RESEARCH PAPER

Global fern and lycophyte richness explained: How regional and local factors shape plot richness

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Abstract

Aim: To disentangle the influence of environmental factors at different spatial grains (regional and local) on fern and lycophyte species richness and to ask how regional and plot-level richness are related to each other.

Location: Global.

Taxon: Ferns and lycophytes.

Methods: We explored fern and lycophyte species richness at two spatial grains, regional (hexagonal grid cells of 7,666 km^2) and plot level (300–500 m^2), in relation to environmental data at regional and local grains (the 7,666 km^2 hexagonal grid cells and 4 km^2 square grid cells, respectively). For the regional grain, we obtained species richness data for 1,243 spatial units and used them together with climatic and topographical predictors to model global fern richness. For the plot-level grain, we collated a global dataset of nearly 83,000 vegetation plots with a surface area in the range 300–500 m^2 in which all fern and lycophyte species had been counted. We used structural equation modelling to identify which regional and local factors have the biggest effect on plot-level fern and lycophyte species richness worldwide. We investigate how plot-level richness is related to modelled regional richness at the plot's location.

Results: Plot-level fern and lycophyte species richness were best explained by models allowing a link between regional environment and plot-level richness. A link between regional richness and plot-level richness was essential, as models without it were rejected, while models without the regional environment-plot-level richness link were still valid but had a worse goodness-of-fit value. Plot-level richness showed a hump-shaped relationship with regional richness.

Main conclusions: Regional environment and regional fern and lycophyte species richness each are important determinants of plot-level richness, and the inclusion of one does not substitute the inclusion of the other. Plot-level richness increases with regional richness until a saturation point is reached, after which plot-level richness decreases despite increasing regional richness, possibly reflecting species interactions.

KEYWORDS
big data, macroecology, pteridophytes, regional-local richness relationship, saturation curves, structural equation modelling

1 | INTRODUCTION

One of the most fundamental questions in plant ecology and biogeography deals with the processes determining species richness patterns at different spatial scales. Even though the importance of scale (i.e. extent and resolution/grain size) in ecological analyses has been acknowledged since the 1950s (e.g. Chase et al., 2019; Hutchinson, 1953; Levin, 1992; Rahbek, 2005; Ricklefs, 1987; Whittaker, 1977), the full implementation of scale effects in global analyses has been hindered by lack of both data and appropriate methods (Beck et al., 2012). Today, advanced statistical methods (e.g. Keil & Chase, 2019) and comprehensive datasets of global extent, fine resolution and

large taxonomic coverage (e.g. Bruelheide et al., 2019) are becoming more widely available, allowing the study of macroecological patterns across scales on a global extent.

An ideal group for the study of diversity patterns across scales on a global extent are ferns and lycophytes. In addition to having a global distribution, the two lineages together contain almost 12,000 currently accepted species with a comparably stable taxonomy (PPG1, 2016). While they are the second largest vascular plant group on Earth after angiosperms (Smith, 1972), the species number is still manageable in plot sampling as well as computational analyses. Additionally, ferns and lycophytes have been the focus of several diversity studies at different spatial resolutions and extents over the last three decades.

At a large grain size of ca. 12,000 km^2, Kreft, Jetz, Mutke, and Barthlott (2010) found regional fern species richness 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. However, their analysis did not include species numbers at local scale.

At finer grain sizes of typically a few hundred square metres, numerous studies have found fern species richness to correlate strongly with climatic variables. The most important of these have been heat-related water deficiency at low elevations, low temperatures that limit diversity at high elevations and cloud cover as an indicator of high humidity (e.g. Kessler, Kluge, Hemp, & Ohlemüller, 2011; Khine, Kluge, Kessler, Miehe, & Karger, 2019; Salazar et al., 2015).

In a study combining regional and local species numbers, Karger et al. (2011) compared five elevational transects within the tropics and found that local and regional richness patterns were almost identical after the effect of the surface area of the relevant elevational belt was accounted for. This suggests that they are either driven by the same factors or that local richness equals a certain subset of regional richness and is directly driven by the size of the regional species pool. In contrast to these results, another study found that on islands of different sizes in the Indo-Malayan archipelago, local species richness was driven by local environmental conditions and not by differences in regional (island-wide) species richness, suggesting that the two are independent (Karger et al., 2014). Studying the species diversity gradients of ferns and lycophytes in the Amazonian rain forests, Tuomisto, Zuquim, and Cárdenas (2014) found that local species richness increased with soil nutrient concentration, and that this increase was paralleled by an increase in the soil-specific regional species pool. However, it has been argued that the interactions between species and their environment can limit the number of locally co-occurring species numbers, leading to local saturation. If this is the case, an increase in regional species richness should not affect local diversity (see Olivares, Karger, & Kessler, 2018; Srivastava, 1999 for details and examples).

The contrasting results and arguments of previous studies show that the cross-scale relationships between regional and local fern and lycophyte richness and their drivers remain puzzling and call for a global analysis of richness patterns across spatial scales. Here,

we use structural equation modelling, a relatively recent statistical approach in complex ecological sciences (Lefcheck, 2016), to understand the influences of environmental predictors at two resolutions ('regional' = 7,666 km^2 grain size and 'local' = 4 km^2 grain size) on fern and lycophyte richness measured at regional (7,666 km^2) and plot (300–500 m^2) grain size. To this end, we combined a large dataset of almost 83,000 vegetation plots with a model of regional fern and lycophyte richness. The model fills in gaps where regional species richness is unknown and increases the comparability of regional species richness estimates based on input species lists of different degrees of completeness. As predictors in the modelling, we used environmental variables related to climate, vegetation structure, locality characteristics and soil. Based on the results of previous studies, we tested the following competing hypotheses represented by competing structural equation models:

Hypothesis 1 *Regional species richness drives plot-level species richness. Regional environment controls regional richness but does not directly impact plot-level richness.*

Hypothesis 2 *Plot-level species richness is influenced by local and regional environment as well as regional richness, indicating that regional environment acts differently at different spatial grain sizes.*

Hypothesis 3 *Plot-level species richness is influenced by local and regional environment but is independent of regional richness.*

Hypothesis 4 *Plot-level species richness is exclusively influenced by the local environment and not by regional environment or richness.*

Additionally, we discuss the relationship between regional and plot-level species richness of ferns and lycophytes as observed in our extensive dataset of almost 83,000 vegetation plots across the globe.

2 | MATERIALS AND METHODS

2.1 | Regional species richness data

We extracted species presence information on 1,243 geographical entities (protected areas, regions, states or countries) from the Global Inventory of Floras and Traits database (GIFT; Weigelt, König & Kreft, 2019). All originally available entities were filtered for those mentioning fern and lycophyte species numbers, including known absences (i.e. geographical entities for which it is known that no fern and lycophyte species occur in them). Entities reporting less than five species were manually double-checked to avoid false under-representation. When an entity spatially overlapped with another one by more than 10%, the larger one was excluded from analyses. Coverage per continent ranged from a minimum of 30 entities in the Antarctic realm to a maximum of 315 in South America. To mitigate the effect of sampling artefacts such as differences in sampling completeness, time since publication of the species list, and overall availability between regional species lists, we built a model of regional species richness. Environmental

predictor variables were extracted from 30-arc second resolution environmental raster layers and summarized across the extent of each geographical 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, Pando, Hollis & Brummitt, 2001) was additionally included as a factor variable to allow continents to have unique richness–environment relationships. This is important since each continent has a unique geographical history and is inhabited by a set of species with a unique diversification history, which affects species richness patterns differently among biogeographical realms. We then used generalized linear models (GLMs with Poisson distribution) to ascertain environment–richness relationships and project regional richness onto an equal area grid with hexagonal grid cells of 7,666 km^2 (Barnes, 2017). The selection of environmental variables was based on previous studies on determinants of global fern richness (Kreft et al., 2010) to prevent considerable overlap between model predictors and the predictors used for the following analyses.

## 2.2 | Plot-level species richness data

To analyse plot-level fern and lycophyte richness, we collated a global dataset of 82,825 vegetation plots ranging in size between 300 and 500 m^2. The data came from the sPlot consortium (Bruelheide et al., 2019), species lists from ground vegetation surveys carried out on Level II plots of the Europe-wide forest monitoring programme ICP Forests (http://www.icp-forests.net, Canullo, Starlinger, Granke, Fischer & Aamlid, 2016; Ferretti & Fischer, 2013), and published and unpublished data from fern and lycophyte inventories carried out by a research network on fern and lycophyte diversity (e.g. Hernández-Rojas et al., 2018; Karger et al., 2014; Kessler et al., 2011; Tuomisto et al., 2014; Zuquim et al., 2014 see Figure 1 for plot distribution). From the sPlot data (sPlot 2.0, accessed on 20th April 2018), we used plots that contained at

least one fern or lycophyte species, had explicit geographical co-ordinates with a location uncertainty less than 5,000 m and whose surface area was between 300 and 500 m^2. ICP Forest data (accessed in October 2016) included Level II ground vegetation data between the years 1994 and 2012. Plots that were sampled repeatedly during this time frame provided multiple data points, but only one of them was selected within any one run of the statistical analyses (see details below). Although the data were collected in the scope of many different projects, they included complete species inventories of fern and lycophyte species, including terrestrials, hemi-epiphytes and epiphytes. Some inventories applied thresholds to juvenile individuals, but we consider any differences this may cause in the actual presence of species to be negligible in comparison to the differences caused by environmental conditions. Only the inventories made in Amazonia were not complete, as they included epiphytes and hemi-epiphytes only up to a height of 2 m. In agreement with the responsible specialists, their species numbers were increased by 10% and rounded to the next full number to make them more comparable with the full inventories.

2.3 | Predictor variables

At the regional grain, we used environmental data that were re-sampled to the same 7,666 km^2 grid cells as the regional species richness data as predictors. At the plot level, species richness was assessed in units of 300–500 m^2. The environmental predictor data corresponding to each plot were obtained as averages for grid cells of 2 × 2 km^2 to account for georeferencing inaccuracies in the plot and environmental data that could otherwise have led to excessive noise in the predictions. The chosen variables are related to climate, vegetation structure, locality characteristics and soil (Table 1).

To identify the most important environmental predictors of species richness, we ran generalized linear models with a Poisson distribution for each response variable (regional and plot-level
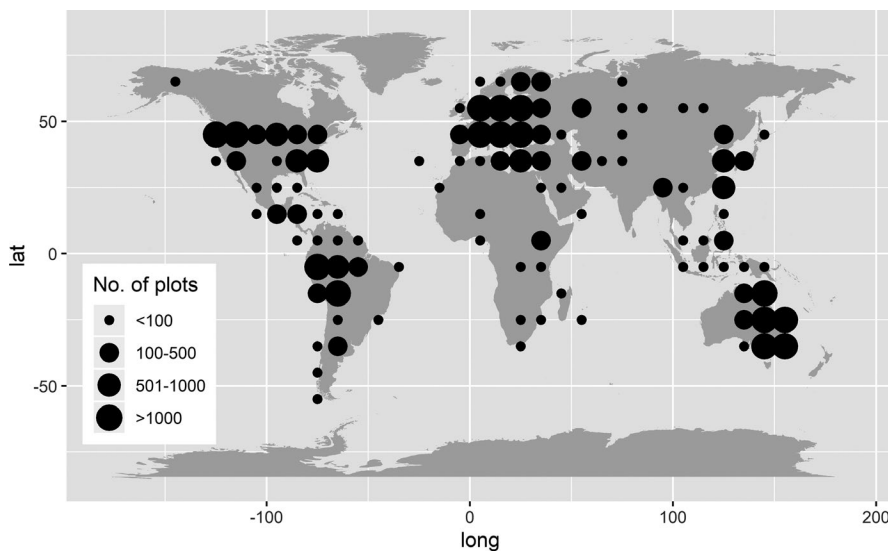

FIGURE 1 Location and number of plots per 10° × 10° grid cell

TABLE 1 Predictor variables tested at the two resolutions

Predictor	Regional	Local	Data source
Actual evapotranspiration	x		Trabucco and Zomer (2010)
Annual Mean Temperature	x	x	Karger et al. (2017)
Annual Precipitation	x	x	Karger et al. (2017)
Area of cloud forest	x		Derived from Wilson and Jetz (2016) (*number of cells including cloud forest*mean of cloud forest cover across regional grid cell*)
Aridity	x	x	Karger et al. (2017)
Biome		x	Crowther et al. (2015)
Canopy height		x	Simard, Pinto, Fisher, and Baccini (2011)
Cloud forest predictions	x		Wilson and Jetz (2016)
Distance to tree line	x	x	Karger et al. (2019)
Elevational	x		Danielson and Gesch (2011)
Elevational range	x		Derived from Danielson and Gesch (2011) (*range between minimum and maximum value per grid cell*)
Habitat homogeneity	x	x	Tuanmu and Jetz (2015)
Isothermality		x	Karger et al. (2017)
Length of growing season	x	x	Karger et al. (2019)
Max Temperature of Warmest Month		x	Karger et al. (2017)
Mean annual cloud frequency	x	x	Wilson and Jetz (2016)
Mean Diurnal Range		x	Karger et al. (2017)
Mean temperature during growing season	x		Karger et al. (2019)
Mean Temperature of Coldest Quarter		x	Karger et al. (2017)
Mean Temperature of Driest Quarter		x	Karger et al. (2017)
Mean Temperature of Warmest Quarter		x	Karger et al. (2017)
Mean Temperature of Wettest Quarter		x	Karger et al. (2017)
Min Temperature of Coldest Month		x	Karger et al. (2017)
Percentage forest cover	x	x	Derived from Tuanmu and Jetz (2014) (*sum of first 4 classes of consensus land cover per grid cell*)
Potential evapotranspiration	x	x	Zomer, Trabucco, Bossio, Straaten, and Verchot (2008)
Precipitation of Coldest Quarter		x	Karger et al. (2017)
Precipitation of Driest Month	x	x	Karger et al. (2017)
Precipitation of Driest Quarter		x	Karger et al. (2017)
Precipitation of Warmest Quarter	x	x	Karger et al. (2017)
Precipitation of Wettest Month		x	Karger et al. (2017)
Precipitation of Wettest Quarter		x	Karger et al. (2017)
Precipitation Seasonality	x	x	Karger et al. (2017)
Soil organic carbon content (ORCDRC)		x	Hengl et al. (2017)
Soil classes based on 'World Reference Base legend' (TAXNWRB)		x	Hengl et al. (2017)
Soil classes based on 'Keys to Soil Taxonomy suborders' (TAXOUSDA)		x	Hengl et al. (2017)
Temperature Annual Range	x	x	Karger et al. (2017)
Temperature Seasonality		x	Karger et al. (2017)

richness) and evaluated the R^2 values for each. For regional predictors, we tested a number of summary statistics (minimum, maximum, mean, median, 95%-quantile, 5%-quantile, 75%-quantile, 25%-quantile, as well as number and range when applicable)

across the 7,666 km^2 grid cells. For regional and local predictors, we always compared the untransformed and the logarithmic transformations to find the best fit. We then selected the variable with the highest R^2 values and excluded all variables that correlated
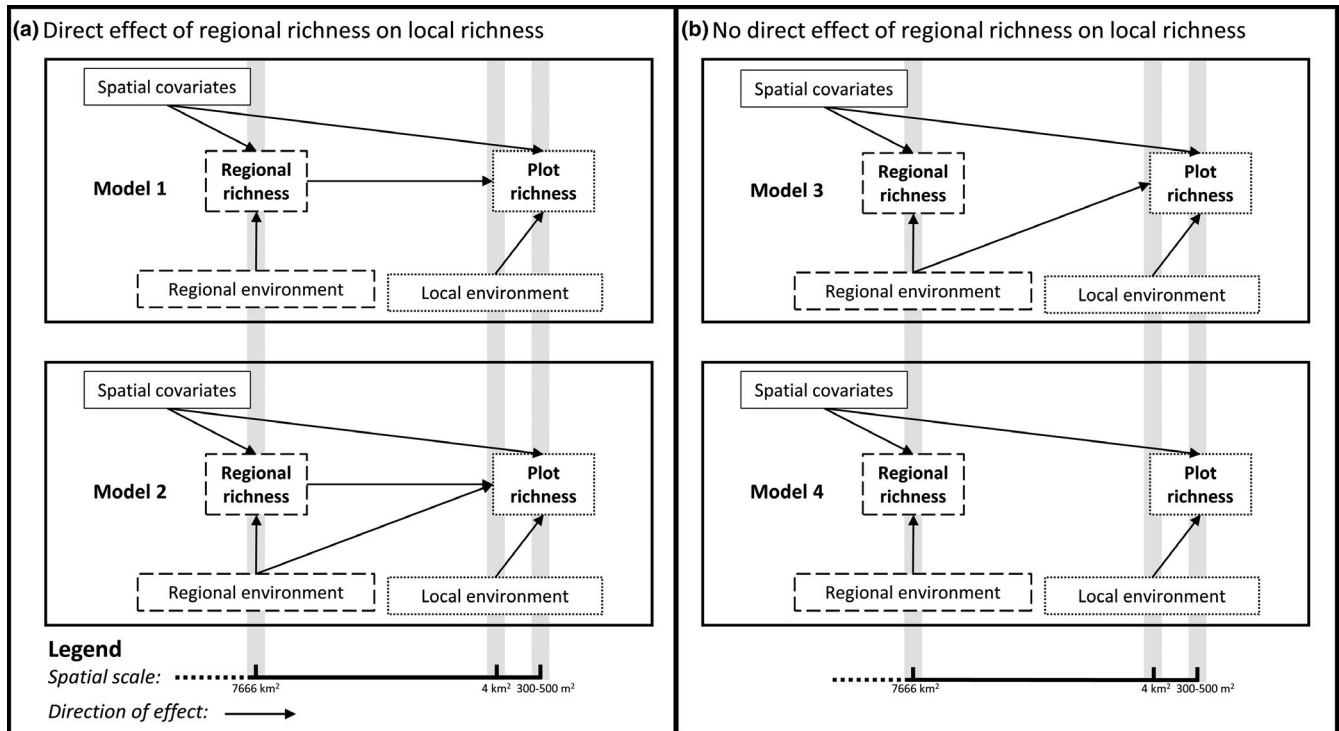
FIGURE 2 A priori conceptual structural equation models depicting environmental influences on fern and lycophyte richness as discussed in the hypotheses. (a) Models 1 and 2 allow direct impact of regional richness on plot-level richness, (b) Models 3 and 4 do not allow direct impact of regional richness on plot-level richness

strongly (correlation above 0.5) with it. Out of the remaining variables, we then selected the one with the next highest R^2 and excluded the ones highly correlated with it and so on. Correlations were evaluated with correlograms (R-package 'corrgram', Wright, 2018). At the local scale, we included the soil classification 'Keys to Soil Taxonomy suborders (TAXOUSDA_250m)', which had relatively few classes compared to other soil classifications and, therefore, the frequency of plots per soil class was sufficient to enable robust predictions. Given that soils can vary considerably over short distances, we did not include soil variables at the regional grain. Additionally, we evaluated the predictive power of the selected regional variables on plot-level richness and included only such regional variables that had an R^2 value above 0.1 as direct predictors of plot-level richness during the path analysis. Finally, we extracted the number of predicted regional species from the regional species richness model for the polygon in which each plot was located.

2.4 | Model testing

Because the spatial distribution of the input plot data was extremely clustered, we used a meticulous data preparation workflow to minimize the effects of sampling bias on the results. Spatial unbalance was reduced by randomly selecting 10 plots from each 10° × 10° grid cell for the analysis (see Figure 1) and repeating the subsampling and analyses 1,000 times. If a grid

cell contained less than 10 plots, all were selected. Plots with identical GPS-coordinates were considered duplicates and only one of them, chosen randomly, could be included in any given subset. The procedure produced subsampled datasets with about 890–1000 plots. We corrected for any spatial autocorrelation within the subsets using Moran Eigenvector GLM filtering (MEs, R-package 'spdep'; Bivand & Wong, 2018), selecting those Eigenvectors that limit residual autocorrelation below an alpha of 0.05. These MEs were then added as additional variables ('spatial covariates') in the competing structural equation models, as direct explanatory variables of regional and plot-level richness to correct the spatial autocorrelation between the GPS points used at both scales. All spatial and statistical analyses were carried out in the programming environment R (version 3.5.1, R Core Team, 2016).

To test our competing hypotheses, we constructed four different structural equation models (SEM; Shipley, 2002). Each consisted of two generalized linear models (GLMs with Poisson distribution, 'paths') as implemented in the R-package 'piecewise-SEM' (Lefcheck, 2016). In each model, regional environment was linked to regional richness, local environment to plot-level richness and spatial covariates to both levels of richness (Figure 2). In addition, models 1 and 2 linked regional richness to plot-level richness and models 2 and 3 linked regional environment to plot-level richness.

We did not allow a link between local environment and regional richness because there is no logical causal link: the local environment

that gets included in the analyses depends entirely on how plot sampling happens to have been done (how many plots are located within each regional cell and where they are situated within it). Local environment was defined as correlated error of regional richness in all models to exclude it as a potential correlate. When a model evaluates variables as correlates, which in fact, should be correlated errors, the goodness-of-fit of the model will be lowered and direct separation values will potentially invalidate models based on these false assumptions. We did not link regional and local environment because we assumed that they are being driven by the same external, global forces rather than being causally connected with each other.

We used AIC (Akaike Information Criterion) as a measure of general model performance. We also used the p value and degrees of freedom of the Fisher's C test of directed separation as implemented in piecewiseSEM to check whether all unlinked paths are indeed statistically independent. The p value summarizes how statistically independent the unlinked paths are, so that a low p value indicates missing links in the evaluated model, and high p values indicate models that do not miss significant links.

We ran all four SEMs separately for each of 1,000 subsampled datasets, extracted AIC and Fischer's C values for each run, and noted which model performed best for each dataset. As the final best model, we took the one that performed best most often across the 1,000 repetitions.

Since the power of the predictors depends strongly on the total range of values of the response variables (0–81 species for plot-level richness and 0–439 for regional richness), we separated the two paths of the SEM and standardized the predictors to evaluate the models and predictor power separately in a later step for the best model.

To model the relationship between regional and plot-level richness, we tested a number of different regressions: linear, polynomial (2nd and 3rd degree) and Michaelis–Menten (R-package 'drc', Ritz, Baty, Streibig, & Gerhard, 2015) on the 1,000 subsampled plot datasets. We used the AIC values of the regression curves to identify the one that gives the best fit. To find potential explanations for the resulting pattern, we also plotted regional and plot-level richness against the most important environmental predictors to identify significant differences.

3 | RESULTS

3.1 | Regional richness model

The predictors chosen for the regional fern and lycophyte richness model following a previous study of Kreft et al. (2010) were surface area of input entity (exported directly from GIFT database), elevational range, potential evapotranspiration, mean annual cloud frequency and habitat homogeneity as well as aridity index, temperature annual range, annual precipitation and precipitation of warmest quarter (find sources in Table 1). The final model of regional richness on a global extent had an explanatory power (R^2) of 74.5% and the predicted species numbers ranged between 0 and 439 for the 7,666 km^2 grid cells (Figure 3).

3.2 | Environmental data

As predictors for fern and lycophyte species richness at the plot level (300–500 m^2), the following local environmental predictors (averaged to grain size of 4 km^2) were chosen based on their performance in the GLM tests (explanatory power $R^2 \geq .1$) and correlation analysis (correlation with other chosen predictors < .46): mean annual cloud frequency ($R^2 = .4$), isothermality ($R^2 = .37$), precipitation of driest quarter ($R^2 = .23$), canopy height ($R^2 = .21$) and distance to tree line ($R^2 = .1$). For regional fern and lycophyte richness at the plot localities, the following regional environmental predictors were found to be strongest ($R^2 \geq .1$; correlation < .4, see Table 2 for summary statistics and transformations): precipitation of warmest quarter ($R^2 = .47$), elevational range of grid cell ($R^2 = .3$), cloud forest cover ($R^2 = .29$), mean temperature during growing season ($R^2 = .16$), length of growing season ($R^2 = .11$) and precipitation seasonality ($R^2 = .1$). All regional predictors, except for elevational range of grid cell and precipitation seasonality, were also included as predictors of plot-level richness ($R^2 \geq .1$). We noted that precipitation variables were important at local as well as regional scale. Given that the regional grid cells cover 7,666 km^2, the elevational range covered by them can be very large (maximum value: 8,534 m, mean: 1,232.8 m, median: 490.5 m). Precipitation and temperature
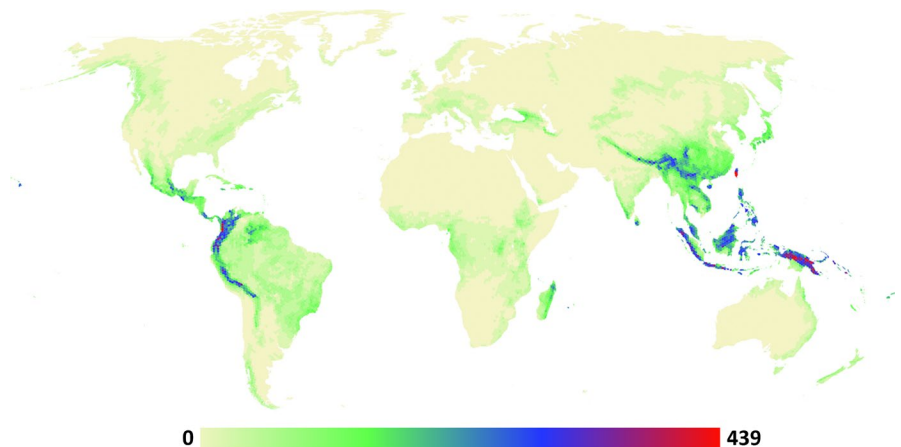
FIGURE 3 Global prediction of regional fern and lycophyte richness model at a grid cell size of 7,666 km^2, Robinson equal area projection, model explanatory value $R^2 = .745$ [Colour figure can be viewed at wileyonlinelibrary.com]

0   439

TABLE 2 Predictors of fern and lycophyte species richness chosen for structural equation modelling (SEM) based on GLM (column 'R^2') and correlation tests

Predictor	Unit	Resolution (km2)	Response	Summary statistic/ interpolation method	Log transf.	R^2
Isothermality	°C	4	Local	Bilinear	x	.37
Mean annual cloud frequency	%	4	Local	Bilinear		.40
Precipitation of driest quarter	mm	4	Local	Bilinear	x	.24
Distance to tree line	M	4	Local	Bilinear		.10
Canopy height	m	4	Local	Bilinear		.21
Soil classes 'Keys to Soil Taxonomy suborders' (TAXOUSDA_250m_II)	*factor*	4	Local	Nearest neighbour		—
Regional fern richness	species	7,666	Local	Bilinear		.10
Precipitation of warmest quarter	mm	7,666	Regional + local	75% quartile	x	.47
Elevational range (derived from GMTED2010)	m	7,666	Regional	Bilinear		.30
Cloud forest cover	m²	7,666	Regional + local		x	.29
Mean temperature during growing season	°C	7,666	Regional + local	75% quartile	x	.17
Length of growing season	days	7,666	Regional + local	75% quartile		.11
Precipitation seasonality	Coefficient of variation	7,666	Regional	75% quartile	x	.10

Note: 'Response' indicates at which grain each variable was linked to fern and lycophyte richness. Variables included in log transformation were not added again without transformation. For sources of the environmental variables, see Table 1.

vary significantly along such elevational ranges and even though the regional richness is going to be related to only one summary variable of this range, the individual precipitation/temperature of the plot can be important as well. We thus consider it necessary to include precipitation at both scales.

3.3 | Structural equation modelling

We repeated the structural equation modelling 1,000 times with different random subsets of the plot data, and the AIC test selected most frequently model 2 as the most likely (77.6% of the runs). This model included direct links from regional richness, regional environment and local environment to plot-level richness. The next frequently most likely model (11.4% of the runs) was model 1 (deltaAIC = 23.3), which was otherwise similar to model 2 but did not allow the link between regional environment and plot-level richness. Model 3 (deltaAIC = 26.3) and model 4 (deltaAIC = 48.9), which did not link regional richness to plot-level richness, were not selected as the best model in any of the runs. In both models, the X^2-distributed Fisher's C statistic indicating the goodness-of-fit after tests of directed separation had a $p > .1$. This indicates that the model was missing a significant link between some variables (Table 3).

By separating the two paths of the most likely model (model 2, Figures 2 and 4) and standardizing them individually to account for the range of the respective response variable (plot-level richness 0–81 species, regional richness 0–439), we were able to measure

the individual power of the predictors (standardized parameter coefficients) on plot-level and regional richness, respectively. After standardization (Figure 4), the local mean annual cloud frequency (coefficient = 0.64) and local canopy height (0.27) were revealed as having the strongest impact on plot-level fern and lycophyte richness, followed by regional mean temperature during growing season (0.19), local distance to tree line (0.17) and regional precipitation of warmest quarter (0.14). Of the significant predictors ($p < .1$), regional richness was the weakest predictor of plot-level richness with a parameter coefficient of 0.09. Local precipitation of driest quarter, local isothermality, regional length of growing season as well as regional area of cloud forest were not found to be significant in the standardized model ($p > .1$). For regional fern and lycophyte richness, the standardization revealed regional precipitation of warmest quarter as

TABLE 3 Mean AIC scores, deltaAIC values between each model and the best one, and p values of X^2-distributed Fisher's C for all models after 1,000 repetitions, ordered from most to least likely

	AIC	deltaAIC	*p* value of Fisher's C	% chosen as best model[a]
Model 2	150.3	0	.24	77.6
Model 1	173.6	23.3	.19	11.4
Model 3	176.6	26.3	< .01	0
Model 4	199.2	48.9	< .01	0

[a]In 11% of the runs, Models 1 and 2 were equally likely to be the best one as their AICs differed by less than 2.

the strongest predictor (coefficient = 0.52), followed by elevational range (0.37), regional length of growing season (0.32) and regional mean temperature during growing season (0.28). Area of cloud forest played a minor role with a coefficient estimate of 0.05. Regional precipitation seasonality was not significant ($p > .1$).

Out of the regression models we used to describe the relationship between plot-level and regional species richness of ferns and lycophytes, the third-order polynomial curve had the best fit in 99.9% of all cases (deltaAIC to next best model: 28; Figure 5). This model showed a gradual increase in plot-level richness with increasing regional richness up to a regional richness of around 300 species and a mean plot-level richness of 23 species, with mean plot-level richness then decreasing to around 12 species at a regional richness of 440 species.

The comparison of relationships between plot-level or regional richness and important environmental predictors showed overall similar patterns. At log-transformed precipitation of warmest quarter values between 0 and 2 the fern and lycophyte species richness at both grain sizes is rather low, while it drastically increases after 2, peaking at 3, and then declining again. For regional habitat homogeneity (measure between 0, very heterogeneous, and 1, very homogeneous), both richness-levels showed a drastic increase between 0 and 0.25, after which it declined again. After 0.75, only plot-level and regional richness values close to 0 were observed. With both regional length of growing season and local mean annual cloud frequency, the two richness levels showed a drastic increase of maximum values but with a large amount of points still ranging in the lower third of species richness values (Figure S1).

4 | DISCUSSION

Our model of regional fern and lycophyte species richness (Figure 3) following the approach of Kreft et al. (2010) reveals that richness (grid cell size of 7,666 km^2) is highest in wet tropical mountains and in regions of high habitat heterogeneity, but much lower in Africa than in other tropical continents. Through an almost 10-fold increase in high-quality input data and finer spatial resolution compared to Kreft et al. (2010), we obtained a realistic model of regional richness across the globe with a high explanatory value ($R^2 = .745$). We used these predicted regional richness values as input data in the regional path of the structural equation models, as they helped to mitigate various biases
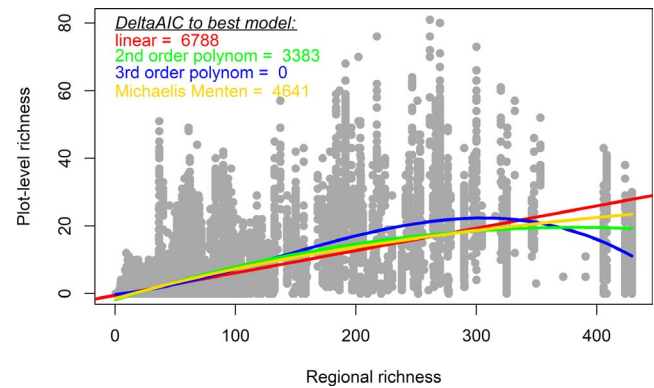
FIGURE 5 Relationship between regional and plot-level species richness of ferns and lycophytes, and curves describing the relationship. DeltaAIC averaged across 1,000 repetitions with different random subsets of the plot data [Colour figure can be viewed at wileyonlinelibrary.com]
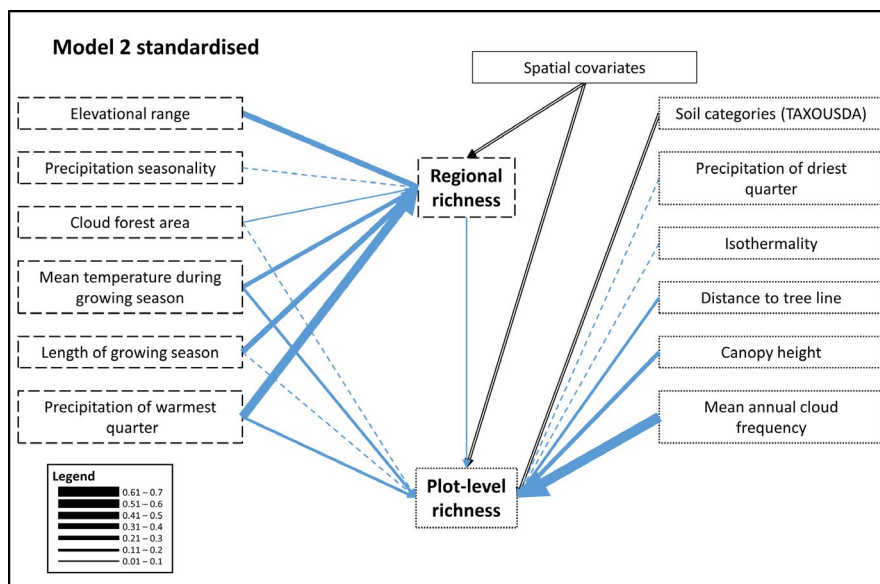
FIGURE 4 Structural equation model describing the influence of environmental variables on regional and plot-level species richness of ferns and lycophytes based on model 2 (see Figure 2), which was the best performing model identified by structural equation models. Standardized predictor power and scaling performed for both paths (response: plot level and response: regional) separately. *Blue solid lines* indicate significant positive effects, with the width of the line being proportional to the standardized parameter coefficient of each predictor in the GLM. *Blue dashed lines* indicate non-significant predictors ($p > .1$) with positive effect and *black double lines* that the power was not directly measured. The use of logarithmic transformation and summary statistics are specified in Table 2 [Colour figure can be viewed at wileyonlinelibrary.com]

in the original species checklists (missing geographical coverage, variation in time since publication and in degree of completeness).

By combining the data obtained from the regional model with our extensive dataset of almost 83,000 vegetation plots (300–500 m^2) across the globe, we were able to analyse the determinants and relationships of plot-level and regional fern and lycophyte species richness through different structural equation models (Figure 2). The best model after 1,000 repetitions of the SEM test showed that regional environment has an important influence not only on regional richness, as expected, but also on plot-level richness (model 2), confirming Hypothesis 2 and rejecting all others. Even though regional environmental predictors affect the number of regionally occurring species, they also seem to have a direct impact on the number of locally occurring species in each plot that cannot be substituted with regional species richness.

After standardizing the best model (model 2), the most significant regional predictor of plot-level richness was regional mean temperature during the growing season, followed by regional precipitation of the warmest quarter and finally regional fern and lycophyte species richness (Figure 4). Locally, mean annual cloud frequency was by far the strongest predictor. Especially at higher elevations, this is related not only to rainfall but also to water input via fog as well as reduced solar irradiance and, therefore, actual and potential evapotranspiration. Previous studies identified rainfall as the strongest predictor of regional richness (Kreft et al., 2010) and of plot-level richness along elevational gradients (Kessler et al., 2011). However, fog can also be of major importance, as shown by the correlation of fern diversity with epiphytic bryophyte cover (Kessler et al., 2011), which is a proxy of air humidity (Karger et al., 2012). Local canopy height as well as local distance to tree line were also significantly related to plot-level richness, which further highlights the importance of forest structure for plot-level richness. Canopy height, which usually correlates with the distance to tree line, can differ drastically within a regional grid cell of 7,666 km^2. This is also reflected in the fact that the elevational range covered by a grid cell was an important regional predictor of regional richness.

Soils are known to have a strong impact on local fern and lycophyte species richness (Tuomisto et al., 2002, 2014) so that areas that have similar regional climatic conditions but differ in soils can be expected to show different plot-level richness values. However, when soil properties have not been measured at the site but their impact needs to be inferred from soil type data derived from digital soil maps, their direct impact is not easy to quantify. This is partly due to accuracy problems and georeferencing errors in the available digital soil data, which themselves have been derived from scant field data (Moulatlet et al., 2017).

Putting the above considerations into context, our study shows that plot-level species richness of ferns and lycophytes is most strongly impacted by local environmental factors, but regional richness and regional environment were also identified as relevant predictors through structural equation modelling. Among the latter two, regional richness has to be considered to be more important as a predictor of plot-level richness than regional environment, as

indicated by the fact that the models without this link (models 3 and 4) were invariably rejected based on the test of direct separation.

We would have expected that plot-level species richness of ferns and lycophytes would either increase linearly with regional richness or reach an asymptote with sufficiently high regional richness. Instead, plot-level richness decreased at high levels of regional richness (Figure 5). Such a pattern has not yet been observed or predicted for global patterns of biodiversity in any group of organisms (Olivares et al., 2018; Srivastava, 1999). Nevertheless, this pattern remained stable through 1,000 random subsets of the plot data so that an obvious sampling effect as the underlying cause seems unlikely. But a detailed analysis of the geographical distribution of the medium species-rich plots in highly species-rich regions is necessary to exclude biases with certainty. Another possible explanation for this unexpected pattern may be that very species-rich regions tend to have a low degree of habitat homogeneity, which would limit the surface area of each habitat in this region and thus via the species–area relationship the number of locally supported species. Additionally, regions with low habitat homogeneity can include habitats that support only a few species, such as alpine outcrops or regions with very poor soils. In such a situation, while these habitats increase overall diversity, they would result in lower average plot-level richness than areas that only have a few locally very species-rich habitats. However, plotting plot-level richness and regional richness against habitat homogeneity (Figure S1a) showed a similar pattern for both spatial grains. We cannot exclude the possibility that the chosen variable does not capture the habitat aspects important for ferns and lycophytes, though.

From another point of view, species tend to overlap in their ecological preferences to some degree so that with increasing regional richness, locally co-occurring species increasingly compete with each other for the same resources, again leading to higher turnover of species between plots (Karger et al., 2015) or locally dominant species preventing many species from co-existing. Thus, we propose that there may be a regional effect on plot-level fern and lycophyte community assembly processes, such as high local species turnover in regionally rich assemblages (Karger et al., 2015). This hypothesis should be tested by targeted sampling. In any case, our data do not support a linear increase of plot-level richness with regional richness as would be expected if plot-level richness is simply a subsample of regional richness (e.g. Bhatta, Grytnes, & Vetaas, 2018; Karger et al., 2011). Rather, the curve shape suggests that ecological species interactions may limit the number of locally co-occurring species at high levels of regional species richness. This effect has indeed been documented for fern and lycophyte assemblages in the Indo-Malayan archipelago, where realized niche widths of species decreased on large islands with large regional species pools (Karger et al., 2014). Also, Kessler, Salazar, Homeier, and Kluge (2014) suggested that competitive species exclusions at high levels of individual densities of ferns and lycophytes occur in the Ecuadorian Andes. Such effects may occur more generally, but experimental approaches are needed to unravel the details of the underlying mechanisms.

In conclusion, our extensive dataset at two spatial resolutions and the use of recent statistical approaches that capture latent relations between

variables gave new insights into the determinants of species richness of ferns and lycophytes at regional and plot-level resolution, and raised new questions on how species interactions act across spatial scales.

DATA AVAILABILITY STATEMENT
The data used in this paper have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.hmgqnk9c3) and will be fully released on November 18, 2020.

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BIOSKETCH

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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.

SUPPORTING INFORMATION

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