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SYNTHESIS

Fighting their last stand? A global analysis of the distribution and conservation status of gymnosperms

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ABSTRACT

Aim Gymnosperms are often described as a marginal and threatened group, members of which tend to be out-competed by angiosperms and which therefore preferentially persist at higher latitudes and elevations. The aim of our synthesis was to test these statements by investigating the global latitudinal and elevational distribution of gymnosperms, as well as their conservation status, using all extant gymnosperm groups (cycads, gnetophytes, ginkgophytes and conifers).

Location Worldwide.

Methods We developed a database of 1014 species of gymnosperms containing latitudinal and elevational distribution data, as well as their global conservation status, as described in the literature. The 1014 species comprised 305 cycads, 101 gnetophytes, the only living representative of ginkgophytes, and 607 conifers. Generalized additive models, frequency histograms, kernel density estimations and distribution maps based on Takhtajan's floristic regions were used.

Results Although the diversity of gymnosperms decreases at equatorial latitudes, approximately 50% of the extant species occur primarily between the tropics. More than 43% of gymnosperms can occur at very low elevations (≤ 200 m a.s.l.). Gymnosperms, considering all species together as well as their main taxonomic groups separately, do not exhibit a latitudinal diversity gradient as commonly observed for many other taxa. Gymnosperms, and especially conifers, are on average less threatened at higher and equatorial latitudes.

Main conclusions Gymnosperms display an unusual latitudinal diversity gradient, which we suggest cannot fully be accounted for by angiosperm dominance and competitive superiority. We hypothesize that other factors explain their present distribution, such as the development of centres of endemism in several regions and the adaptation of certain taxa to cold and arid climates.

Keywords

Angiosperm domination, conifers, cycads, *Ginkgo*, global diversity patterns, elevational distribution, gnetophytes, latitudinal distribution, latitudinal diversity gradient.

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INTRODUCTION

The increase in angiosperm diversity during the Cretaceous period, between 145 and 65 Ma, resulted in the dominance of flowering plants observed today in the majority of ecosystems (Coiffard *et al.*, 2012). The sudden appearance and rapid spread of angiosperms, and therefore the replacement of gymnosperms, in the fossil record has attracted the attention of naturalists for centuries, including Charles Darwin (Darwin & Seward, 1903). The rapid radiation of flowering plants meant that gymnosperms were almost exterminated (Friedman, 2009; Coiffard *et al.*, 2012) and it is often reported in the literature that gymnosperms are today confined almost exclusively to high latitudes and high elevations and have been virtually eliminated from tropical regions (Bond, 1989; Enright & Hill, 1995; Coomes *et al.*, 2005; Farjon, 2008; Lusk, 2011). The superior reproductive strategies and rapid reproduction cycles, varied arrays of biochemical

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defences and high diversity of growth forms, as well as anatomical and physiological novelties, mean that angiosperms are much better competitors than gymnosperms (Bond, 1989; Enright & Hill, 1995; Williams, 2009; Lusk, 2011; Turner & Cernusak, 2011), particularly in habitats with a high frequency of disturbance regimes and in aquatic habitats (Kozlowski *et al.*, 2015). It is accepted that, in terms of diversity, gymnosperms have manifestly been outdistanced by angiosperms (Brodribb *et al.*, 2012). Further study of the marginality, low diversity (with only *c.* 1000 extant species) and assumed competitive inferiority of gymnosperms might, however, expand our understanding of the biogeographical and evolutionary processes of seed plants (Soltis & Soltis, 2004; Soltis *et al.*, 2005; Kozlowski *et al.*, 2015).

Information regarding spatial distribution and biodiversity is central to many fundamental questions in biogeography, macroecology and conservation biology (Mutke & Barthlott, 2005; Collen *et al.*, 2014). Nevertheless, biodiversity maps and analyses at continental to global scales are scarce (e.g. Kreft & Jetz, 2007; Jenkins *et al.*, 2013; Safi *et al.*, 2013; Collen *et al.*, 2014; Pimm *et al.*, 2014). Regarding gymnosperms, little synthetic work has been conducted at a global scale, so only broad conclusions about their patterns of diversity and vulnerability can be formulated (Rumeu *et al.*, 2014; Wang & Ran, 2014). One of the main reasons for this shortfall is that the geographical distributions of many gymnosperm taxonomic groups remain poorly documented (Kreft & Jetz, 2007). Recently, several comprehensive compilations of gymnosperms have been published (e.g. Jones, 2002; Eckenwalder, 2009; Farjon, 2010; Debreczy & Racz, 2011; Farjon & Filer, 2013; Earle, 2014), providing an extraordinary wealth of data for exploring various aspects of the biological, biogeographical and evolutionary processes and patterns of this ancient plant group.

We present a detailed global synthesis of all extant gymnosperm species that have been described in the literature, and their biogeographical and conservation status patterns. Specifically, we addressed the following questions. (1) What are the global latitudinal and elevational distribution patterns of all extant gymnosperm groups and species? (2) Are gymnosperms following the latitudinal diversity gradient (LDG) observed in the majority of groups of organisms? (3) What are the threat levels and conservation status for all extant gymnosperms? More generally, the results of this review should provide an important, new perspective on the long-standing discussion regarding the reasons for the hypothesized competitive superiority and dominance of angiosperms over gymnosperms.

MATERIALS AND METHODS

Study taxa: gymnosperms and their extant groups

Gymnosperms represent an ancient seed-plant group that originated approximately 300 Ma in the late Carboniferous (Kramer & Green, 1990; Bowe *et al.*, 2000). Recent analyses of molecular data show that all living gymnosperms are monophyletic (Bowe *et al.*, 2000; Chaw *et al.*, 2000; Ran *et al.*, 2010). They are significantly diverse and can be divided into four groups recognizable at divisional or subclass levels: conifers, cycads, ginkgophytes and gnetophytes.

Conifers are by far the largest gymnosperm group, with more than 600 extant species, and show a cosmopolitan distribution (Farjon, 2008, 2010; Eckenwalder, 2009; Debreczy & Racz, 2011). Conifers of the Northern Hemisphere comprise mainly cone-bearing, long-living trees and shrubs, typical of mountainous and boreal environments (Farjon, 2010). Tropical and southern conifers, in contrast, show a much larger morphological and ecological diversity (Enright & Hill, 1995; Farjon, 2008).

Cycads are characterized by a palm-like habit, with stout trunks and crowns formed by large, evergreen and pinnate leaves (Jones, 2002). Cycads are divided into three families and comprise almost 300 extant species. They occur across much of the tropical and subtropical regions (Hill *et al.*, 2014).

Ginkgophytes were represented by various families and genera during the Mesozoic (252–66 Ma). Only one species has survived, *Ginkgo biloba* L., which is now endemic to south-east China (Del Tredici *et al.*, 1992; Zhao *et al.*, 2010).

Gnetophytes consist of only three extant and, at first sight, very different genera, comprising approximately 100 species (Roskov *et al.*, 2013; Earle, 2014). *Gnetum* species are woody climbers (rarely trees) that occur in tropical forests. *Ephedra* species are small shrubs (rarely climbers) that grow preferentially on shores and sandy soils, mainly in the Northern Hemisphere, but some species also occur in South America. The third genus, *Welwitschia*, is endemic to the desert regions of Angola and Namibia (McCoy *et al.*, 2008; Earle, 2014).

Data collection

We developed a database that included 1014 extant gymnosperm species; we did not include hybrids, subspecies, varieties and aggregates. The species comprised 305 cycads, 101 gnetophytes, 607 conifers and the only extant Ginkgoales, *Ginkgo biloba* (see Appendix S1 in Supporting Information for the complete database and list of references). The database took advantage of open-access online resources (e.g. eFloras, 2008; IUCN, 2013; Roskov *et al.*, 2013; Earle, 2014; Hill *et al.*, 2014) and recently published monographs, as well as research on ecological and biogeographical aspects of all taxonomic groups of gymnosperms (e.g. Jones, 2002; Eckenwalder, 2009; Farjon, 2010; Debreczy & Racz, 2011; Farjon & Filer, 2013). For each species, we compiled data on its elevational and geographical distribution. Elevational data included the minimum and maximum elevation documented for each species and the mean elevation of a species within its elevational range. We assumed that species had continuous ranges between their recorded minimum and maximum elevations.

Takhtajan's floristic regions (Takhtajan, 1986), commonly used in biogeographical studies (e.g. Pärtel, 2002; Feuerer & Hawksworth, 2007; Meyer *et al.*, 2012), were used as the basic geographical units. Patterns of historical isolation and evolutionary divergence in the global distribution of vascular plants are represented in this system, which is preferable to using geopolitical boundaries (Fridley, 2008). We related each species to one single floristic region. All maps presented are in the Robinson projection (Robinson, 1974). The mean latitude for each species was estimated from published and unpublished data (Appendix S1). In cases where a distribution map was available, the latitude of the area centroid was estimated. Estimations were rounded to the nearest integer.

The International Union for Conservation of Nature's (IUCN) Red List conservation status was indexed for each species (Farjon & Filer, 2013; IUCN, 2013) using IUCN Red List version 2013.2 (http://www.iucnredlist.org). The IUCN uses a large number of criteria (e.g. population size, area of occupancy and known threats) to assign a status to each taxon using the following categories: least concern (LC), near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), data deficient (DD) and not evaluated (NE). Gymnosperms are well documented in comparison with other organisms, and the overwhelming majority are included in the most recent IUCN Red List (IUCN, 2013). Only a few species were evaluated in previous versions against old criteria and had not been re-evaluated, so they were categorized as NE or DD in this study [e.g. *Agathis australis* (D. Don) Steud.]. Species belonging to categories VU, EN and CR are referred to as threatened species.

Statistical analyses

Statistical analyses were performed in R (R Core Team, 2013). We used the kernel density estimation (KDE) method to add a smooth approximation curve on histograms of species richness plotted along the latitudinal gradient. KDE is a nonparametric technique for density estimation in which a known density function (i.e. the kernel) is averaged across the observed data points to create a smooth approximation (SAS Institute Inc., 2004). The kernel function was multiplied by the best constant value to fit the frequency histograms.

Data were modelled using generalized additive models (GAMs), implemented in the R package MGCV (Wood, 2006, 2011). The nonparametric GAMs are more suitable for exploring data and visualizing the relationship between dependent and independent variables than parametric linear models (SAS Institute Inc., 2004). In GAMs, the linear form $\Sigma\beta_j X_j$ of the covariates (independent variables) is replaced by a sum of smoothed functions $\Sigma s_j(X_j)$ with $s_j(\cdot)$ being unspecified functions that are estimated in an iterative procedure from a scatterplot smoother (Hastie & Tibshirani, 1986). All models were constructed from a single covariate (i.e. latitude) and we chose the identity function associated with the Gaussian family as the link function. Univariate penalized cubic regression spline smoothers were used. These have a cubic spline basis defined by a modest sized set of knots (the default of 10 knots was used) spread evenly through the covariate values. They are penalized by the conventional integrated square second derivative cubic spline penalty (Wood, 2006). All models were checked for normal distribution of residuals. To assess the significance of the models, we used approximate *P*-values implemented in the MGCV package (Wood, 2013); for the null hypotheses the smooth term was zero ($^{***}P < 0.001$; $^{**}P < 0.01$; $^{*}P < 0.05$).

The best estimate (IUCN, 2013) was used to calculate proportions of threatened species. This is the percentage of threatened extant species if DD and NE species are assumed to be subject to equivalent degrees of threat as data-sufficient species, i.e.:

$$\%\text{ of threatened species} = \frac{n_{\mathrm{VU}} + n_{\mathrm{EN}} + n_{\mathrm{CR}}}{n_{\mathrm{total}} - n_{\mathrm{DD}} - n_{\mathrm{NE}}}$$

where $n\ldots$ is the species richness in the corresponding IUCN category. For the statistical analysis, a continuous linear scale was used: 0, LC; 1, NT; 2, VU; 3, EN; 4, CR; 5, EW (Purvis *et al.*, 2000; Davies *et al.*, 2011). The mean threats were therefore calculated with:

$$\text{Mean threats} = \frac{0 \times n_{\mathrm{LC}} + 1 \times n_{\mathrm{NT}} + 2 \times n_{\mathrm{VU}} + 3 \times n_{\mathrm{EN}} + 4 \times n_{\mathrm{CR}} + 5 \times n_{\mathrm{EW}}}{n_{\mathrm{total}} - n_{\mathrm{DD}} - n_{\mathrm{NE}}} \cdot$$

RESULTS

Latitudinal distribution

Of the 1014 gymnosperms species, 342 (33.7%) are mostly distributed in the Southern Hemisphere and 672 (66.3%) mostly in the Northern Hemisphere. A total of 506 species (50%) are present between the tropics (i.e. between 23.5° N and 23.5° S). Two peaks in gymnosperm diversity can be observed around the tropics (Fig. 1a). Four floristic regions show very high species richness around the Tropic of Cancer (Fig. 1b): the Eastern Asiatic (156 species), Caribbean (115 species), Madrean (74 species) and Indochinese (61 species) regions. Around the Tropic of Capricorn, the north-east Australian region exhibits very high gymnosperm diversity, with 99 species. The Neocaledonian (43 species) and Usambara–Zululand (40 species) regions are smaller in size but also rich in species. At equatorial latitudes, the Malesian region is the most important, with 107 species. At temperate latitudes, the Rocky Mountain region shows the highest diversity of gymnosperms, with 43 species (all conifers). In fact, gymnosperms are found in virtually every floristic region, with the exception of several island regions such as St Helena and Ascension, the Hawaiian Islands and

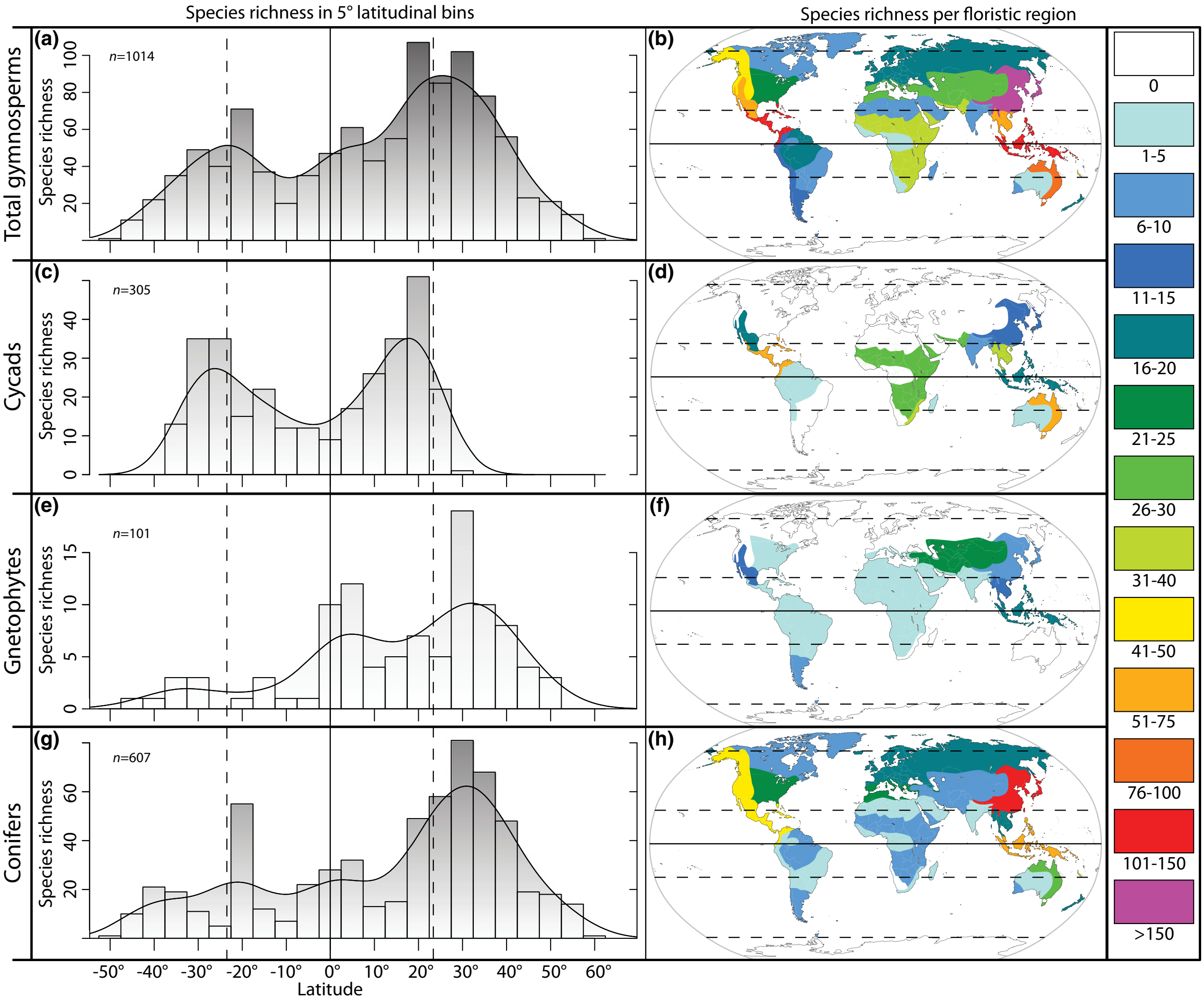

Figure 1 The global latitudinal distribution of gymnosperms. The left-hand panels show species richness along the latitudinal gradient. Histogram bars indicate the number of species with a mean latitude included within each 5° latitude bin. The smooth approximation above the histogram was calculated using the kernel density estimation method. The two vertical dashed lines represent the tropics circles, and the vertical solid line the equator. The right-hand panels show the global species richness per Takhtajan's floristic region (Takhtajan, 1986). The right colour scale indicates the number of species in each region: blue and dark-green indicate low species richness; light-green, yellow, red and pink indicate high species richness; white indicates regions without any species. (a, b) All gymnosperm species in the database (1014 species); (c, d), cycads (305 species); (e, f), gnetophytes (101 species), (g, h), conifers (607 species). *Ginkgo biloba* is not shown; its mean latitude is 30° N, in the eastern Asiatic region. The equator is represented by the solid horizontal line and the dashed horizontal lines indicate the tropics and polar circles.

Antarctica. The species richness of all floristic regions is shown in Appendix S2.

Cycads show a near symmetrical latitudinal distribution around the equator: species richness is relatively low at the equator but markedly higher around the tropics, with peaks at *c.* 27° S and 18° N latitude), and no species can be found at temperate latitudes (Fig. 1c). The Caribbean and north-east Australia represent the two most diverse floristic regions, with 68 Zamiaceae species (*Zamia*, *Ceratozamia* and *Dioon*) and 70 species (essentially *Macrozamia* and *Cycas*), respectively. The Usambara–Zululand and Indochinese regions are also particularly important, with 38 *Encephalartos* species and 31 *Cycas* species, respectively (Fig. 1d).

Gnetophytes show much larger species density in the Northern Hemisphere, with two peaks of diversity (Fig. 1e). The first diversity peak is visible at equatorial latitudes at *c.* 4° N. Gnetaceae are found mainly at these latitudes, with, for example, 16 *Gnetum* species in the Malesian floristic region (Fig. 1f). The second is located at roughly 33° N and is caused by the presence of Ephedraceae in subtropical and temperate regions. In particular, 21 species can be found in the Irano-Turanian region. Only eight gnetophytes

(Ephedraceae) are found south of the Tropic of Capricorn, mainly in the Chile–Patagonian region. *Welwitschia*, the only living genus of Welwitschiaceae (the third family of gnetophytes), is the only gymnosperm found in the Karoo–Namib region.

Conifers also have many more species in the Northern than the Southern Hemisphere and exhibit a strong peak in diversity between 20° and 40° N (Fig. 1g). The eastern Asiatic floristic region, the major conifer hotspot with six families and 137 species (Fig. 1h), falls within these latitudes. Western and central North America are also particularly rich in conifers, in particular the Rocky Mountain (43 species), Madrean (44 species) and Caribbean (46 species) regions. A small peak of diversity is observable at equatorial latitudes, reflective of the species richness found in the Malesian region (74 species, mainly Podocarpaceae). The peak observed at *c.* 22° S reflects the Neocaledonian region, which is yet another conifer hotspot (42 species). Conifers have a broader latitudinal distribution than the other gymnosperm groups, such that the mean latitude of certain species can reach 60° N and 48° S. Nevertheless, a large minority of 247 (40.7%) conifer species is still mainly found between the tropics.

Ginkgo biloba, the only living Ginkgoales, has a relictual distribution in the eastern Asiatic region at *c.* 30° N, where it occurs in the Zhejiang province (eFloras, 2008) and in the Dalou Mountains, between the Guizhou and Sichuan provinces in China (Tang *et al.*, 2012).

Elevational distribution

Elevational information was available for 1010 species. The mean elevation for all these gymnosperms was 1145 m a.s.l. Some species can reach very high elevations, such as *Ephedra gerardiana* Wall. ex Stapf (up to 5300 m) and *Juniperus indica* Bertol. (up to 5050 m). GAMs (Fig. 2a) showed significant elevational trends along a latitudinal gradient. In the Southern Hemisphere, gymnosperms occur more often at elevations below 1000 m. At equatorial latitudes, we saw a peak in mean elevation of species occurrence at around 1500 m. At *c.* 30° latitude, another peak indicated that gymnosperms generally occur between 1000 m and 2300 m in the subtropics of the Northern Hemisphere. They are found on average at *c.* 1400 m in the northern temperate latitudes, but within a large elevational range. Gymnosperm mean elevation is significantly higher in the Northern Hemisphere than in the Southern Hemisphere (Wilcoxon rank sum test, $P < 0.001$). Furthermore, 437 species (43.3%) can occur at very low elevations (minimal elevation ≤ 200 m); the minimal elevation is ≤ 1000 m for 777 species (76.9%). A total of 678 species (67.1%) are found only below 2000 m (maximal elevation ≤ 2000 m) and 57 species (5.6%) only above 2000 m (minimal elevation > 2000 m) (Fig. 2b).

Cycads occur at relatively low elevations, with a mean elevation of 565 m. The minimum occurred at *c.* 13° S latitude (Fig. 2c). Only four species grow above 2000 m (Fig. 2d). The mean elevation of occurrence of gnetophytes is 1324 m. Overall, many *Gnetum* species occur at lower elevations between the tropics, and many *Ephedra* species occur at higher elevations in subtropical or temperate latitudes. Both GAMs (Fig. 2e) and bar plots (Fig. 2f) showed this pattern. The gnetophyte mean elevation is significantly lower between the tropics (Wilcoxon rank sum test, $P < 0.001$).

Conifers occur at a mean elevation of 1407 m. They are found principally between sea level and 1000 m a.s.l. below 20° S latitude; otherwise, they occur at higher elevations, on average at *c.* 1600 m at equatorial latitudes and at *c.* 1900 m around the Tropic of Cancer (Fig. 2g). Frequencies of minimum, maximum and mean conifer elevations roughly follow a Poisson distribution (Fig. 2h). A total of 290 conifer species (47.8%) have maximum elevations that are > 2000 m, but only 49 (8.1%) are found exclusively above 2000 m, i.e. have a minimum elevation > 2000 m. Finally, *Ginkgo* occurs in the wild between *c.* 300 and 1100 m.

Conservation status

Of the 1014 species, only 19 were evaluated as DD and seven as NE by the IUCN. The number of species per IUCN category is summarized for each gymnosperm group in Table 1 and for each floristic region in Appendix S2.

Globally, 40.3% of all extant gymnosperms are threatened (398 species). The GAM 'm'-shaped curve (Fig. 3a) shows an obvious tendency for gymnosperms to be on average less threatened at equatorial latitudes (between *c.* 15° S and 5° N) than around the tropics. The mean threat decreases again at higher latitudes, with only 10 species (all conifers) classed as threatened at latitudes exceeding 40° S and 40° N. Gymnosperms of the Uzambara–Zululand floristic region are on average the most threatened (Fig. 3b). The mean threat is also very high in some island floristic regions (Polynesian, Madagascan, Neocaledonian and Macronesian regions), in the Caribbean region and in the Indian region. Regarding the absolute number of threatened species, the Caribbean region has the maximum number of threatened species (78 species), followed by the eastern Asiatic (60 species), Malesian (37 species) and north-east Australian (36 species) regions.

Cycads are by far the most endangered group, with 63.2% threatened species. Apart from an area at *c.* 12° S, where the threat level is relatively low, cycads generally have high threat levels throughout their area of distribution (Fig. 3c). Except for the Madagascan and south-west and central Australian regions, the situation is very serious in all other floristic regions (Fig. 3d).

In contrast, only 4.6% of the gnetophytes are considered threatened. A slight peak was visible between the tropics (Fig. 3e) because several NT, VU and one EN *Gnetum* species occur in the Malesian, Indian and Guineo-Congolian regions (Fig. 3f). However, our knowledge of gnetophytes is still incomplete, with 13.9% of the species categorized as DD or NE.

The mean threat level of conifers is greater close to the tropics, with a maximum at *c.* 23° S and 18° N (Fig. 3g).

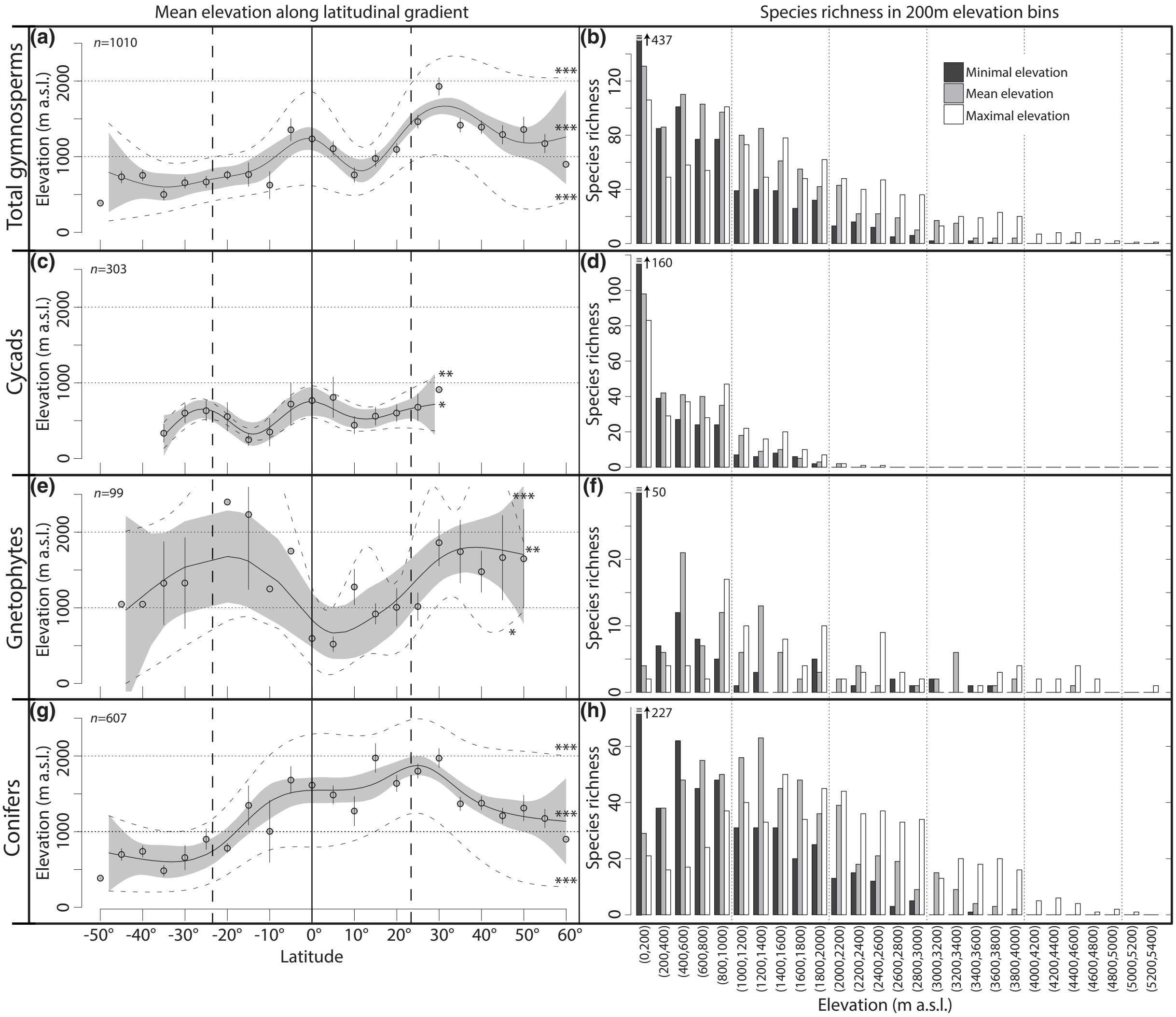

Figure 2 The global elevational distribution of gymnosperms. The left-hand panels show generalized additive models (GAMs) of species elevation as a function of the mean latitude. Three GAMs are displayed on each plot. Species mean elevation data were used to calculate the middle GAM. The solid curve represents GAM fits and shading represents 95% confidence intervals. Mean species elevation and standard error in 5° latitude bins are represented by circles and error bars. To calculate upper and lower GAMs (dashed curves), the maximum and minimum elevations, respectively, of species occurrence were used. The approximate significance of the smoothing term is indicated by asterisks (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$). The two vertical dashed lines show the tropics and the vertical solid line the equator. On the right-hand panels, grey bars indicate the number of species for which the mean elevation is in the corresponding 200-m elevation interval. Species minimum elevation frequency is shown by the black bars and species maximum elevation frequency by the white bars. (a, b) All gymnosperm species with available elevation data (1010 species); (c, d), cycads (303 species); (e, f), gnetophytes (99 species), (g, h), conifers (607 species). *Ginkgo* is not shown; it occurs from 300 m to 1100 m.

The mean threat is very high in the Indian and Saharo-Arabian regions, because one single EN species occurs in each of these regions (Fig. 3h). Thus, conifers could become extinct in these two floristic regions in the near future. Furthermore, the mean threat of conifers is high in island floristic regions. Finally, *Ginkgo* is evaluated as EN.

Correlation between conservation status and elevation

A significant negative correlation was seen between the gymnosperm mean elevation (for all taxonomic groups taken together) and the threat level (Spearman's correlation $r_s = -0.15$, $P < 0.001$), indicating that gymnosperm species living at higher elevations are on average less threatened. Cycads, which occur at low elevations and are highly threatened, have obviously driven this correlation.

When calculated for specific gymnosperm groups separately, the correlation between conservation status and elevation shows large differences. It is not significant when only conifers are considered ($r_s = -0.04$, $P = 0.34$), but correlations become positive and highly significant for cycads ($r_s = 0.25$, $P < 0.001$) and negative and highly significant for gnetophytes ($r_s = -0.39$, $P < 0.001$).

Table 1 The IUCN Red List conservation status of gymnosperms. The number of species is given, with the percentage within each group indicated in parentheses. Best estimates of the percentage threatened species are used (IUCN, 2013).

Category	LC	NT	VU	EN	CR	EW	DD	NE	Threatened
Gymnosperms	420 (41.4)	167 (16.5)	158 (15.6)	161 (15.9)	79 (7.8)	3 (0.3)	19 (1.9)	7 (0.7)	398 (40.3)
Cycads	45 (14.8)	63 (20.7)	76 (24.9)	63 (20.7)	52 (17)	3 (1)	3 (1)	–	191 (63.2)
Ginkgo	–	–	–	1 (100)	–	–	–	–	1 (100)
Gnetophytes	76 (75.2)	7 (6.9)	3 (3)	1 (1)	–	–	10 (9.9)	4 (4)	4 (4.6)
Conifers	299 (49.3)	97 (16)	79 (13)	96 (15.8)	27 (4.4)	–	6 (1)	3 (0.5)	202 (33.8)

IUCN categories: LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; EW, extinct in the wild; DD, data deficient; NE, not evaluated. Threatened refers to species classified as VU, EN and CR.

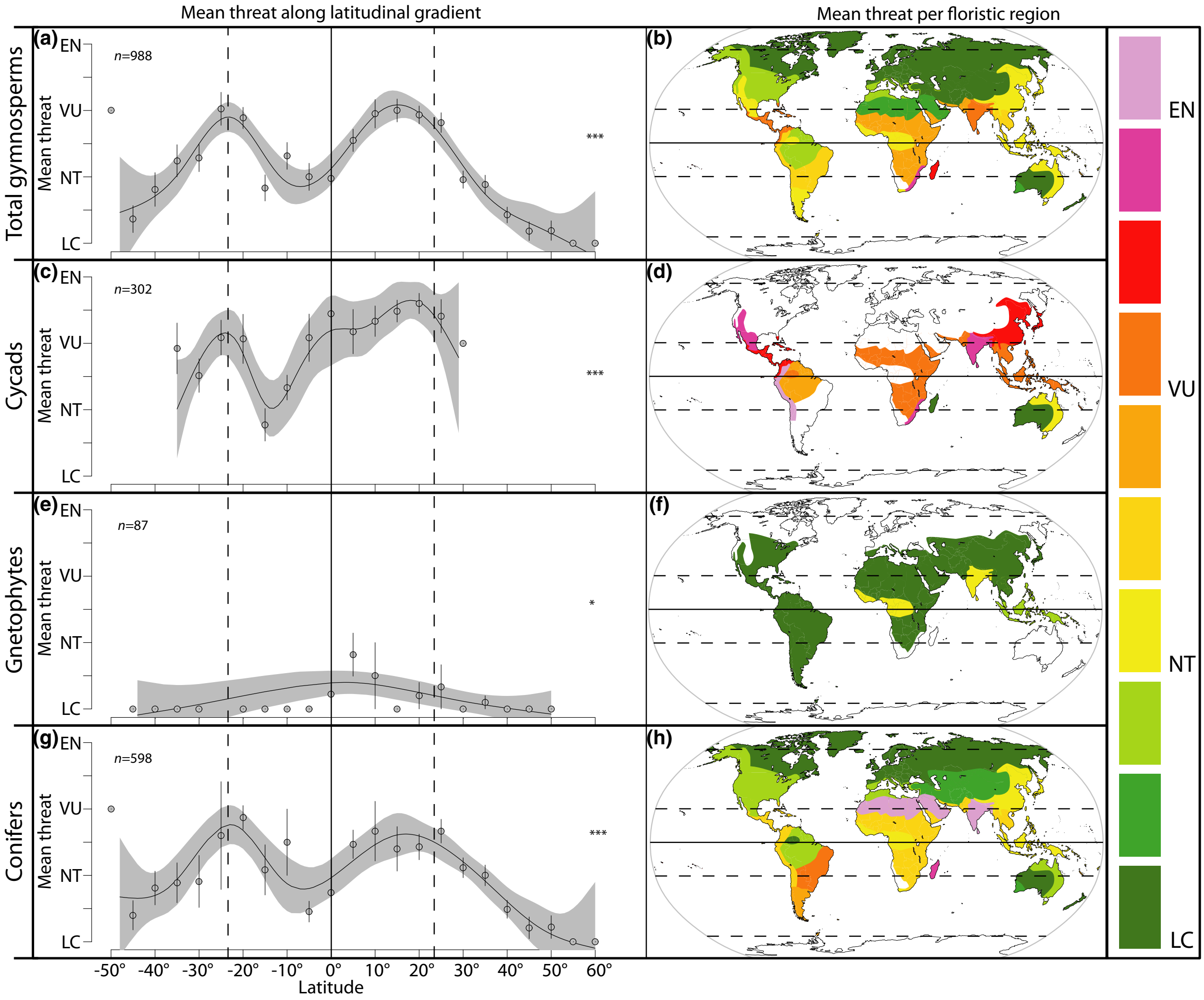

Figure 3 Global threat status of gymnosperms. The left-hand panels show the generalized additive model (GAM) of species threat as a function of mean latitude. The solid curve represents GAM fits and shading represents 95% confidence intervals. Mean threat and standard error in 5° latitude bins are represented by circles and error bars. The approximate significance of the smoothing term is indicated by asterisks (***$P < 0.001$; *$P < 0.05$). LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered (IUCN, 2013). The two vertical dashed lines show the tropics and the vertical solid line the equator. The right-hand panels show the mean threat per Takhtajan's floristic region (Takhtajan, 1986). The colour scale indicates the mean threat for each floristic region, from dark-green (LC) to violet (EN). White indicates no data. (a, b) All gymnosperm species assessed in the IUCN Red List (988 species); (c, d), cycads (302 species); (e, f), gnetophytes (87 species), (g, h), conifers (598 species). *Ginkgo* is not shown; it is classified as EN. The equator is represented by the solid horizontal line and the dashed horizontal lines indicate the tropics and polar circles.

DISCUSSION

In this synthesis we investigated the latitudinal and elevational distribution along with the conservation status of gymnosperms, using our own newly constructed database containing all extant gymnosperm groups (cycads, gnetophytes, ginkgophytes and conifers). We have demonstrated that half of all gymnosperms are found principally between the tropics, despite the fact that their species richness gradually decreases at equatorial latitudes. In the case of the cycads, the vast majority of species grow between the tropics (69.8%), while considerable minorities of gnetophytes (45.5%) and conifers (40.7%) are also found at these latitudes. The survey also shows that the remaining species are found largely at subtropical latitudes. Moreover, we have demonstrated that Gnetaceae and Podocarpaceae have peaks in diversity at equatorial latitudes (Appendix S1) and confirmed that several conifer families are able to compete with angiosperms (Cernusak *et al.*, 2011; Coomes & Bellingham, 2011; Brodribb *et al.*, 2012). Thus, even if the rapid radiation and competitive ability of angiosperms induced a large decline in gymnosperms (Bond, 1989; Lusk, 2011), it can no longer be accepted that gymnosperms would consequently have been eliminated from lower latitudes. Furthermore, our study demonstrates that the mean threat status of gymnosperms decreases at equatorial latitudes, a pattern that would not be possible if angiosperm domination was predominant under equatorial climates (Fig. 3g). We acknowledge that as the base map used is not equal area, the description of geographical gradients of diversity is in part confounded by variation in sample area across the different floristic regions.

There are four main elevational richness patterns described in the literature: a decreasing, low-elevation plateau, a low-elevation plateau with a mid-peak, and mid-elevation peak patterns (Lomolino, 2001; McCain & Grytnes, 2010). With respect to the mean elevation bar plots (Fig. 2b,d,f,h), gymnosperms show a low-elevation plateau pattern, cycads a decreasing pattern, and conifers and gnetophytes a low-elevation plateau with a mid-peak pattern. All groups have standard elevational gradient patterns and do not exhibit peaks at higher elevations or gaps at lower elevations. Moreover, 43.3% of all extant gymnosperms species are growing at elevations below 200 m under current climatic conditions. Only gnetophytes show a small peak at higher elevations, because of the relatively large number of *Ephedra* species that are particularly well adapted to extreme elevations as a result of the near-vessellessness of their wood (Carlquist, 1988; Motomura *et al.*, 2007).

The elevational distribution of all gymnosperm species is largely driven by conifers, but cycads reduce the mean around the tropical region. The low cycad richness at equatorial latitudes is, in contrast, responsible for the elevational peak in gymnosperms. The reduced numbers of gnetophytes and *Gingko* species do not have much influence on the mean elevational distribution of gymnosperms in general.

Conifers are found at relatively high elevations at latitudes from 10° S to 60° N, where they largely exceed the mean Earth elevation (Fig. 2g). It thus seems that the adaptation of certain species to cold environments and their competition with angiosperms could be possible explanations for their distribution. We consider that our findings are incompatible with the hypothesis that the distribution of gymnosperms is largely a by-product of the presumed general competitive superiority of angiosperms (Friedman, 2009; Coiffard *et al.*, 2012). A total of 102 tropical conifers were found at elevations < 500 m and no correlation existed for the assumption that conifers at higher elevations are less threatened.

In contrast to conifers, cycads appear to be particularly poorly adapted to higher elevations. They are found mainly below 1000 m and are significantly less threatened at lower elevations, for example at *c.* 12° S (Figs 2c & 3c). The reasons for these findings remain unclear and further studies are called for. Among the gnetophytes, the distribution patterns can be explained by the existence of three very different families: the Gnetaceae, species of which generally occur at lower elevations between the tropics and are rarely threatened; the Ephedraceae, species of which generally occur at higher elevations at temperate latitudes and are not threatened; and the Welwitschiaceae, comprising one species that grows at lower elevations, with a very restricted distribution area in southern Africa. *Welwitschia mirabilis* Hook. f., the only extant member of the Welwitschiaceae, shows a set of remarkable physiological, anatomical and ecological adaptations for surviving in the arid fog-desert of the Namib. It collects droplets of dew and absorbs them through the stomata, the fog water run-off is taken up with shallow hair roots below the leaves, and ground water is tapped with deep roots (Henschel & Seely, 2000). Additionally, *W. mirabilis* exhibits crassulacean acid metabolism (CAM) and its anticlinal and inner periclinal cell walls are thickened, minimizing cuticular transpiration (von Willert *et al.*, 1982, 2005). The plant forms two broad and long strap-shaped leaves, creating a microhabitat, microclimate cooling. Furthermore, the upper surfaces of these leaves have high solar reflectivity, preventing overheating (Gibson, 1996; Henschel & Seely, 2000).

Our results show that gymnosperms from the Northern Hemisphere grow at higher latitudes than gymnopserms of the Southern Hemisphere. However, the reason for this distribution pattern and species diversity might simply reflect the fact that very little land surface is available at temperate latitudes exceeding 56° S. Available land area could therefore be an important factor in understanding the high gymnosperm richness in the Northern Hemisphere (Leslie *et al.*, 2012), consistent with well-known general relationships between species number and area (e.g. Connor & McCoy, 1979; Rybicki & Hanski, 2013; Gerstner *et al.*, 2014). In this context we note the existence of a highly significant correlation between the number of gymnosperm species and the land area in a 1° latitudinal bin between the polar circles (see Appendix S3).

One of the most famous large-scale patterns in biological diversity is the dramatic increase in the number of species from the poles to the equator, a trend that has been called the latitudinal diversity gradient (LDG; Rohde, 1992; Hillebrand, 2004; Jablonski *et al.*, 2006; Wright *et al.*, 2006; Mittelbach *et al.*, 2007). Species richness does indeed increase gradually from the poles to the equator for the great majority of taxonomic groups, with exceptions being limited primarily to small taxonomic scales (Sax, 2001). In the present analyses, based on a map of Takhtajan's floristic regions, we show that neither gymnosperms considered globally, nor cycads, gnetophytes and conifers analysed separately, follow this classical latitudinal diversity gradient. In fact, gymnosperm diversity increases from *c.* 50° to 20° S and from *c.* 60° to 20° N, and decreases at equatorial latitudes (Fig. 1a). While this pattern is not based on an equal-area system of sample areas and thus is confounded to a degree by variation in area, we regard it as a reasonable first approximation of the underlying pattern. Multiple mechanisms are probably driving this atypical latitudinal gradient. Only a few other higher taxonomic groups show a similar distributional pattern, including grasses (Poaceae, angiosperms), where certain lineages, historical biogeography and topographical heterogeneity all seem to play a role in their adaptation to cold and arid environments (Visser *et al.*, 2014).

The same elements might be determinants for gymnosperms. A number of conifers and many gnetophytes are well adapted to the cold, and many xerophytes can be found within the three main gymnosperm groups (Kramer & Green, 1990; Bigras & Colombo, 2000; Jones, 2002). The explanation could be found in their wood and stem anatomy (Ewers, 1985; Sperry, 2003). As the transport properties of conifer tracheids are superior to those of angiosperm vessels in water- and nutrient-limited habitats and under freezing stress (Sperry *et al.*, 2006; Stoffel & Hitz, 2008), conifers have largely colonized arid, boreal and mountain ecosystems of the Northern Hemisphere (Farjon, 2010; Kozlowski *et al.*, 2015).

The historical biogeography of gymnosperms has presumably also favoured the development of many centres of endemism. Such hotspots include, among others, the north-east Australian and Usambara–Zululand regions for the cycads, and the eastern Asiatic and Neocaledonian regions for the conifers. Topographical heterogeneity appears to be particularly important between *c.* 28° and 45° N, with the presence of the Himalayan Mountains, which offer various niches for specialized conifer and *Ephedra* species.

These elements together could have led to this particular latitudinal diversity gradient. However, the theory of angiosperm competitive superiority (Bond, 1989; Coomes *et al.*, 2005) does provide another explanation for the reduced number of gymnosperms at equatorial latitudes.

From a global perspective, nearly 58% of all extant gymnosperm species are not threatened (IUCN categories LC and NT; Table 1). At the same time, however, our results show that certain taxonomic groups, such as the cycads, represent some of the most endangered groups of organisms. In addition, and with respect to geography, the Usambara–Zululand, Caribbean and entire south-east Asian regions should be of primary importance for conservation action. Our study also highlights the fact that a large number of threatened gymnosperms occur on oceanic islands (e.g. Malesian, Neocaledonian, Macronesian, Madagascan and Polynesian regions), including a high proportion of endemic species, which is in agreement with Rumeu *et al.* (2014). Notably, the only obligate aquatic gymnosperm, *Retrophyllum minus* (Carrière) C.N. Page, possesses no more than four localized natural populations on New Caledonia (Kozlowski *et al.*, 2015). These hotspots of biodiversity and species richness should be given priority in future conservation efforts.

CONCLUSIONS

The results of our global survey demonstrate that exactly 50% (506 species) of all extant gymnosperms occur in the tropics. Even among conifers, often showcased as an example of a non-tropical plant group, more than 40% (247 species) of all species currently grow between the tropics. In addition, we demonstrate that gymnosperms are present in each and every biogeographical region (with the exception of several small and isolated oceanic islands and Antarctica). Furthermore, our results put the putative elimination of gymnosperms from lower elevations into perspective, as more than 43% (437 species) of all extant species occur at sea level (0–200 m a.s.l.). Only 5.6% (57 species) of all gymnosperms (mainly conifers, 49 species) are typically inhabitants of higher elevations (above 2000 m a.s.l.).

Despite the fact that several gymnosperm species and taxonomic groups (especially cycads) are at the brink of extinction, approximately 60% of all extant species are not currently threatened. Our study highlights the fact that the mean threat of gymnosperms decreases at equatorial latitudes. Gymnosperms are thus not fighting their last stand and will probably continue to play an important role in future ecosystems on all continents and in all biogeographical regions.

Although gymnosperms show an atypical latitudinal diversity gradient, we conclude that the competitive superiority of angiosperms cannot fully explain the observed global latitudinal and elevational distribution patterns of extant gymnosperms. We hypothesize that other aspects could be equally important, such as (1) the presence of regions with great evolutionary radiation, leading, for example, to high endemic species richness, (2) the species–area relationship, and (3) the adaptations to cold and arid climates of certain taxa, providing them with the potential to occur at higher elevations and latitudes and in water-poor regions. Some of these adaptations have possibly been favoured by the expansion of angiosperms in certain families or genera. Generalizations for all gymnosperms are, however, problematic and further studies are clearly needed to clarify the situation and identify the drivers of adaptations at lower taxonomic scales.

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SUPPORTING INFORMATION

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

Appendix S1 Details of the 1014 study species and the full list of references from the gymnosperm database.

Appendix S2 A summary of gymnosperm IUCN Red List status and species richness by floristic region.

Appendix S3 Details of gymnosperm species richness versus land area.

BIOSKETCH

This research group was formed through collaboration between the Natural History Museum and the Botanical Garden of the University of Fribourg (Switzerland). The five authors are biologists, dendrochronologists and/or biogeographers, mainly interested in the conservation biogeography and conservation biology of woody, relict and endemic plant taxa.

Author contributions: G.K. developed the research ideas; S.B., L.C. and Y.F. collected the data; Y.F. and G.K. analysed the data; and Y.F., M.S. and G.K. led the writing of the manuscript.

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