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Environmental and historical determinants of fern richness across spatial grains

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Abstract

Aim

To disentangle the hierarchy of historical and environmental factors determining fern richness at regional and plot scale.

Location

Global.

Time Period

Present.

Major Taxa studied

Ferns and lycophytes (together called "ferns").

Methods

We collated a global dataset of nearly 83,000 vegetation plots of similar area size ($300-500m^2$) in which all fern species were counted. For the regional grain size, we constructed a global fern richness model based on environment-richness relationships obtained from 1243 regional floras in combination with climatic, topographical, and biogeographical predictors. Environmental and historical/biogeographical determinants of species richness per plot were assessed at two spatial resolutions: regional grain size (7666 km^2) and local grain size (4 km^2). We used structural equation modelling to identify the direct and indirect effects of these factors on fern species richness per plot worldwide.

Results

Plot fern richness showed a hump-shaped relationship with regional richness. The comparison of different structural equation models revealed that botanical realm as a summary variable for historical processes was an important direct predictor of regional richness, but not of plot richness. Models allowing a link between regional (large grain size) environment and plot richness performed better than models without this link.

Main Conclusions

Plot fern richness increases with regional richness until a saturation point is reached, after which plot richness decreases despite increasing regional richness, possibly reflecting species interactions. Historical determinants do not affect plot fern richness directly but indirectly through the mediating effect of regional richness being strongly determined by biogeographical processes. Regional environment is an important determinant of plot richness, and cannot be replaced by including regional richness.

Introduction

One of the most fundamental questions in plant ecology and biogeography asks which processes determine species richness patterns at different spatial scales (i.e. extents and resolutions/grain sizes). Regional and local species richness are interlinked through a hierarchy of historical, environmental and biotic processes but their relative influences on both regional and local richness remain unknown (Cornell & Lawton, 1992). Even though the importance of scale in ecological analyses has been commonly acknowledged since the 1950s (e.g. Hutchinson, 1953; Whittaker, 1977; Ricklefs, 1987; Levin, 1992; Rahbek, 2005; Chase et al., 2019), detailed global analyses of the processes influencing biodiversity patterns at different spatial scales have long been hindered by lack of data and appropriate statistical methods (Beck et al., 2012). Today, advanced statistical methods (e.g. Keil & Chase, 2018) and comprehensive datasets (e.g. Bruelheide et al., 2018) at different spatial scales have become available, allowing the study of macroecological patterns across scales for many organism groups;.

Ferns and lycophytes (hereafter together referred to as "ferns") have a global distribution, and with around 10,500 and 1350 currently accepted species, respectively (PPG1, 2016), make up the second and third largest vascular plant lineages on Earth after angiosperms (Smith, 1972). With an estimated age of about 400 Myr, ferns are an exceptionally old group of vascular plants that - together with gymnosperms - dominated terrestrial vegetation before the rise of the angiosperms (Niklas, Tiffney & Knoll, 1983). Large portions of their extant diversity, however, are of recent origin and their diversification happened "in the shadow of angiosperms" (Schneider et al., 2004), commonly as understorey or epiphytic species in the newly developing angiosperm forests (Schuettpelz & Pryer, 2009).

Over the last three decades, several studies have focussed on the spatial distribution of fern diversity at different spatial resolutions and extents: At a global extent, Kreft, Jetz, Mutke & Barthlott (2010) found regional fern species richness (i.e. the number of species occurring in regions with an extent of hundreds to thousands of square kilometres) to be strongly and positively related to water-energy variables such as potential evapotranspiration and precipitation. They also found a strong positive relationship with geographical habitat heterogeneity, whereas the total surface area of the focal region only had moderate effects. Together, their results confirmed a strong latitudinal gradient in fern species richness, which peaked in tropical regions, especially in tropical mountains. Beyond effects of contemporary environment, significant differences between biogeographical realms (e.g. tropical Africa being less diverse than other tropical regions), pointed to a strong role of biogeographical and

133 historical processes. This pattern is also known from other plant groups, such as palms
134 (Couvreur & Baker, 2013) or vascular plants in general (Kreft & Jetz, 2007).

135 Also for small grain sizes of typically a few hundred square metres, numerous studies have
136 shown that fern diversity typically peaks in tropical regions and that especially the mid-
137 elevations along elevational gradients are particularly species-rich (e.g. Salazar et al., 2015;
138 Kessler, Kluge, Hemp & Ohlemüller, 2011, and references therein). For instance, in a
139 comparison of 20 elevational gradients on different continents, Kessler et al. (2011) found that
140 the fern species richness correlated most strongly with climatic variables, mainly heat-related
141 water deficiency at low elevations and predictors related to low temperatures that limit diversity
142 at high elevations. The authors compare the elevational gradient to the latitudinal gradient in
143 that temperatures decline towards higher elevations/latitudes. They also noted differences in
144 local species richness among continents. Going one step further, Karger et al. (2011) compared
145 five elevational transects within the tropics and found that after the effect of area of the
146 representative elevational belt was accounted for, local and regional richness patterns were
147 almost identical, suggesting that they are either driven by the same factors or that local richness
148 equals a certain subset of regional richness and is directly driven by the size of the regional
149 species pool. In contrast to these results, Karger et al. (2014) found that on islands of different
150 sizes in the Indo-Malayan archipelago, local species richness was driven by local environmental
151 conditions and not by differences in regional (island-wide) species richness, suggesting that the
152 two are independent. However, Tuomisto, Zuquim & Cárdenas (2014) found that local fern
153 species richness in Amazonian rain forests increased with soil nutrient concentration, and that
154 this was paralleled by an increase in the total number of species (substrate-specific species pool
155 size).

156   In a broader context, it has been argued that the environment can strongly limit the
157 number of locally co-occurring species numbers, thus leading to local saturation in that
158 increases of regional species richness will not be reflected at the local scale (Srivastava, 1999;
159 Olivares, Karger & Kessler 2018). Nevertheless, the cross-scale relationships between regional
160 and local fern richness and their drivers remain puzzling. As mentioned above, environmental
161 predictors at different resolutions have been discussed as underlying causes, but whether factors
162 at larger grain size only act on regional richness or also on local/plot richness remains widely
163 untested. Similarly, it has been shown that historical factors are correlated with both regional
164 and local species richness. But it is unclear whether these factors, which typically act at large
165 spatial extents and over long time periods, do not only influence regional richness but may also
166 have more local effects. To understand the causal relationships, we analysed the hierarchical

structure of environmental and biogeographical determinants of fern species richness at two resolutions, "regional" (at a large grain size of 7666 km^2) and "local" (i.e. at a fine grain size resolution of 4 km^2) on regional (7666 km^2) and plot fern richness (300-500 m^2). We combined a large dataset of almost 83,000 vegetation plots with a model of regional fern richness, which fills in gaps of unknown regional species richness in some areas, and makes regional richness comparable independently of age and completeness of the input species lists. Using structural equation modelling, we tried to answer the following main questions:

Q1: How do plot and regional fern richness relate to each other on a global scale? Can we observe saturation?

Q2: Do historical factors, summarised in biogeographical/botanical realms, act on regional and plot fern richness or is only regional richness impacted, which in turn shapes plot richness?

Q3: Do regional environmental conditions (at large grain size) impact regional and plot fern richness or only regional, which in turn impacts plot richness?

Material and methods

Regional fern richness data

In order to bridge differences in completeness, age, and overall availability between regional species lists of protected areas, regions, states or countries, we built a model of regional fern species richness. For this, we extracted species presence information on 1243 geographic entities from the Global Inventory of Floras and Traits database (GIFT; Weigelt, König & Kreft, 2019). All originally available entities were filtered for those mentioning fern species numbers, including true absences. Entities with less than five occurring fern species were double checked to be certain that false underrepresentation is avoided. When an entity overlapped with another one by more than 10%, the larger one was excluded from analyses. Environmental predictor variables were extracted from 30-arc second resolution environmental raster layers and summarised across the extent of each geographic entity (as mean, median, 75% quantile or 95% quantile; the best fitting summary was chosen for each predictor). Botanical continent (continental scheme level 1 of the Taxonomic Database Working Group (Brummitt, 2001) was additionally included as a substitute variable of not directly measurable historical influences, which might influence vegetation patterns differently across biogeographical realms until today. Global coverage ranged from a minimum of 30 entities in the Antartic realm to a maximum of 315 in South America. In order to assess regional diversity independently from

199 the covered geographical extent of the regional entity, we used generalised linear models
200 (GLMs, with Poisson distribution) to ascertain environment–richness relationships and project
201 regional fern richness on a hexagon equal area grid with a grid cell size of 7666 km^2 (Barnes,
202 2017). Based on what is known about determinants of global fern richness (Kreft et al., 2010),
203 we tested environmental predictors (Supp. Table 1) variables from for the models and the best
204 performing ones were included in the final model.

205 **Plot richness data**

206 To analyse plot fern richness, we collated a global dataset of almost 83,000 vegetation
207 plots ranging in size between 300 m^2 and 500 m^2 from the sPlot consortium (Bruelheide et al.,
208 2018), species lists from ground vegetation surveys carried out on Level II plots of the Europe-
209 wide forest monitoring programme ICP Forests (http://www.icp-forests.net, Ferretti & Fischer,
210 2013; Canullo, Starlinger, Granke, Fischer & Aamlid, 2016), and published and unpublished
211 data from fern inventories carried out by a research network on fern diversity (e.g. Kessler et
212 al., 2011; Karger et al., 2014; Zuquim et al., 2014; Tuomisto et al., 2014; Hernández-Rojas et
213 al., 2018; see Figure 1 for plot distribution and Supp. Table 2 for full plot list). For the sPlot
214 data (sPlot version 1.2, 20th April 2018), the following filters applied: at least one fern species
215 occurring, explicit geographical coordinates with a location uncertainty below 5,000 m and an
216 area size between 300 m^2 and 500 m^2. ICP Forest data included Level II ground vegetation data
217 between the years 1994 and 2012, accessed in October 2016. Plots that were sampled repeatedly
218 throughout this time frame were kept, but never selected within the same run of the statistical
219 analyses (see details below). For the Amazon plots that originally only included terrestrials and
220 hemi-epiphytes up to 2 m height, species numbers were increased by 10% and rounded to the
221 next full number in agreement with the responsible specialists. Although the data were collected
222 in the scope of many different projects, they all included complete species inventories of fern
223 and lycophyte species. Some of them applied thresholds to juvenile species, but as we are
224 dealing with species presence numbers instead of abundance, we consider these differences to
225 be negligible in comparison to the differences caused by environmental conditions.
226 Environmental data for each plot were extracted on a 2x2 km^2 scale due to potential GPS
227 inaccuracies. Additionally, we extracted the number of predicted regional fern species from the
228 regional model for the polygon in which each plot was located. Soil properties were not
229 included due to the small-scale variation in soils in many regions of the Earth and the fact that
230 soil samples from the plots were only available for a very small number of plots.

231 **INSERT TABLE 1 AND FIGURE 1 AROUND HERE.**

232

Statistical analyses

234   All spatial and statistical analyses were carried out in the programming environment R
235   (version 3.5.1, R Core Team 2016). To analyse the hierarchical relationships between regional
236   (coarse grain size: 7666 km^2) and local (fine grain size: 4 km^2) environment as well as fern
237   richness at regional and plot scale, we used structural equation modelling (SEM; Shipley, 2002)
238   of GLMs as implemented in the R-package "piecewiseSEM" (Lefcheck, 2016).

239   We constructed multiple competing models to test the direction of environmental
240   influences, allowing for coarse-grain size environment to only impact regional richness which
241   in turn impacts plot richness (Figure 2A), or allowing coarse-grain size environment to
242   additionally impact plot richness (Figure 2B).

243   **INSERT FIGURE 2 AROUND HERE.**

244   We did not link coarse-grain size and fine-grain size environment because we assume
245   that they are being driven by the same external forces and are not causally connected. Fine-
246   grain size environment was tested as predictor of regional richness in model 6 (Figure 2B), but
247   was defined as correlated error of regional richness in all other models to exclude it as a
248   potential correlate. We also tested one model without a direct impact of regional fern richness
249   on plot fern richness for completeness (model 7). To identify the most important environmental
250   predictors for the models, we ran generalised linear models with a Poisson distribution for each
251   response variable against all explanatory factors and evaluated the R-squared-values for each
252   (Table 1). Afterwards, we used principal component analysis (PCA, R package ade4, Dray &
253   Dufour, 2007) to choose from the strongest predictors those that were not strongly correlated.
254   Even though it had a comparably low R^2-value, we included habitat homogeneity on a regional,
255   large grain size, as it was shown to be a strong predictor of regional richness in previous studies
256   (Kreft et al., 2010, Table 1). Additionally, we tried to prevent the use of the same predictors at
257   different grain sizes to prevent circularity (except for annual precipitation, which on both grain
258   sizes was found to be extremely important). Since the structural equation models do not test
259   whether the link between regional environment and regional richness exists but rather measures
260   the strengths for the plot richness numbers, we believe that using the same predictors for the
261   regional model as well as in the SEM is not problematic. However, the estimates of these
262   relationships, which demonstrate how strong the predictors were for regional richness at the
263   83,000 plot localities, are less independent than for local environment and plot richness.

264   To prevent spatial unbalance in the input plot data, we randomly selected 10 plots from

265   each 10° x 10° grid cell (see Figure 1). When less than 10 plots fell into a cell, all were selected.

266   Plots with identical GPS-coordinates were considered duplicates and all but one were excluded.

267   This resulted in a final number of roughly 890-1000 plots for each run. This selection as well

268   as the subsequent model testing was repeated 1000 repetition in order to account for differences

269   in species richness of plots in the same grid cell as well as model uncertainty. We corrected for

270   spatial autocorrelation using Moran Eigenvector GLM filtering (MEs, R-package "spdep";

271   Bivand & Wong, 2018), selecting those Eigenvectors that limit residual autocorrelation below

272   an alpha of 0.05. These MEs were then added as additional variables in the competing SEMs,

273   with links on regional and plot richness. The AIC-values of each model as well as the p-value

274   and number of degrees of freedom of the Fisher's C-test of directed separation, which validates

275   whether all unlinked paths are indeed independent, were extracted for each run, and the best

276   performing model per run was noted. The final best model was the one that performed best

277   most often in AIC and Fischer's C, averaged across all repetitions. Since the strength of the

278   predictors depends strongly on the total range of values, we separated the two paths of the SEM

279   and standardised the predictors to evaluate the models and predictor strengths separately in a

280   later step.

281   To find the best curve shape describing the relationship between regional and plot

282   richness, we tested a number of different regressions: linear, polynomial (2nd and 3rd degree) as

283   well as Michaelis-Menten (R-package "drc", Ritz, Baty, Streibig & Gerhard, 2015) on the same

284   subsampled plot dataset repeated 1000 times. We compared the AIC of the curves to identify

285   the best fit.

Results

The predictor testing for the regional fern richness model revealed area size of input entity, elevational range, potential evapotranspiration, mean annual cloud frequency (Wilson & Jetz, 2016), and habitat homogeneity (second order, Tuanmu & Jetz, 2015) as well as aridity index, temperature annual range, annual precipitation, and precipitation of warmest quarter obtained from the Climatologies at high resolution for the earth's land surface areas database (CHELSA; Karger et al., 2017; Table 1) as strongest predictors. The final generalized linear model (Poisson distribution) of regional fern richness on a global extent had an explanatory power of 74.5% (R^2) and predictions ranged in species numbers between 0 and 439 at a spatial grain size of 7666 km^2.

INSERT FIGURE 3 AROUND HERE.

For the environmental predictors on the fine grain-size of 4 km^2, the GLM tests and principal component analyses (PCAs) revealed fine-grain size mean annual temperature, temperature seasonality, temperature annual range as well as mean annual cloud frequency and mean annual precipitation as strong predictors of plot fern richness. The coarse-grain size median of habitat homogeneity, of precipitation of warmest quarter, of annual precipitation, and the elevational range of each 7666 km^2 grid cell were identified as strong predictors of the regional richness at the plot localities.

The comparison of the regression models used to answer Q1 showed the polynomial curve of 3rd degree to have the best fit in 99.9% of all cases (deltaAIC to next model: 28; Figure 4). The best model showed a gradual increase of plot richness with increasing regional richness up to a regional richness of around 300 species and a mean of plot richness of 23 fern species, with plot richness then decreasing to around 12 species at a regional richness of 440 species.

INSERT FIGURE 4 AND TABLE 2 AROUND HERE.

In the structural equation model, the AIC test as well as the X^2-distributed Fisher's C statistic indicating the goodness-of-fit after tests of directed separation revealed the following order from most to least likely model (Table 2): The model chosen most frequently as the most likely (55.7%) was model 5, in which the coarse-grain size environment directly affects regional as well as plot richness (Q3) and botanical continent affects regional richness (Q2). The second most likely model was model 4 (44.2% chosen, deltaAIC = 19), which also included coarse-grain size environment affecting both regional and plot richness, but did not include an effect of botanical continent. Both models were almost equally often chosen as the most likely. However, the low Fisher's C value for model 4 indicates that a significant path is being missed

319   in the model – including this link makes model 4 equal to model 5, supporting model 5 as the

320   most likely again. The third most likely model (model 7, deltaAIC = 38) included effects of

321   coarse-grain size and fine-grain size environment on regional and plot richness, as well as of

322   botanical continent on regional richness. The next most likely model (model 1, deltaAIC = 43)

323   included botanical continent as well as coarse-grain size environment as predictors of regional

324   richness, but without a direct connection between coarse-grain size environment and plot

325   richness, followed by model 6 (deltaAIC = 56), model 2 (deltaAIC = 63), and model 3

326   (deltaAIC = 111).

327   **INSERT FIGURE 5 AROUND HERE.**

328   The most likely model (model 5, Figures 2 and 5) revealed that botanical continent had

329   the strongest impact on regional richness (Q2). Comparing continents (Table 3), temperate and

330   tropical Asia were modelled to be more species rich (indicated by positive estimates) compared

331   to Africa, which as the baseline had an estimate of 0. North America and South America had

332   weaker positive estimates, whereas Europe and Australasia had negative estimates when

333   referenced against Africa. The test of directed separation showed that botanical continent did

334   not have a significant effect on plot richness.

335   Overall, the effect of the predictors on plot richness in the structural equation model was

336   smaller than for regional richness (Figure 5A). However, this depended strongly on the range

337   of the response variables; in the case of plot richness 0–81 species and for regional richness 0–

338   439 species. So, in order to identify the predictor strength independent of the range of the

339   response variable, we standardised each model-path individually. After standardisation (Figure

340   5b, Table 3), fine-grain size temperature seasonality and temperature annual range were

341   revealed as having the strongest impact on plot fern richness, followed by temperature diurnal

342   range, regional fern richness, annual precipitation, and coarse-grain size cloud frequency. The

343   standardisation also relativised the differences between the strengths of coarse-grain size

344   predictors on regional richness, revealing annual temperature range as the strongest factor.

345

346   **INSERT TABLE 3 AROUND HERE.**

347

348   Discussion

349   Using our extensive dataset of almost 83,000 vegetation plots with the regional fern

350   richness model at a resolution of 7666 km^2, we were able to analyse the determinants and

351 relationships of plot and regional fern richness. In the following, we will focus on the three
352 aspects outlined in our focal questions, namely the relationship of plot and regional richness,
353 the impact of historical or biogeographical factors at different scales and the impact of regional
354 environment on richness at regional and plot scale. Overall, the results of our regional model
355 corresponded with those of Kreft et al. (2010) who used a broadly similar modelling approach,
356 although the higher quantity and quality of the input data and the finer spatial resolution of the
357 model imply that our model has higher explanatory value, as also reflected by the high R^2 values
358 obtained for the model. In essence the model confirms that regional fern richness is highest in
359 wet tropical mountains, in regions of high habitat heterogeneity, and is much lower in Africa
360 compared to other tropical continents.

361 Focussing on the relationship of regional and local/plot fern richness, surprisingly, plot richness
362 did not show a linear relationship and neither reached a saturation asymptote (Q1), but rather
363 decreased at high levels of regional richness. To our knowledge, such a pattern has not yet been
364 observed or predicted for global patterns of biodiversity of any group of organisms (Srivastava,
365 1999; Olivares et al., 2018). By showing that this pattern remained stable through 1000 different
366 plot subsets, we can exclude sampling effects as the underlying cause. Additionally, our dataset
367 included 1860 plots from 43 regional polygons with over 250 regional species with most of
368 these plots having been conducted within the scope of fern-oriented studies. It thus seems
369 unlikely that locally super-rich plots were coincidentally missed in super-rich regions. A
370 possible explanation for this unexpected pattern may be that very species-rich regions tend to
371 have a high degree of habitat heterogeneity, which would limit the surface area of each habitat
372 in this region and thus via the species-area relationship the number of locally supported species.
373 Additionally, regions with high habitat heterogeneity can include habitats that support only few
374 species, such as alpine outcrops or regions with very poor soils. Indeed, the underlying soils are
375 an important factor known to impact fern richness (e.g. Tuomisto et al., 2002) especially at the
376 local scale, but at regional grain sizes, these local differences are harder to detect, leading to
377 high turnover of local species pools that are only small subsamples of the regional species pool,
378 which might be even larger because of the diversity of different soils occurring in a region.

379 From another point of view, species tend to overlap in their ecological preferences to some
380 degree so that with growing regional richness, locally co-occurring species increasingly
381 compete with each other for the same resources, again leading to higher turnover of species
382 between plots (Karger et al., 2015) or locally dominant species prevent many species from co-
383 existing. Thus, we propose that there may be a regional effect on plot fern community

384   assemblage processes, such as high local species turnover in regionally rich assemblages

385   (Karger et al., 2015). This hypothesis should be tested by targeted sampling. In any case, our

386   data does not support a linear increase of plot richness with regional richness as would be

387   expected if plot richness is simply a subsample of regional richness (e.g. Karger et al., 2011;

388   Bhatta, Grytnes & Vetaas, 2018). Rather, the curve shape suggests that ecological species

389   interactions may limit the number of locally co-occurring fern species at high levels of regional

390   species richness. This effect has indeed been documented for fern assemblages in the Indo-

391   Malayan archipelago, where realized niche widths of species decreased on large islands with

392   large regional species pools (Karger et al., 2014). Kessler, Salazar, Homeier & Kluge (2014)

393   suggest that competitive species exclusions at high levels of individual densities of ferns occur

394   in the Ecuadorian Andes. Such effects may occur more generally, but potentially experimental

395   approaches are needed to unravel the details of the underlying mechanisms.

396   Considering the influence of inter-continental differences, our analysis confirmed that

397   continents differ in "base levels" of fern species richness, with Africa long known to be the

398   "odd man out" with much lower richness than other tropical continents (Kreft et al., 2010).

399   Indeed, South America and tropical Asia were found to be more species rich when measured

400   against Africa in our analyses. Due to its geological past and history of climate oscillations,

401   tropical Africa is known to have a lower regional richness of ferns (Kreft et al., 2010) but also

402   of many other plant groups (Couvreur, 2015) than found on other tropical continents. However,

403   it has also been established that especially eastern Africa can have high local species diversity

404   as well as high levels of endemism (Couvreur, 2015), which is in agreement with our results

405   that local richness is not defined by the biogeographic past of the region (Q2): Local richness

406   does not appear to be directly influenced by geographical position, but only indirectly via

407   regional richness.

408   Finally, focussing on the impact of environmental factors, the comparison of different

409   structural equation models revealed that models allowing a direct impact of regional

410   environmental predictors on both regional and plot fern richness were the only ones capturing

411   all paths and thus performing best (Q3): Even though regional environmental predictors shape

412   the number of regionally occurring fern species, they also have a direct impact on the number

413   of locally occurring species in each plot that cannot be substituted with the regional species

414   richness. The most significant coarse-grain size predictor impacting local richness was annual

415   precipitation, followed by precipitation of warmest quarter. Locally, mean annual cloud

416   frequency was the strongest predictor, which especially in higher elevations is related not only

417   to rainfall but also to water input via fog as well as reduced solar irradiance and therefore also

418   actual and potential evapotranspiration. Previous studies found that rainfall is the strongest

419   predictor of regional fern richness (Kreft et al., 2010) and of local fern richness along

420   elevational gradients (Kessler et al., 2011). However, fog can also be of major importance, as

421   shown by the correlation of fern diversity with epiphytic bryophyte cover (Kessler et al., 2011),

422   which is a proxy of air humidity (Karger et al., 2012). The influence of fog on water relations

423   of ferns is presumably two-fold, on the one side via direct water input and on the other via

424   reduced transpiration. Habitat homogeneity and the elevational range within one coarse-grain

425   grid cell only have significant influence on regional richness. Both variables measure

426   differences between habitats within the same grid cell, so that their influence on plot richness

427   is mechanistically limited. Another aspect we could not include in the analyses, but which is

428   likely to act more strongly on plot richness than on regional richness, are the local soil

429   properties. As mentioned above, soils strongly act on local fern richness (Tuomisto et al., 2002),

430   so that differences in soil could lead to different numbers of local richness at otherwise similar

431   regional climatic conditions.

432   Putting the above considerations into context, our study shows that among the factors

433   considered by us, regional fern richness is primarily driven by climatic factors in combination

434   with strong inter-continental differences that reflect historical influences. Local richness is most

435   strongly impacted by fine-grain size climatic factors, but regional fern richness as well as

436   coarse-grain size environmental factors were also identified through structural equation

437   modelling. Interestingly, we did not find evidence of historical influences acting directly on

438   local richness. Such grain size-dependent differences in factors are commonly invoked in

439   general terms (Hutchinson, 1953; Whittaker, 1977; Ricklefs, 1987; Levin, 1992; Field et al.,

440   2004; Rahbek, 2005), but are still poorly understood for different groups of organisms.

441   Structural equation modelling as applied here has proven a suitable tool to differentiate between

442   direct and indirect influences of various factors at different spatial resolutions.

443

Biosketch

Anna Weigand is a PhD student in the working group of Michael Kessler. Her research focuses on historical and current processes shaping distribution patterns of ferns.

Author contributions

AW, MK, and HK designed the study, AW compiled the database and performed the analysis with help from SN and JL, PW helped with the regional model, PW and HK provided regional data. All other authors provided plot data. AW led the writing; all authors provided critical comments to the manuscript.

Supplementary material

Suppl. Table 1: List of environmental variables tested for predictions.

482   **Suppl. Table 2:** Plot information.

483

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615   **Table 1:** Predictors chosen for structural equation modelling.

| Predictor	Resolution (km²)	Data source
Annual mean temperature [°C]	4	Karger et al., 2017
Mean annual cloud frequency	4	Wilson & Jetz, 2016
Temperature seasonality [°C]	4	Karger et al., 2017
Temperature annual range [°C]	4	Karger et al., 2017
Annual precipitation [mm]	4	Karger et al., 2017
Regional fern richness	7666	This study, Fig. 3
Precipitation of warmest quarter [mm]	7666	Karger et al., 2017
Median habitat homogeneity	7666	Tuanmu & Jetz, 2015
Annual precipitation [mm]	7666	Karger et al., 2017
Elevational range (derived from GMTED2010)	7666	Danielson & Gesch, 2010
Botanical continent	-	Brummitt, 2001

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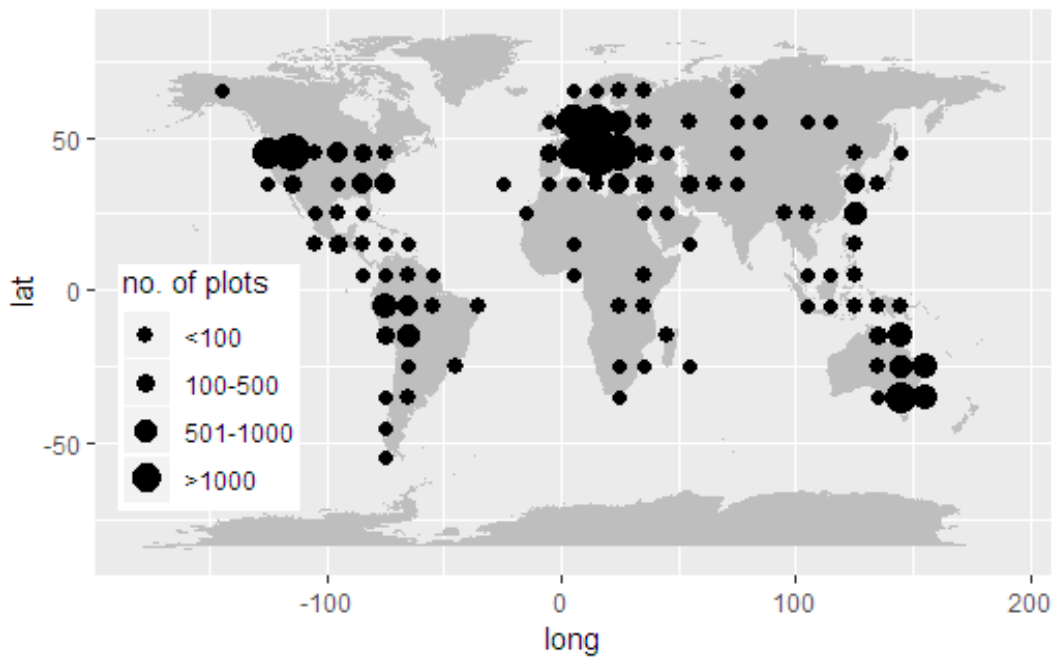
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619   **Figure 1:** Location and number of plots per 10°x10° grid cell.

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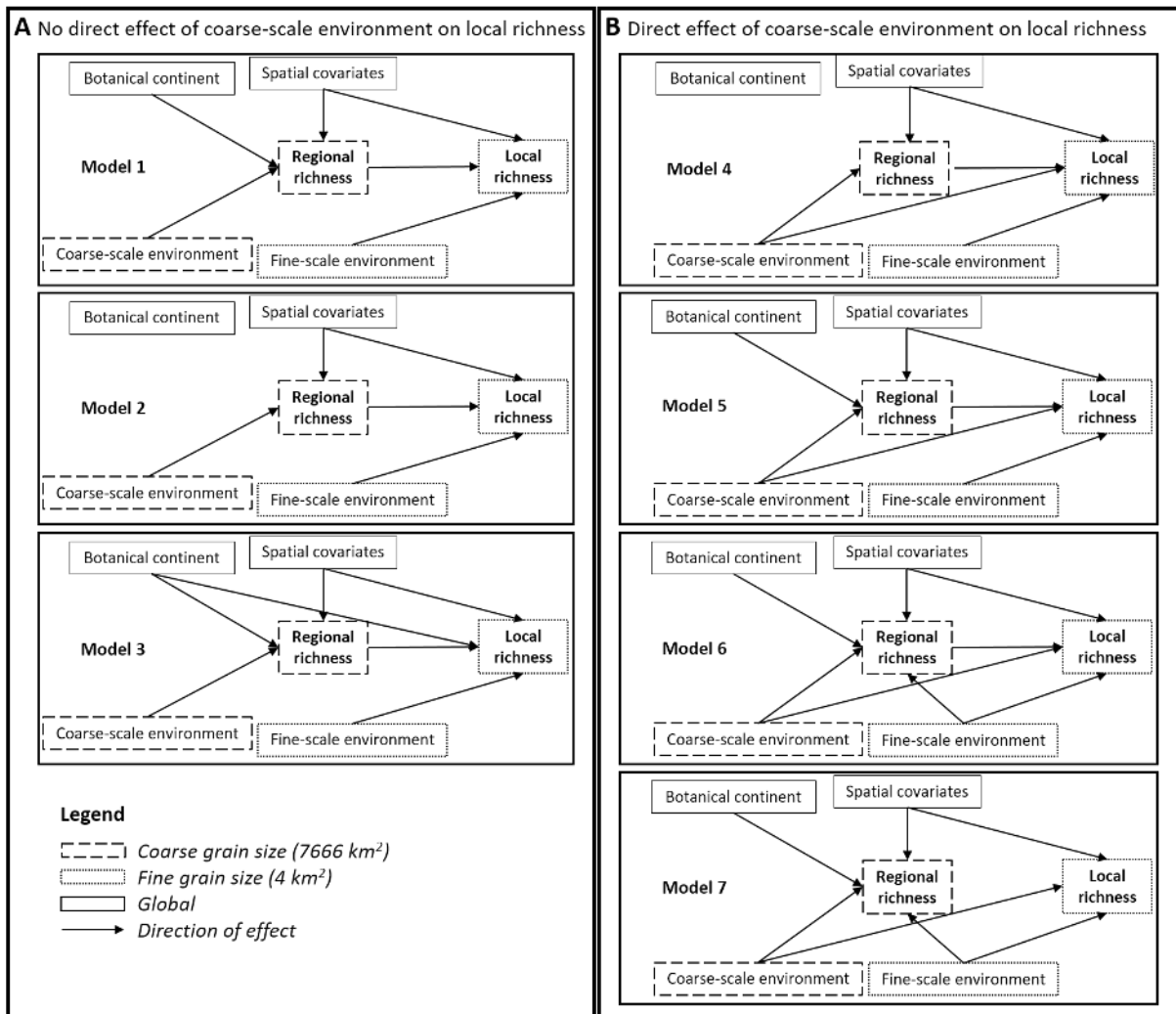
623   Figure 2: A priori conceptual structural equation models depicting environmental influences on fern regional
624   richness. **A.** Model 1-3: without allowing direct impact of coarse-grain size environment on plot richness, **B.** Model
625   4-7: allowing direct impact of coarse-grain size environment on plot richness as well as other variations.

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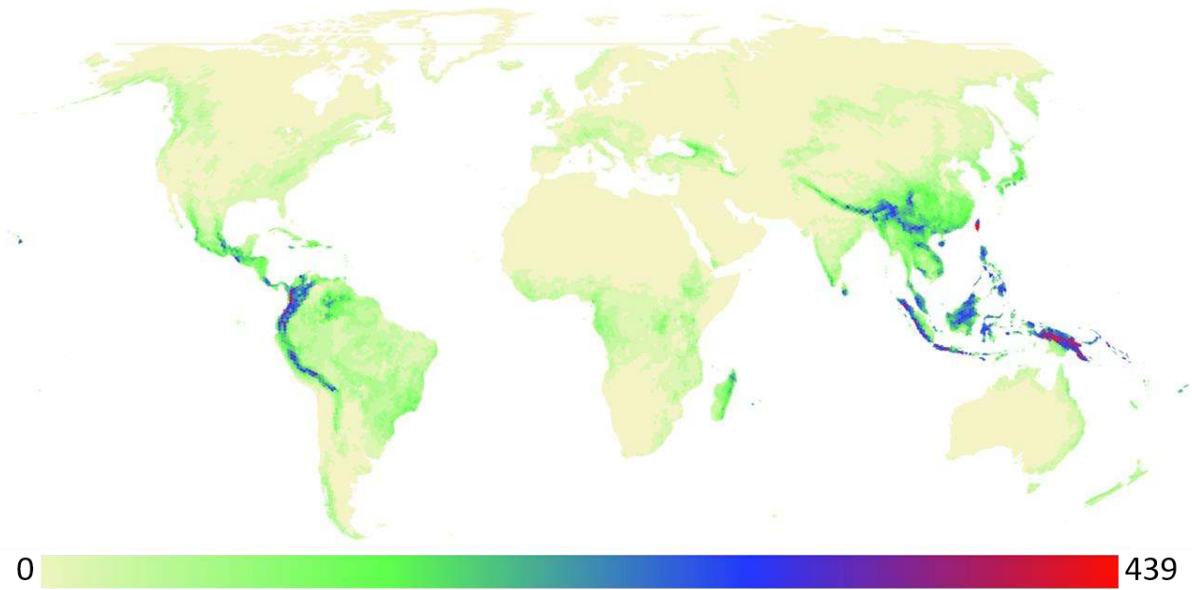
Figure 3: Global prediction of regional fern richness at a grid cell size of 7666 km^2, Robinson equal area projection, R^2 = 0.745.

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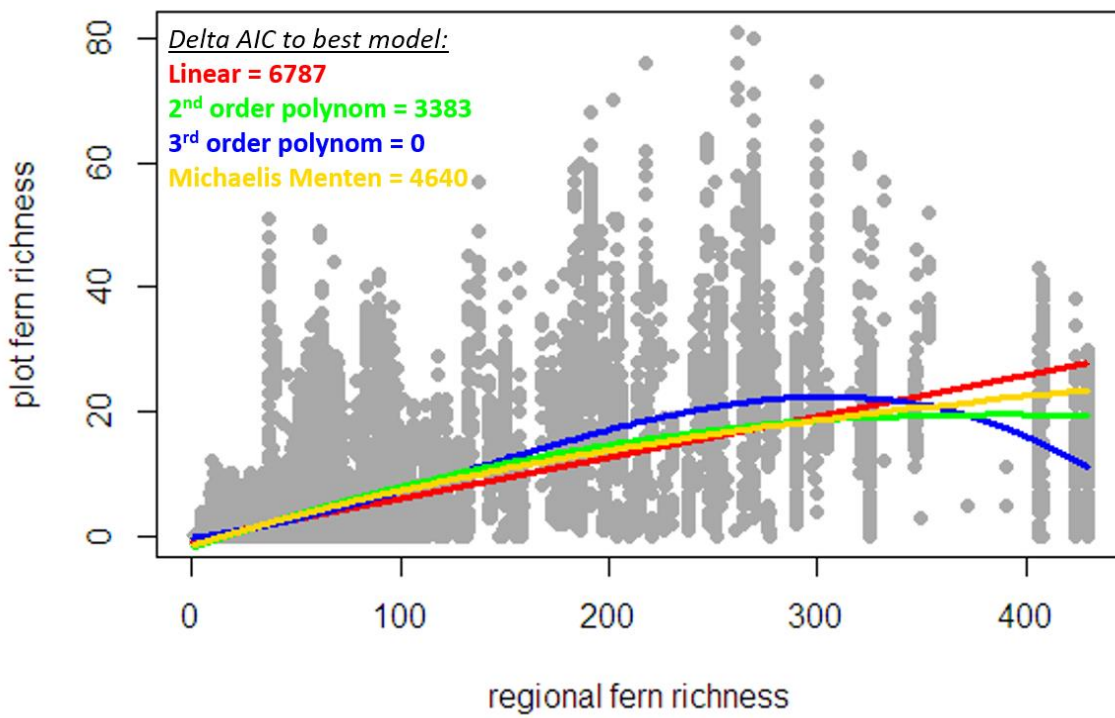
Figure 4: Relationship between regional and plot fern richness, and curves describing the relationship. DeltaAIC averaged across all repetitions.

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Table 2: Mean AIC scores, deltaAIC values between each model and the likeliest, and p-values of X^2 distributed Fisher's C for all models after 1000 repetitions, ordered from most to least likely.

	AIC	deltaAIC	p-value Fisher's C
Model 5	94	0	0.110803
Model 4	113	19	0.028600
Model 7	132	38	0.000338
Model 1	137	43	<0.00001
Model 6	150	56	<0.00001
Model 2	157	63	<0.00001
Model 3	205	111	<0 .00001

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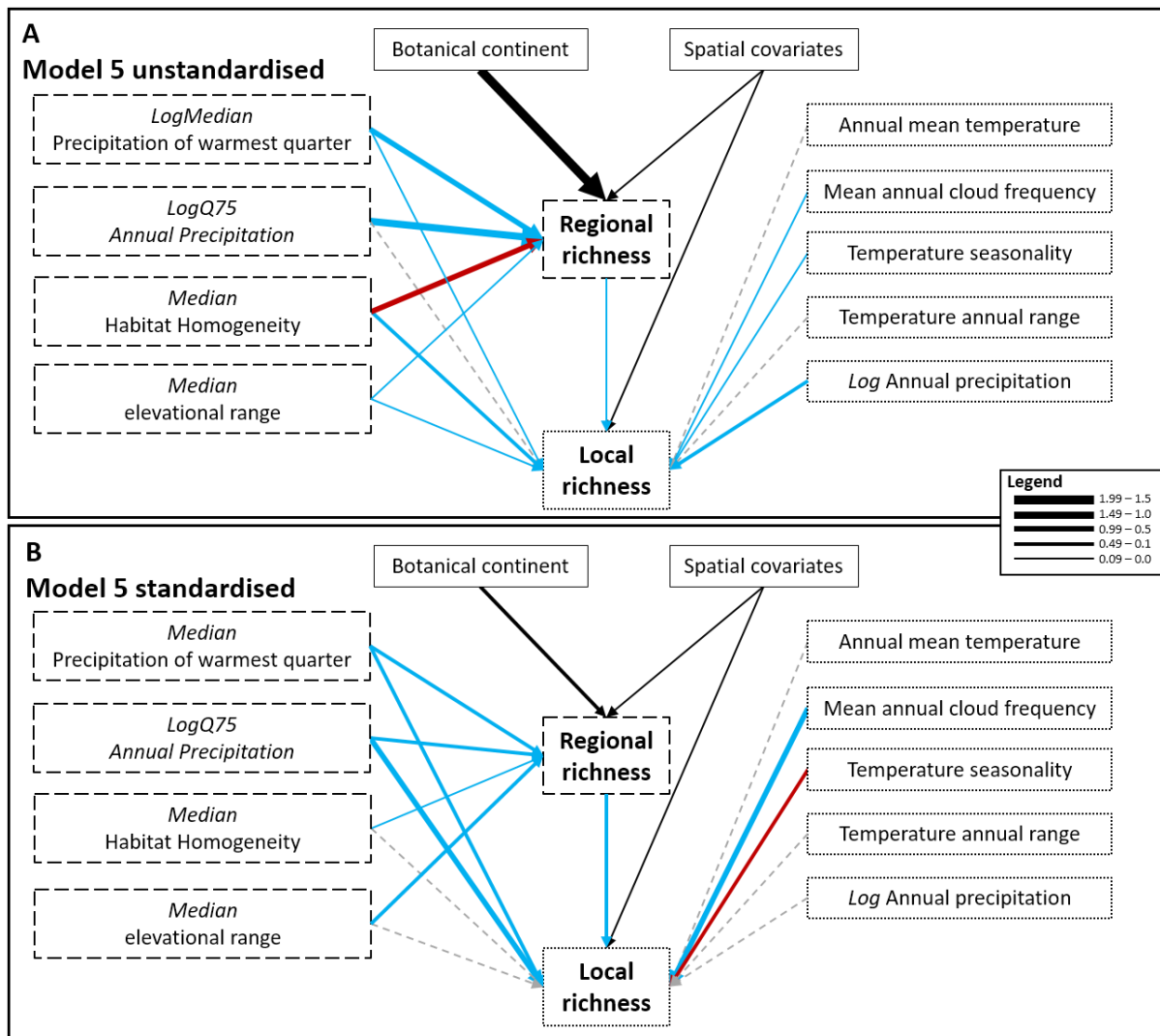
Figure 5: Structural equation models describing the influence of environmental variables on fern regional and plot richness based on the model 5, which was the best performing model identified by SEM. **A.** Unstandardised predictor strength. **B.** Standardised predictor strength and scaling performed for both paths (response: plot and response: regional) separately. *Blue* indicates positive and *red* negative correlations. The width to the arrows indicate the estimates of each predictor in the GLM. *Q75* indicates predictors that were aggregated based on the 75% quantile across each coarse grain size grid cell. *log* indicates log-transformed predictors.

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644 **Table 3:** Standardised estimates for each response variable. Estimates equal predictor strength. Predictors in italics
645 indicate coarse-grain size variables. *Q75* indicates predictors that were aggregated based on the 75% quantile
646 across each coarse grain size grid cell. *log* indicates log-transformed predictors. 0.1-0.05 (.), 0.049-0.01 (*), 0.009-
647 0.001 (**), <0.0009 (***).

	Predictor	Estimate	Std..Error	z.value	Pr...z..	
Pl ot ric hn es s	Temperature seasonality	-0.426	0.084	-5.178	0.057	.
	Annual Precipitation [mm]	-0.109	0.062	-1.720	0.304	
	Median habitat homogeneity	0.082	0.058	2.862	0.119	
	Annual temperature range [°C]	0.095	0.084	1.209	0.164	
	Annual mean temperature [°C]	0.113	0.031	3.726	0.152	
	Q75 Precipitation of warmest quarter [mm] (log)	0.175	0.042	4.187	0.015	*
	Elevational range [m]	0.183	0.053	7.021	0.528	
	Regional fern richness	0.319	0.061	10.703	0.019	*
	Mean cloud frequency	0.578	0.035	16.673	0.000	***
	Q75 annual precipitation [mm] (log)	0.594	0.121	9.839	0.040	*
Re gi on al ric hn es s	*Median habitat homogeneity*	0.090	0.007	12.926	0.002	**
	Elevational range [m]	0.320	0.005	68.208	0.000	***
	Q75 Precipitation of warmest quarter [mm] (log)	0.400	0.009	45.358	0.000	***
	Q75 annual precipitation [mm] (log)	0.419	0.010	43.687	0.000	***
	EUROPE	-0.364	0.024	-15.313	0.000	***
	AUSTRALASIA	-0.289	0.028	-10.451	0.000	***
	SOUTHERN AMERICA	0.110	0.017	6.125	0.053	.
	NORTHERN AMERICA	0.196	0.019	10.396	0.000	***
	ASIA TROPICAL	0.341	0.017	20.335	0.032	*
	ASIA TEMPERATE	0.396	0.017	23.866	0.000	***

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