical ecoregions) were selected compared with temperate realms (Nearctic 53%; Palaeartic 30%). Ecoregions of high relative need are found in Southeast Asia, Central America, the Tropical Andes and the Cerrado of South America, and the East African montane

Table 2 Overview of the 747 ecoregions analysed in this study.

No.	Parameter analysed	Min.	Max.	Mean	SD
1	Area (km ²)	907	4,629,000	175,200	340304.9
2	Number of vascular plant species	80	10,000	2066	1616.27
3	Population density change (% per annum)	-4.73	13.62	1.06	1.52
4	Historical habitat loss (proportion)	0	0.999	0.269	0.271

No.	Biogeographical realms	No. of ecoregions
1	Australasia (AA)	78
2	Afrotropical (AT)	99
3	Indo-Malayan (IM)	97
4	Nearctic (NA)	115
5	Neotropical (NT)	159
6	Oceania (OC)	7
7	Palaeartic (PA)	192

No.	Biomes	No. of ecoregions
1	Tropical and subtropical moist broadleaf forests	203
2	Tropical and subtropical dry broadleaf forests	51
3	Tropical and subtropical coniferous forests	16
4	Temperate broadleaf and mixed forests	79
5	Temperate coniferous forests	53
6	Boreal forests/taiga	28
7	Tropical and subtropical grasslands, savannas and shrublands	45
8	Temperate grasslands, savannas and shrublands	40
9	Flooded grasslands and savannas	24
10	Montane grasslands and shrublands	49
11	Tundra	30
12	Mediterranean forests, woodlands and scrub	38
13	Deserts and xeric shrublands	91

Minimum (Min.), maximum (Max.), mean and standard deviation (SD) of the variables considered in the plant species assessment analysis are presented, as are the number of ecoregions in each biogeographical realm and biome.

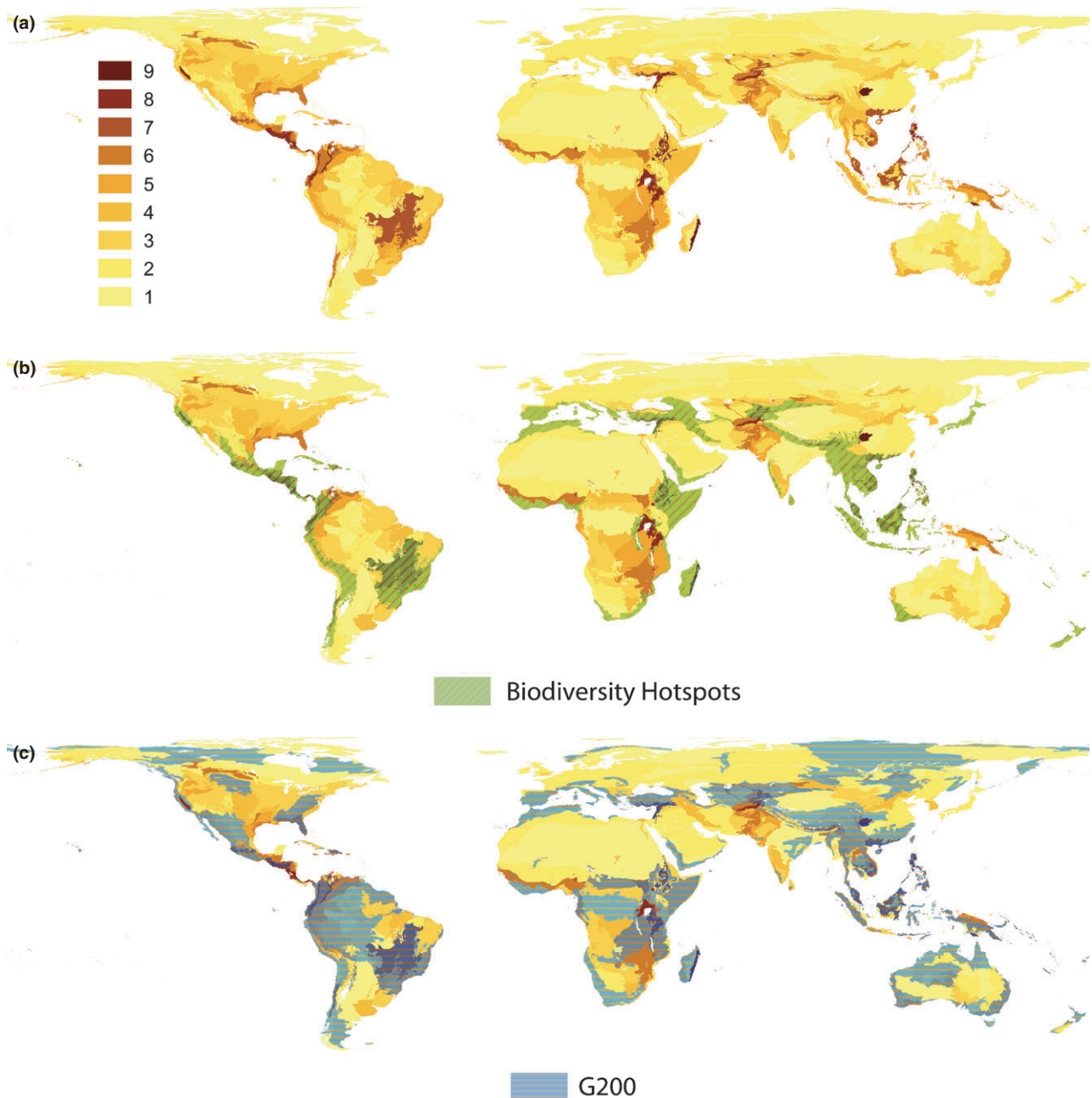


Figure 2 (a) Relative need for the conservation assessment of plant species among 747 global ecoregions. Ecoregions are placed in nine categories, from 1 = lowest relative need (pale yellow) to 9 = highest relative need (dark brown). Ecoregions that are ranked above the 80th percentile in plant species richness, historical habitat loss, and future human population increase are placed in category 9. Ecoregions ranked above the 70th percentile but lower than the 80th percentile in all three criteria are placed in category 8, and so on. Our scheme is overlaid with (b) the BH template and (c) the Global 200 template for comparison. The map uses a cylindrical equal-area projection.

region and its surrounding areas (ecoregions shaded dark brown in Fig. 2). Notable extra-tropical, highly important ecoregions are found in the mountains of Central Asia and central valley of California, USA (Fig. 2). Trends were similar using the 40th and 60th percentile thresholds – tropical and subtropical dry broadleaf forests, and moist forests, were deemed important for plant assessments (Appendix S2). The ecoregion-by-ecoregion findings are available for download

(Appendix S3). The associated GIS shapefile can be obtained from the corresponding author upon request.

Species–area models used in ranking vascular plant species richness

Compared with the nonlinear fixed-effects models, the nonlinear mixed-effects models displayed a reduction in positive

spatial autocorrelation. Only three mixed-effects SAR models (one in the temperate coniferous forests biome, two in the boreal forests/taiga biome) showed evidence for spatially autocorrelated residuals (Mantel permutation test, $P < 0.05$; Legendre & Legendre, 1998) while 21 ecoregion fixed-effects SAR models had spatially autocorrelated residuals (exact P values presented in Appendix S4).

Every SAR model considered was top-ranked in at least one biome. The exponential model was the top-ranked model in six (tropical and subtropical dry broadleaf forests; temperate broadleaf and mixed forests; temperate coniferous forests; boreal forests/taiga; temperate grasslands, savannas and shrublands; flooded grasslands and savannas) out of the 13 biomes according to $wAIC_c$, followed by the power model in five biomes (tropical and subtropical moist broadleaf forests; tropical and subtropical coniferous forests; tropical and subtropical grasslands, savannas and shrublands; montane grasslands and shrublands; deserts and xeric shrublands), and the negative exponential and monod models were each top-ranked in one biome (Mediterranean forests, woodlands and scrub; and tundra, respectively). In most biomes, there is no one dominant SAR model ($wAIC_c$ values were spread more or less evenly across models). Only in the tropical and subtropical

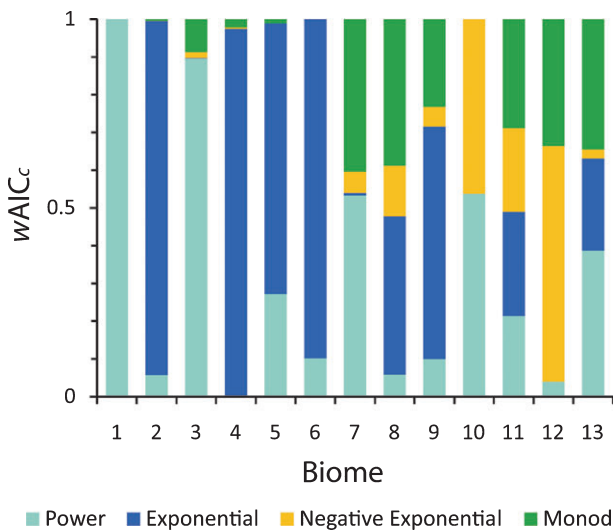


Figure 3 The Akaike information criterion corrected for small sample sizes weights ($wAIC_c$) for candidate species–area relationship (SAR) models across each biome. The $wAIC_c$ values represent the relative likelihood of candidate models and can vary from 0 (no support) to 1 (complete support) relative to the entire model set. The biome numbers correspond to the numbers denoting biomes in Table 2: (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 coniferous forest, (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.

moist broadleaf and dry broadleaf forests, and temperate broadleaf forests, was the information-theoretic weighting > 0.90 for a single model (Fig. 3). The power model was dominant in the tropical and subtropical moist broadleaf forests, while the exponential model was dominant in the tropical and subtropical dry broadleaf forests, and temperate broadleaf forests.

The nonlinear mixed-effect models exhibited both homoscedastic and heteroscedastic error structures. Out of the 49 models which converged, 32 were modelled with heteroscedastic errors and 17 were modelled with homoscedastic errors (Appendix S4).

Overlap with the biodiversity hotspots and G200 templates

Among the 406 ecoregions selected using the 20th percentile threshold, 217 (53%) overlap with the ecoregions identified in WWF’s G200; 294 (72%) are contained in the BH, whilst 81 are excluded from both G200 and BH templates (Appendix S5). Among the 168 ecoregions selected using the 40th percentile threshold, 101 (60%) overlap with those designated in the G200, and 148 (88%) are contained in BH. Nineteen ecoregions selected in our analysis are excluded from both G200 and BH (Appendix S6). Using the 60th percentile threshold, 29 of 44 (66%) ecoregions overlap with G200, and 40 (91%) overlap with BH. Only three ecoregions are excluded by both G200 and BH – the Louisiade Archipelago rain forests (AA0110), Jos Plateau forest–grassland mosaic (AT1010), and South Malawi montane forest–grassland mosaic (AT1014) (Appendix S7). The two ecoregions selected using the 80th percentile threshold overlap with both BH and G200. The overlap between the relative importance of ecoregions derived from our present analysis and the BH and G200 prioritization schemes are shown in Fig. 2b,c), respectively. Ecoregions and their respective overlapping G200 and BH are presented in Appendix S5.

Lack of financial resources in ecoregions that are important for conservation assessments

Two hundred and seven countries overlapped with the 747 ecoregions assessed in our analyses. After eliminating 41 countries with unavailable GNI–PPP data, 166 countries remained for the financial resources analysis (Appendix S8). At the 20th to 70th percentile thresholds, the GLM containing per capita wealth was always ranked higher than the null model (Akaike’s model weights, $wAIC_c = 0.97 - \approx 1$ for all cases; Table 3). At all thresholds, increasing per capita wealth was negatively correlated with the odds of a country overlapping with ecoregions deemed important for conservation assessments. We did not model the importance status of the 10th and 80th percentile thresholds owing to small sample sizes (four countries that did not overlap with important ecoregions, and two countries that overlapped with important ecoregions, respectively).

Table 3 Generalized linear models (GLMs) investigating the correlation of per capita wealth with whether a country overlaps with important ecoregions selected using multiple percentile thresholds.

Rank	Structure	k	LL	AIC_c	ΔAIC_c	$wAIC_c$	%DE
20th percentile threshold							
1	~GNI	2	-66.70	137.48	0	1	20.7
2	~1 (null model)	1	-84.16	170.35	32.87	7.3×10^{-8}	
30th percentile threshold							
1	~GNI	2	-88.96	182.00	0	1	15.0
2	~1	1	-104.71	211.45	29.45	4.0×10^{-7}	
40th percentile threshold							
1	~GNI	2	-96.30	196.68	0	1	15.6
2	~1	1	-114.08	230.19	33.51	5.3×10^{-8}	
50th percentile threshold							
1	~GNI	2	-99.65	203.38	0	1	13.2
2	~1	1	-114.87	231.76	28.38	6.9×10^{-7}	
60th percentile threshold							
1	~GNI	2	-96.60	197.28	0	0.99	5.7
2	~1	1	-102.40	206.82	9.54	0.01	
70th percentile threshold							
1	~GNI	2	-75.57	155.22	0	0.97	5.4
2	~1	1	-79.92	161.87	6.65	0.03	

Important ecoregions identified using a 20th percentile threshold are ranked above the 20th percentile in plant species richness, historical habitat loss and future human population. GLMs are ranked by sample size-corrected Akaike's information criterion model weights ($wAIC_c$), which represent the probability of the model being the best in the candidate set. GNI, per capita GNI-PPP. Also shown are the number of parameters (k), log-likelihood (LL), AIC_c , difference between the top-ranked model's AIC_c and that of the model under consideration (ΔAIC_c), and percentage deviance explained by each model (%DE).

DISCUSSION

Our prioritization approach incorporates future human population pressure explicitly into a categorization of the relative need for global-scale plant conservation assessment, and in this way we incorporate both past and future (latent) threat (*sensu* Cardillo *et al.*, 2006). Our reactive approach (*sensu* Brooks *et al.*, 2006) depends on the premise that highly biodiverse ecoregions that have experienced high habitat degradation, and at the same time are projected to have high rates of human population increase over the next few decades, are most likely to have the largest numbers of species that are declining in numbers and range, and hence are most susceptible to extinction. These ecoregions thus require immediate attention in terms of assessing the population size and the distribution of native plant species to be able to quantify the relative threats to biodiversity. With a shortage of conservation funds (Balmford *et al.*, 2003; Bruner *et al.*, 2004), we believe it is prudent to acquire knowledge about species that are most likely to be affected by current and future habitat loss, and do this in areas where the most threatened species are found. It would not be as important to assess the population status of species that are in pristine forests (a proactive approach, *sensu* Brooks *et al.*, 2006) because their populations are less likely to decline owing to habitat stability. However, our analysis excludes small ecoregions, most of them islands, owing to the uncertainty in human population and habitat loss trends. Following the precautionary principle, it is important to assess the plant species, while at the same time incorporating high-resolution

trends in population and land-use change in these ecoregions. This study focuses on vascular plant species which, as a group, account for most of Earth's terrestrial plants. The number of non-vascular plant species (15,000, *c.* 5% of the world's flora; Rozzi *et al.*, 2008) is small compared with the number of vascular plant species; therefore it is unlikely to affect our results. Furthermore, there is no information on the global distribution of non-vascular plant species, hence it was not possible to incorporate them in our analysis.

Our work has also demonstrated the utility of nonlinear mixed-effect models for overcoming spatial autocorrelation owing to the shared evolutionary history of ecoregions in the same biogeographical realm. Spatial autocorrelation can lead to incorrect model parameter estimates (Dormann *et al.*, 2007), and thus lead to incorrect conclusions about the conservation importance of ecoregions. The commonly used fixed-effects models (Guilhaumon *et al.*, 2008) displayed residual autocorrelation, in some biomes across all four forms of the SAR models considered. This is not unexpected, as the ecoregions in each biome fall into several spatially distinct biogeographical realms (Olson *et al.*, 2001). Ecoregions in each biogeographical realm broadly share a similar evolutionary history and contain distinct species assemblages (Olson *et al.*, 2001; Millennium Ecosystem Assessment, 2005). Species richness in ecoregions within each biogeographical realm is therefore likely to be similar, resulting in spatial correlation. If a fixed-effects modelling framework was employed to identify species-rich ecoregions, the exclusion of spatially autocorrelated SAR would result in the entire exclusion of four biomes

(tropical and subtropical moist broadleaf forests; temperate coniferous forests; boreal forests/taiga; flooded grasslands and savannas), thus compromising the comprehensiveness of the assessment. As in the case of fixed-effects models used by Guilhaumon *et al.* (2008), we showed that it is important to consider a suite of candidate mixed-effects SAR models when identifying species-rich ecoregions because no one form of SAR was consistently top-ranked across all biomes. We also illustrated the utility of model averaging to account for the uncertainty in the top-ranked SAR form, given the similar weighting across models applied in many biomes. Lastly, we found that the SAR models exhibited both homoscedastic and heteroscedastic errors. Our results demonstrate that it is important to account for the variability in the error structure, and we provided a possible approach through nonlinear mixed-effects modelling.

Instead of setting a single and arbitrary threshold, we allocated ecoregions to nine levels of relative need so that conservation assessors (e.g. in the IUCN and other organizations involved in conservation assessments) can make sound decisions in selecting focal ecoregions for species assessment projects – moving down the percentiles as funds and logistics permit. By modelling the SAR and ranking the species richness in ecoregions within each biome, we ensure a more representative template akin to the G200 (Olson & Dinerstein, 2002). Our template shows moderate spatial congruence with both G200 and BH (Myers *et al.*, 2000), but identifies some important differences. The overlap between the ecoregions selected by our algorithms and the BH template was greater than with the G200 template. A possible explanation is that the BH template shares our emphasis on conserving plant species and choosing areas with high historical habitat loss. Another reason might be that the BH template covers more ecoregions (451) than the G200 (369). We identified some ecoregions that merit conservation attention which are currently excluded from the list of high-priority areas designated by one or both templates. For example, the South Malawi montane forest–grassland mosaic (WWF eco-code: AT1014) is ranked above the 60th percentile in terms of plant species richness among ecoregions of its biome, historical habitat loss, and future population increase, but it has not been identified by either the BH or the G200 template. The region has had 36% of its natural habitat already altered, and its human population density is projected to be increasing by almost 2% annually from 2005 to 2015.

Countries that overlap with ecoregions of high relative need for conservation assessments are relatively poorer as measured by their gross national income; therefore funds might not be available locally for the implementation of conservation assessment programmes in ecoregions facing high habitat loss. Our results, which are directed at plant species assessments, support the general conclusions of Bode *et al.* (2008), who found that global conservation priorities are weighted towards poorer countries when socioeconomic factors are taken into account. We urge international funding agencies such as the World Bank and Global Environment

Facility to cooperate with the IUCN and various botanic gardens to facilitate the transfer of funds and scientific expertise from wealthier to poorer countries across high-importance ecoregions in need of conservation assessments. Plant Red List assessments in southern Africa (Siebert & Smith, 2005) and other biodiversity hotspots (Missouri Botanical Gardens, 2009) are examples of projects arising from international cooperation and funding. Ecoregions of high plant assessment need often span two or more countries (for example, Apure-Villavicencio dry forests along the slopes of the Colombian and Venezuelan Andes), so partnerships between countries, in addition to international institutions, are needed to coordinate assessment projects. Besides improving the efficacy of assessing species by sharing knowledge on plant distributions and status, cross-country collaborations also lower conservation costs (Bladt *et al.*, 2009; Kark *et al.*, 2009). These multilateral projects also contribute to the long-term conservation of plant species by transferring scientific and management knowledge from international organisations to local conservation practitioners. However, a major barrier to implementing species assessment projects in such regions is the sociopolitical instability of these countries. Poorer countries are at higher risk of experiencing a civil war (Rice *et al.*, 2006), and such political disturbances will undoubtedly disrupt species assessment efforts. As the international community cannot dictate the political stability of countries, we suggest that species assessment programmes should be built into existing debt-for-nature swap programmes (Miles, 2005) as they fulfil concomitant goals in financing assessment projects and improving economic conditions to improve political stability.

We did not explicitly incorporate cost into our scheme, owing to the lack of data on the cost of plant conservation assessments across a range of countries (Siebert & Smith, 2005). Moreover, the cost of conservation assessments tends to be flexible depending on the decision to include or exclude non-essential components such as disseminating information at no charge in the form of books and CDs (Siebert & Smith, 2005). However, our highly important ecoregions – such as the high-priority watersheds identified using an ecosystem-services approach to prioritization (Luck *et al.*, 2009) – are located in areas characterized by having a high conservation benefit-to-cost ratio (i.e. developing countries with low per capita wealth: Balmford *et al.*, 2003; and where labour costs are low: Naidoo *et al.*, 2006). This observation argues for even greater motivation for investment in these areas. Cooperation among international funding agencies, botanic gardens, and local and international scientists is imperative for the implementation of conservation assessment programmes in highly biodiverse and highly threatened ecoregions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Nonlinear mixed-effects models for 12 of the 13 biomes (excludes the tropical and subtropical moist broadleaf forests biome, shown in Fig. 1) to control for area in ranking vascular plant species richness.

Appendix S2 Supplementary methods and results.

Appendix S3 Full dataset used in allocating the relative conservation assessment need of ecoregions.

Appendix S4 Mantel permutation test for fixed-effects and mixed-effects SAR models fitted to each biome.

Appendix S5 List of ecoregions and their respective overlapping biodiversity hotspots and Global 200 ecoregions.

Appendix S6 List of 19 important ecoregions excluded from biodiversity hotspots and Global 200 templates.

Appendix S7 Location of the three ecoregions excluded from both Global 200 and biodiversity hotspots templates.

Appendix S8 Countries overlapping with important ecoregions at multiple thresholds.

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BIOSKETCH

Our research group consists of scientists from the National University of Singapore and the University of Adelaide. We have broad and varied research interests, including biotic endangerment, conservation management and policy, climate change impacts on biodiversity, invasive species and urban ecology, and we work on a variety of taxa both globally and locally.

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