

Species-richness patterns of the living collections of the world's botanic gardens: a matter of socio-economics?

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- **Background and Aims** The botanic gardens of the world are now unmatched *ex situ* collections of plant biodiversity. They mirror two biogeographical patterns (positive diversity–area and diversity–age relationships) but differ from nature with a positive latitudinal gradient in their richness. Whether these relationships can be explained by socio-economic factors is unknown.
- **Methods** Species and taxa richness of a comprehensive sample of botanic gardens were analysed as a function of key ecological and socio-economic factors using (a) multivariate models controlling for spatial autocorrelation and (b) structural equation modelling.
- **Key Results** The number of plant species in botanic gardens increases with town human population size and country Gross Domestic Product (GDP) per person. The country flora richness is not related to the species richness of botanic gardens. Botanic gardens in more populous towns tend to have a larger area and can thus host richer living collections. Botanic gardens in richer countries have more species, and this explains the positive latitudinal gradient in botanic gardens' species richness.
- **Conclusions** Socio-economic factors contribute to shaping patterns in the species richness of the living collections of the world's botanic gardens.

Key words: Biodiversity loss, global priorities, hotspots conservation, large-scale patterns, local and regional diversity, macroecology, plant biogeography, rarity, species–people correlation, species–time relationship, tropical ecosystems, urban ecology.

INTRODUCTION

Botanic gardens devote their resources to studying, conserving and making known the world's plant species diversity (e.g. Ingram, 1992; Frankel *et al.*, 1995; Dosmann, 2006). Although the extraordinary diversity of the collections of the world's botanic gardens is mostly due to deliberate planting (e.g. Heywood, 1990; Maunder, 1994, 2008; Heyd, 2006), their species richness has been shown to match two major geographical patterns often found in natural ecosystems (Pautasso and Parmentier, 2007). Larger and older botanic gardens tend to have more species than smaller and younger ones, as expected from the many positive species–area (Connor and McCoy, 1979; Lawton, 1999; Crawley and Harral, 2001) and species–time (McKinney and Frederick, 1999; Adler and Lauenroth, 2003; Carey *et al.*, 2007) relationships observed in nature. However, the living collections of the world's botanic gardens show an increase in species richness with increasing latitude, and this goes against most latitudinal gradients in species diversity documented in natural ecosystems (Rohde, 1992; Hillebrand, 2004).

Today, there are approx. 2500 botanic gardens in the world (Fig. 1). These cultivate over 6 million accessions of living plants, representing around 80 000 taxa in cultivation, which is about one-quarter of the estimated number of vascular plant species in the world (Wyse Jackson, 2001). Botanic gardens thus play a central role in the *ex situ* conservation and exploration of the global plant biodiversity. They also have an important role in preserving species that support human needs and well-being (Waylen, 2006). This role is likely to become increasingly important due to climate change (Donaldson 2009; Primack and Miller-Rushing, 2009). Understanding the determinants of collection richness can help us to predict what actions are required to ensure that the plant collections of botanic gardens are aligned with their aims for conservation and sustainable development. Moreover, investigating the relationships between biogeography, garden characteristics, socio-economic factors and species richness might help to derive recommendations for strengthening the role of botanic gardens in the framework of several international agreements and political debates such as the Global Strategy for Plant Conservation (GSPC). One of the targets of this strategy is to have 60 % of the world's threatened

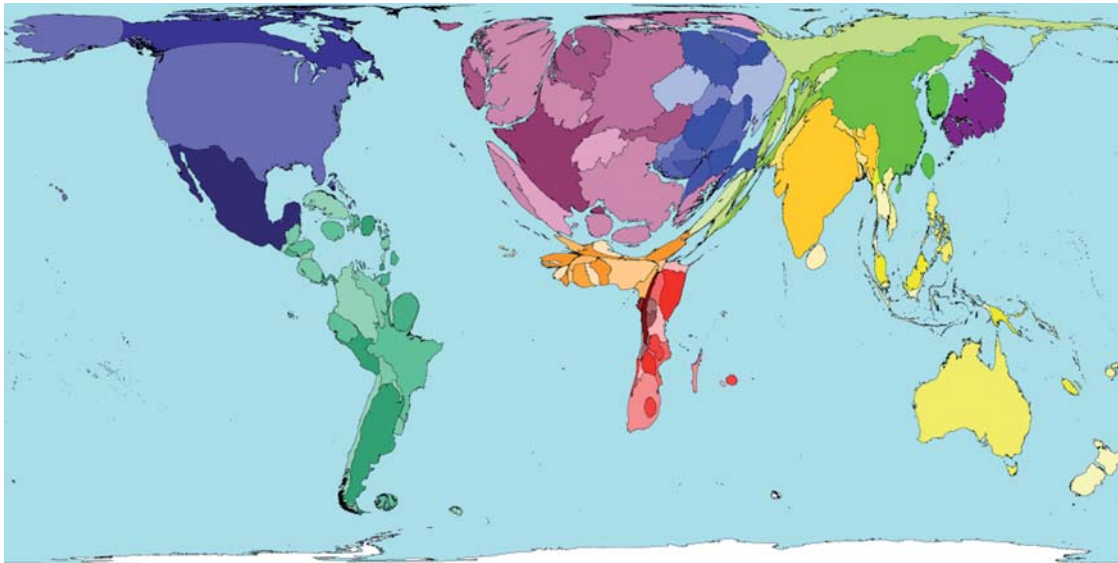


FIG. 1. World map of botanic gardens (territory size is proportional to number of gardens). From <http://www.worldmapper.org/>, accessed August 2008. Creative Commons License, copyright 2006 SASI Group (University of Sheffield, UK) and Mark Newman (University of Michigan, USA).

plant species conserved *ex situ* (Heywood and Iriondo, 2003; Callmender *et al.*, 2005; Hunter and Gibbs, 2007; Sharrock and Jones, 2009). Hence botanic gardens have an important role in the preservation of global plant biodiversity in the face of the current mass extinction.

The wide variation in species richness among botanic gardens (from hundreds to tens of thousands of species; Fig. 2) and the reversed latitudinal gradient in this species richness prompt the question of whether such variation is mainly controlled by ecological or socio-economical factors. We inquire here whether the biogeographical patterns of the living collections of the world's botanic gardens (positive species–area, –time and –latitude relationships) documented in Pautasso and Parmentier (2007) is still present when accounting for variations in socio-economic factors. Also the flora of the country in which a botanic garden is located is considered as an additional explanatory factor. The main questions addressed in this paper are as follows.

- (a) Is there a relationship between the species richness of a botanic garden and the human population size of the town in which the garden is located? There has been a recent increase in the interest of macroecologists and biogeographers in ecosystems modified by human beings and in the degree to which biodiversity and human population overlap spatially (e.g. Araújo, 2003; Luck, 2007). Surprisingly, over large scales of analysis many studies have reported a positive correlation between the species richness of various taxa and the human population size or density located in the same area (e.g. Kühn *et al.*, 2004; Pautasso and McKinney, 2007; Fjeldså and Burgess, 2008). The population size of a town may be correlated with the budget of a botanic garden (information which it was not possible to obtain) and might thus be associated with the allocation of more resources for the collection of new plant species and for the maintenance of the species

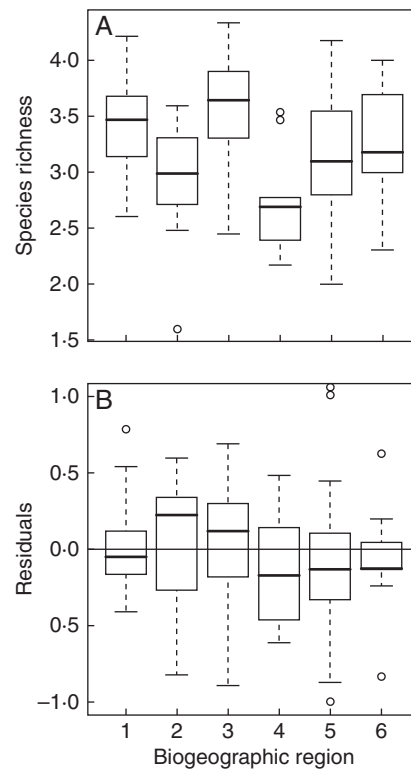


FIG. 2. Box-and-whisker plots in the different biogeographical regions (1, Nearctic; 2, Neotropical; 3, Palearctic; 4, Ethiopian; 5, Oriental; 6, Australasian) of (A) botanic garden species richness ($n = 179$) and (B) residuals of the models presented in Table 1 for the same gardens.

already acquired. On the other hand, more populous towns may struggle to find sufficient room to house the collections of botanic gardens.

- (b) Is there a relationship between the species richness of a botanic garden and the Gross Domestic Product (GDP)

per person of the country in which the garden is located? Biodiversity loss in natural ecosystems, poverty and the associated lack of conservation funding are known to be linked problems (e.g. Adams *et al.*, 2004; Roe, 2008; Sodhi, 2008). However, unless they incorporate patches of natural vegetation, most botanic gardens are artificial ecosystems where the presence and location of most plants is the result of a gardener's decision, in some cases related to the focus of a botanic garden on certain taxa or geographic regions. Given that importing, propagating and maintaining material is costly and difficult, gardens in more affluent countries may have been able to collect more species in the course of their existence, as they may afford the employment of a higher number of skilled gardeners. On the other hand, labour costs are substantially lower in developing countries (Wells, 1992), so that botanic gardens in these regions may be able to counterbalance their lower resources.

- (c) Is there a relationship between the species richness of a botanic garden and the flora of the country in which the garden is located? Regional richness, which can often contribute in explaining local richness (e.g. Caley and Schluter, 1997), is a control factor in the present analysis: if the species richness of the world's botanic gardens is dependent on the national flora due to seed availability, financial constraints and restrictions concerning international transport of plants and their propagules, the richness of the botanic gardens should correlate with the richness of the national floras. If instead the species richness of botanic gardens is mainly a consequence of financial factors (larger resources to buy and collect specimens and seeds from other regions and gardens), then it is expected that the flora of the region around a botanic garden is not related to the species richness of a botanic garden.

MATERIALS AND METHODS

The botanic garden data used in these analyses are the same as those in Pautasso and Parmentier (2007). The identities of approx. 2500 botanic gardens were obtained from the database 'Garden Search', publicly available via the website of Botanic Garden Conservation International (BGCI; <http://www.bgci.org/>). Many of these gardens are arboreta, and these were not included in the analyses. The present analysis did not include national parks and nature reserves. Data on (a) the species richness of the living collections, (b) the total area, (c) the year of establishment, and (d) the geographical co-ordinates of 704 gardens were retrieved from publications and/or web-pages. To fill the gaps in the database, 292 e-mails and 209 letters were sent to botanic gardens at the beginning of 2006 (with 127 and 33 replies, respectively). For the present analyses, recent (2000 onwards) estimates were also collected of the population size of the town (United Nations Statistics Division) and of the GDP per person (Purchasing Power Parity; CIA World's Factbook) of the country in which the botanic garden is located. Estimates of the vascular plant species richness of the country where the botanic garden is located were obtained from Gleich *et al.* (2000).

For only 179 gardens was it possible to retrieve all the data of interest [species richness of the living collections, range 40–22 000 species (mean 4300); area, 0.14–600 ha (mean 24); year of establishment, 1545–2003 (mean 1901); population size of the town, 2000–10 000 000 inhabitants (mean 1100 000); GDP per person, 1000–38 000 US \$ (mean 22 000); flora of the country, 250–56 000 species (mean 8000)]. For an additional 93 gardens, information on these variables and the number of taxa instead of species, i.e. including cultivars, forms and varieties, were obtained. Nearly the majority of the botanic gardens in the database are European (45%) and half of the gardens analysed are located in only ten countries (Australia, China, France, Germany, India, Italy, Japan, Russian Federation, UK and USA). However, the data analysed reflect the distributional patterns of the world's botanic gardens: according to BGCI, 35% of the world's botanic gardens are in Europe and 55% of them are in the ten countries just listed. Moreover, the 55 (species richness) and 30 (taxa richness) countries covered in the analysis have 80 and 64% of the botanic gardens in the world (according to BGCI). Furthermore, there is a good positive correlation between the number of botanic gardens in a country included in the analysis and the number of botanic gardens provided by BGCI for that country, both for the analysis of species and taxa richness (Fig. 3A, B). The sample is thus likely to be representative of the botanic gardens existing in the world. If a botanic garden was enlarged during the course of its history, its current size was recorded as its area. In case a botanic garden was moved to a different location, the year of establishment was dropped in favour of the year of the opening at the new location.

Species and taxa richness, area, and age of the botanic garden, population size of the town, GDP per person and vascular plant species richness of the country in which the botanic garden is located were log-transformed before analysis to conform to general assumptions of statistical tests. Analyses were run in SAS 9.1. The non-significant variables were included in models in order to prove that these were not affecting significantly the response variable. Mixed models with exponential co-variance structure were used to test the null hypotheses described above controlling for spatial autocorrelation within biogeographical regions with absolute distances (as, for example, in Pautasso and Weisberg, 2008). Spatial non-independence of data, by conflating the degrees of freedom, can lead to misleading parameter estimates (e.g. Pandit and Laband, 2007). Significant Moran's I of model residuals were observed at short distances, which justifies the use of spatial models to control for spatial autocorrelation (Hawkins *et al.*, 2007). There may be spatial autocorrelation among botanic gardens in intensity of management, funding availability and other factors such as the relative importance of scientific versus recreational use. Botanic gardens might be collaborating more with those in the same country and in neighbouring ones than with those elsewhere, if only because of linguistic reasons. Moreover, even if many botanic gardens have glasshouses, in many cases climate is a limiting factor for the living collections outside glasshouses and climate is spatially autocorrelated.

In addition, structural equation models (SEM) were performed with the software AMOS v. 5.0 (Arbuckle, 2003).

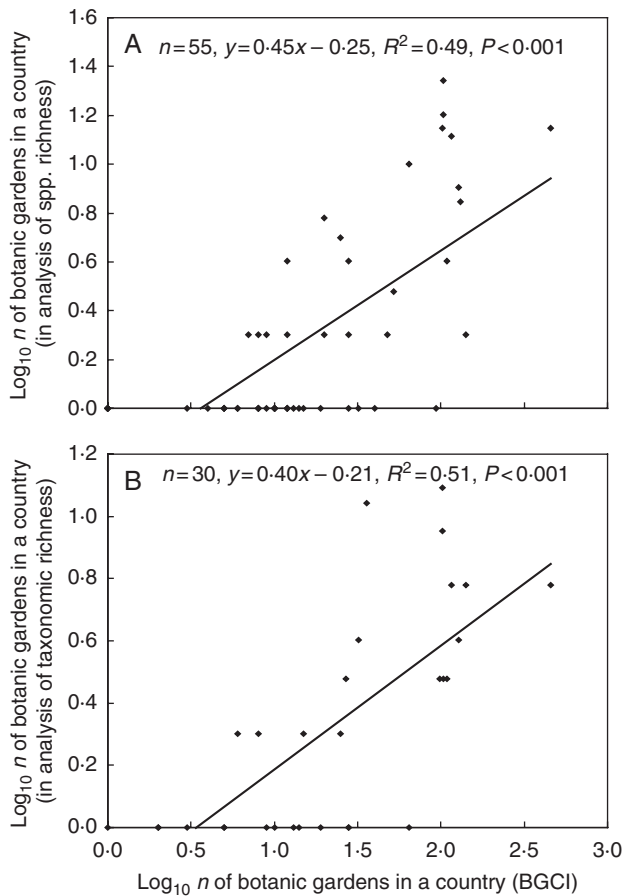


FIG. 3. Correlation between number of botanic gardens in a country according to BGCI and number of botanic gardens included in the present analysis for (A) species and (B) taxa richness.

SEM is a methodology to test various hypotheses regarding multivariate directional relationships. It allows to tackle multicollinearity among predictor variables in a more satisfactory way as it teases out direct and indirect effects of explanatory variables (Grace, 2006; Jetz *et al.*, 2008). Our SEMs were designed to test the hypotheses that (a) rich countries have rich gardens, (b) garden features such as area and age matter most, and (c) diverse gardens mirror a diverse country flora. Also a path analysis combining all these hypotheses together was run. Town population was used as an explanatory variable for variations in area among gardens and not the other way around, because it can be reasonably hypothesized that towns with more inhabitants may have the resources to maintain larger botanic gardens. On the other hand, more densely built towns may not have the physical space for a large botanic garden.

RESULTS

The species richness of the living collections of the botanic gardens analysed significantly increases with increasing population size of the town (Fig. 4A) and with increasing GDP per person of the country (Fig. 4B). There is a significant decrease of the species richness of the botanic gardens with increasing species richness of the flora of the country, but when controlling

for spatial autocorrelation this relationship is non-significant (Fig. 4C). When including all three explanatory factors in a multivariate model, the species richness of botanic gardens significantly increases with increasing town population size and country GDP per person [$n = 179$, $R^2 = 0.35$, $\log(\text{spp}) = 0.58 + 0.26 \log(\text{pop}) + 0.63 \log(\text{GDP}) - 0.19 \log(\text{flora})$; $P = 0.07$ for $\log(\text{flora})$ and < 0.001 for the other factors].

The generality of these results is corroborated by repeating the same analyses for an independent set of botanic gardens for which only an estimate of taxa (and not species) diversity was obtained ($n = 93$). The number of taxa of these gardens increases with increasing town population size (Fig. 4D) and country GDP per person (Fig. 4E) [$R^2 = 0.31$, $\log(\text{taxa}) = 1.34 + 0.25 \log(\text{pop}) + 0.50 \log(\text{GDP}) - 0.14 \log(\text{flora})$; $P = 0.09$ for $\log(\text{flora})$ and < 0.001 for the other factors]. There is no significant variation of number of taxa with increasing species richness of the country flora, also when not controlling for the other two factors (Fig. 4F).

These results are broadly confirmed when controlling for the area, age and absolute latitude of the botanic gardens (Table 1). In this model, the species richness of the gardens still increases significantly with town population size and country GDP per person, whereas there is no significant variation with increasing species richness of the country flora. The increase in species richness with garden area and age is still present when including town population, country GDP per person and flora in models, whereas there is no significant association with absolute latitude (Table 1A). For number of taxa, a similar pattern arises, with the exception of (a) country flora, which in this case is significantly negatively associated with number of taxa of botanic gardens, and (b) garden age, which drops together with absolute latitude as a significant factor from the model (Table 1B).

As for the interrelationships among the explanatory variables, for the botanic gardens for which an estimate of the species (and not taxa) richness was available, when controlling for spatial autocorrelation there is no significant correlation of absolute latitude with the town population size and with the number of species of the country flora, but there is a significant increase of the country GDP per person with absolute latitude [$R^2 = 0.41$, $\log(\text{GDP}) = 3.56 + 0.01\text{abs}(\text{lat})$; $P < 0.001$]. Town population size is not significantly correlated with garden age, but there is a significant increase of garden area with town population size [$R^2 = 0.27$, $\log(\text{area}) = -1.52 + 0.35 \log(\text{pop})$; $P < 0.001$]. There are no significant correlations of country plant species richness with town population size and of town population size with country GDP per person, but there is a significant decrease of country plant species richness with increasing country GDP per person [$R^2 = 0.10$, $\log(\text{flora}) = 6.44 - 0.63 \log(\text{GDP})$; $P < 0.001$]. Table 2 shows the correlation matrix of botanic garden species richness and all explanatory variables (without controlling for spatial autocorrelation).

Results from SEM (Fig. 5) confirmed the importance of socio-economic factors both in a direct way (country GDP per person) and in an indirect way (town population through garden area) in shaping the diversity of the world's botanic gardens. As with mixed models, SEM did not provide evidence that the diversity of the botanic gardens analysed (at least in terms of their number of species) tends to mirror the

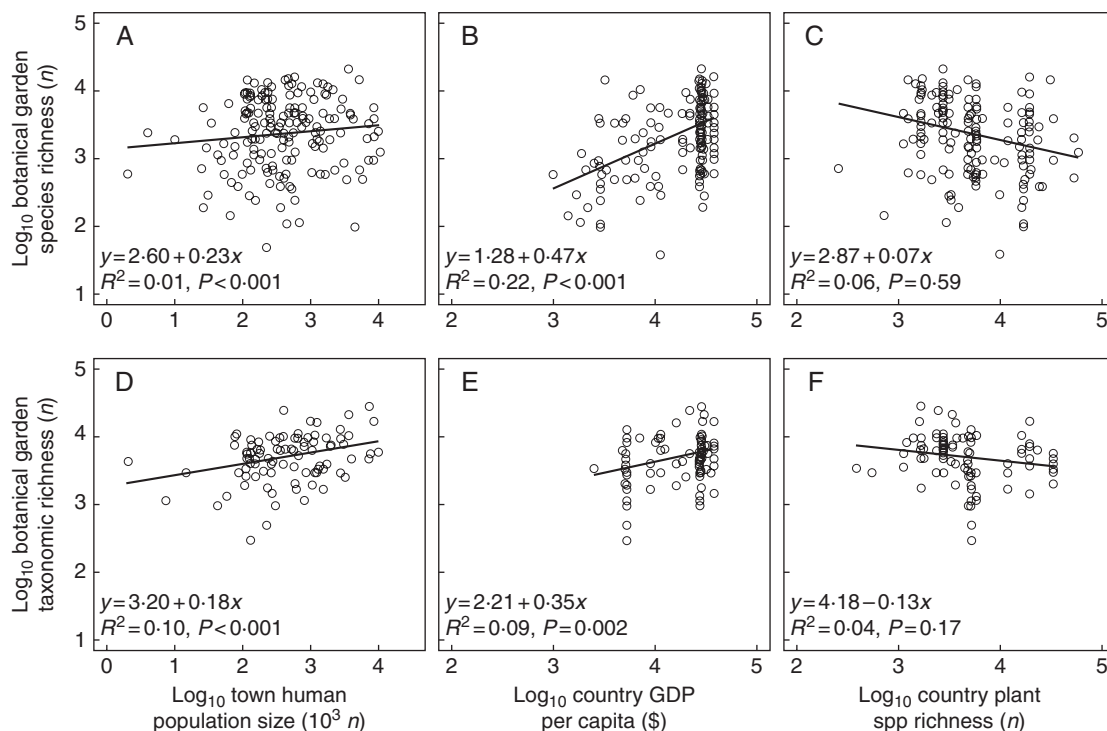


FIG. 4. The species (A–C; $n = 179$) and taxa (D–F; $n = 93$) richness of the living collections of botanic gardens as a function of the (A, D) town population size, (B, E) country GDP per person and (C, F) species richness of the flora of the country. Parameter estimates and P values, but not the R^2 values, were determined after accounting for spatial autocorrelation (this explains the negative slope and the positive parameter estimate of C).

TABLE 1. Results from mixed models of the (A) species ($n = 179$) and (B) taxa ($n = 93$) richness of botanic gardens as a function of town population size (thousand individuals), country Gross Domestic Product per person (\$, Purchasing Power Parity), species richness of the country flora (n), garden area (km^2), age (years, as of 2006) and absolute latitude

R^2	$y =$	log(pop)	log(GDP)	log(flora)	log(area)	log(age)	Abs. lat.
(A) Species							
0.48	0.93	0.15	0.48	-0.14	0.25	0.27	0.004
s.e. =	0.58	0.05	0.12	0.10	0.05	0.06	0.004
	$P =$	0.006	0.001	0.17	0.001	0.001	0.27
	part. R^2	0.05	0.11	0.03	0.10	0.10	0.02
(B) Taxa							
0.46	2.07	0.13	0.57	-0.26	0.28	0.08	-0.005
s.e. =	0.72	0.05	0.11	0.10	0.05	0.07	0.004
	$P =$	0.01	0.001	0.005	0.001	0.28	0.19
	part. R^2	0.08	0.26	0.09	0.18	0.01	0.02

s.e., Standard error of the parameter estimate.
Significant values are highlighted in bold.

diversity of the flora of the country in which the gardens are located. Moreover, the path models showed that the positive latitudinal gradient in species richness of botanic gardens can be attributed to the positive latitudinal gradient in country GDP per person. SEM thus helped in disentangling the interrelationships between latitude and other explanatory variables. Absolute latitude is positively correlated to country GDP per person because most rich countries (in terms of money) are located outside the tropics. Conversely, absolute latitude is negatively correlated to country flora species richness because most rich countries (in terms of plant species) are located in the tropics.

DISCUSSION

The key role of botanic gardens in the conservation of plant biodiversity is widely recognized (e.g. Mistretta *et al.*, 1991; Melzheimer, 1996; Ingram, 1999; He, 2002; Meda, 2005; Stevens, 2007). Each botanic garden is irreplaceable given its individual history, its particular living collection, its spatial display of different plant taxa and flora of various geographic regions, its age, area and microclimate, its location, current team, educational activities and research programmes (e.g. Mamaev and Andreev, 1996; Wyse Jackson, 2001; Dosmann, 2006). Botanic gardens are planted, tramped,

TABLE 2. Correlation matrix (Pearson product moment correlation) between botanic garden species richness, town population, country GDP per person, country flora species richness, garden area, age and absolute latitude

	log(spp)	log(pop)	log(GDP)	log(flora)	log(area)	log(age)	Abs. lat.
log(spp)	1.00						
log(pop)	0.11	1.00					
log(GDP)	0.48	-0.27	1.00				
log(flora)	-0.25	0.33	-0.20	1.00			
log(area)	0.18	0.39	-0.19	0.23	1.00		
log(age)	0.41	0.02	0.27	-0.16	-0.07	1.00	
Abs. lat.	0.47	-0.24	0.64	-0.55	-0.19	0.26	1.00

Significant correlations ($P \leq 0.05$) are highlighted in bold. These correlations were obtained without accounting for spatial autocorrelation.

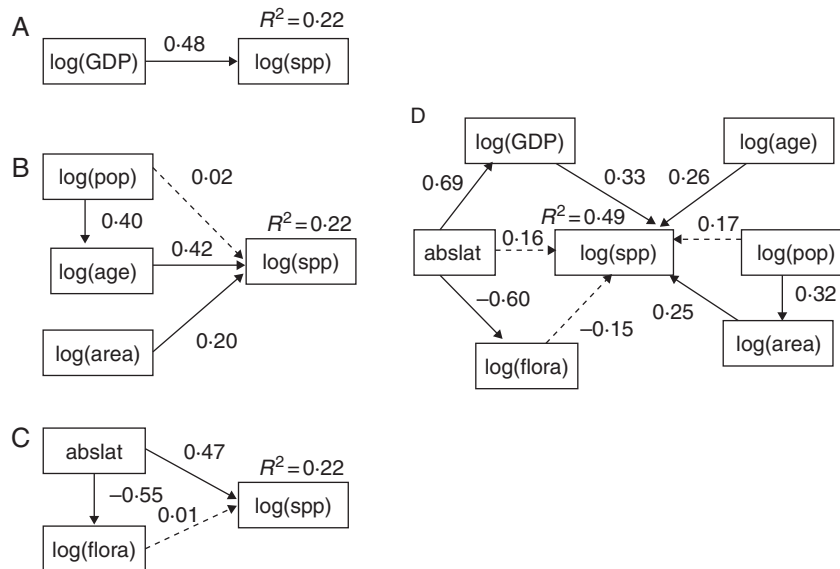


FIG. 5. Standardized path coefficients and squared multiple correlations for path models explaining botanic garden species richness under the hypotheses (A) 'rich countries have rich gardens', (B) 'garden characteristics (area and age) matter most', (C) 'diverse gardens mirror a rich country flora', and (D) all hypotheses combined. Dotted lines: $P > 0.05$. Abbreviations: spp, species richness of the living collections; age, number of years since the foundation of the garden; area, area of the garden; abslat, absolute latitude; flora, number of species of the country flora; GDP, Gross Domestic Product per person; pop, town population.

pruned and tended, but so are other urbanized ecosystems (Williams *et al.*, 2008). The analyses presented here suggest that two of three main large-scale patterns in the number of species of these managed ecosystems (species–area and –age, but not the species–latitude relationship) are still present when controlling for confounding factors such as town population size, country GDP per person and country plant species richness.

The botanic gardens of the world are no exception to the common finding that, over large extents of analysis, more populated regions also have more species (e.g. Luck, 2007; Pautasso, 2007; Knapp *et al.*, 2008). The proportion of variance in the species/taxa richness of the living collections of the botanic gardens of the world explained by the population size of the town in which they are located is negligible (Fig. 4A and D), but the effect is highly significant when controlling for spatial autocorrelation. In many places, towns are now located in larger metropolitan areas, so that botanic gardens revenues and visitors are not confined to the local administrative area. However, town size is likely to be often correlated with the size of the larger metropolitan area.

Given that there is a positive garden area–town population size relationship, and given that larger gardens have more species/taxa (Table 1), higher population size of the town appears to be associated with the creation and maintenance of larger gardens (Fig. 5). Whether botanic garden area and budget are in turn positively correlated is an open question. In developed countries, such a correlation between garden budget and area may be the case, and this will allow the space and the human and financial resources for the collection of new species/taxa and for the reintroduction of those which have died. However, there are large botanic gardens in developing countries where only a fraction of the whole surface area is maintained because of lack of money. In this case, tropical botanic gardens can still provide an important conservation example if they manage to preserve the natural vegetation inside their boundaries in the face of encroaching urbanization.

A higher proportion of variance (at least in terms of species richness) is explained by country GDP per person (Fig. 4B, E). This is evidence for the importance of national financial resources in shaping the living collections of the botanic gardens of the world. The GDP of the country is of course a

limited predictor, as botanic gardens obtain resources also at local and regional levels. However, there is an overall association between the general affluence of a country and the plant diversity exhibited in its botanic gardens. This result is likely to be conservative as many gardens have been cumulatively created over the centuries, but it can be reasonably assumed that countries with currently high GDPs were also relatively rich in the past. The positive correlation between the species richness of botanic gardens and country GDP per person could result from the tendency of countries becoming more affluent to increase their demand for environmental services such as, in this case, botanical conservation (e.g. Dietz and Adger, 2003; McPherson and Nieswiadomy, 2005).

The mismatch between the latitudinal gradient in plant species richness in the natural environment and in botanic gardens (Pautasso and Parmentier, 2007) is likely to be a consequence of the lower GDP per person of countries at tropical latitudes (Miller and Diamond, 2006; Fisher and Christopher, 2007). Even if the pool of regional plant species from which tropical botanic gardens can collect species for their living collections tends to be larger, these gardens are generally fewer and dispose of fewer resources than their counterparts in the developed world (Holdgate, 1993; Crawley, 1997; Kuzevanov and Sizykh, 2006; Chen et al., 2009). Many botanic gardens are set to entertain and this is typically accomplished by creating plantings that differ from the local flora. However, as the GSPC states that 60% of threatened plant species should be preserved in *ex situ* collections, preferably in the country of origin (Sharrock and Jones, 2009), it is likely that there will be a shift of focus in the collection policies towards the conservation of local threatened species. It is also possible that developed countries may have a higher number of botanists and skilled gardeners, but as there is no reliable information on the number of botanists and trained gardeners in different countries, it is not possible to be confident about whether there really is a positive correlation of country GDP with number of botanists and gardeners.

The absence of a positive relationship between the species/taxa richness of botanic gardens and the number of plant species of the flora of the country in which they are located thus confirms that the richness of botanic gardens is more due to socio-economic than to ecological factors. This is also manifest from the results of the SEM, which led to rejecting the hypothesis that the richness of botanic gardens mirrors the richness of the country flora. Moreover, since there is a positive correlation between botanic garden area and species richness, the result that botanic gardens at lower latitudes tend to be species-poorer than those at higher latitudes is not affected by influence variations in area. In other words: one would expect botanic gardens in extra-tropical regions to be less able to host species as they tend to be smaller, but this does not happen to be the case, hence the importance of socio-economic variables.

Since botanic gardens are essential in the conservation of plant biodiversity, there is a need for an increase in their activity in hotspots of biodiversity in the tropics (Bramwell, 1995; Miller et al., 2004; Chen et al., 2009). This does not mean that the best allocation of conservation money is necessarily the creation of new botanic gardens in the tropics, if this is money that could have saved threatened plant species by

directly avoiding deforestation. Nonetheless, there is a manifest mismatch between the number of botanic gardens and their living collections in developed and developing countries. For example, according to BGCI, Brazil has only about 40 botanic gardens, which is three times fewer than the UK (whose flora in turn has about 30 times fewer species than Brazil has). Similarly, South Africa has only 20 botanic gardens compared with >100 gardens in Germany (whose flora has roughly 8 times fewer species than South Africa has). Botanic gardens in (sub)tropical countries could be much more cost-efficient than those located in cold and affluent regions: they do not need greenhouses to cultivate cold-intolerant species and labour in developing countries is much cheaper. However, botanic gardens in the (sub)tropics still need technical, scientific and financial support.

Botanic gardens are of course much more valuable than the number of species or taxa they harbour, given their educational, research and conservation activities (e.g. Ashton, 1988; Dosmann, 2006; Havens et al., 2006; Waylen, 2006). Worldwide, botanic gardens attract visitors from their surrounding regions and, for the largest and most famous gardens, from all over the world (e.g. Garrod et al., 1993; Kohlleppel et al., 2002; Lindemann-Matthies and Bose, 2007). Further study is needed to investigate patterns in rarity, endemism, threat, turnover, genetic, plant pathogen and phylogenetic diversity in the living collections of the world's botanic gardens. The relationships established between the species/taxa richness of a botanic garden and the town population size, country GDP per person and flora are general trends and should not be used to criticize the management of any botanic garden. Botanic gardens with relatively few species in comparison to other gardens are still much species-richer than their surroundings and pursue important recreational, educational and scientific goals.

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