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Global maps and factors driving forest foliar elemental composition: the importance of evolutionary history

Helena Vallicrosa[1,2] , Jordi Sardans[1,2] , Joan Maspons[1,2] , Paolo Zuccarini[1,2] , Marcos Fernández- Martíınez[3] , Marijn Bauters[3] , Daniel S. Goll[4] , Philippe Ciais[4] , Michael Obersteiner[5] , Ivan A. Janssens[3] and Josep Peñuelas[1,2]

[1]CSIC, Global Ecology Unit CREAF-CSIC-UAB, Bellaterra, Catalonia 08913, Spain; [2]CREAF, Cerdanyola del Vall`es, Catalonia 08913, Spain; [3]Research Group PLECO (Plants and

Ecosystems), Department of Biology, University of Antwerp, Wilrijk B-2610, Belgium; [4]Universit´e Paris-Saclay, Saint-Aubin 91190, France; [5]Ecosystems Services and Management, International Institute for Applied Systems Analysis (IIASA), Schlosspplatz 1, Laxenburg A-2361, Austria

Summary

Consistent information on the current elemental composition of vegetation at global scale and the variables that determine it is lacking.

To fill this gap, we gathered a total of 30 912 georeferenced records on woody plants foliar concentrations of nitrogen (N), phosphorus (P) and potassium (K) from published databases, and produced global maps of foliar N, P and K concentrations for woody plants using neural networks at a resolution of 1 km2. We used data for climate, atmospheric deposition, soil and morphoclimatic groups to train the neural networks.

Foliar N, P and K do not follow clear global latitudinal patterns but are consistent with the hypothesis of soil substrate age. We additionally built generalized linear mixed models to investigate the evolutionary history effect together with the effects of environmental effects. In this comparison, evolutionary history effects explained most of the variability in all cases (mostly > 60%).

These results emphasize the determinant role of evolutionary history in foliar elemental composition, which should be incorporated in upcoming dynamic global vegetation models

Key words. Climate change; neural networks; global map; leaf; nitrogen; phosphorus; potassium

Introduction

In the Earth system, forests store close to 80% of all the biomass on Earth, store 50–65% of terrestrial organic carbon (C) and occupy a third of the terrestrial vegetated surface (Reichstein & Carvalhais, 2019). Despite its importance in C cycles large uncer- tainties exist regarding stocks, turnover times and the C sink function in forest (Reichstein & Carvalhais, 2019). Recent stud- ies show that accounting for stocks, fluxes, and availability of nitrogen (N), phosphorus (P) and potassium (K) in the plant–soil system can largely improve projections of C cycles, especially when simulating global change impacts (Sardans & Penuelas, 2015; Jiang et al., 2017; Penuelas et al., 2017, 2020; Sun et al., 2017; Wang et al., 2018; Terrer et al., 2019). In fact, empirical evidence suggests that the availability of N, P and K limits the capacity of globally increasing C fixation by the rising atmospheric CO2 concentrations (Vicca et al., 2012; Fernández- Mart´ınez et al., 2014; Zhu et al., 2016; Bellassen et al., 2017; Wang et al., 2020), which was recently addressed in Earth-system models (Meyerholt & Zaehle, 2015; Walker et al., 2015; Goll et al., 2017). Several studies have reported improvements in accuracy of the projections of the Earth-system models when information on N and P has been coupled to that of the C cycle (Zaehle et al., 2010, 2011, 2015; Piao et al., 2013; Huang et al., 2016; Wang et al., 2017; Fernandez-Martınez et al., 2019). The con- tent/concentration of these elements in photosynthetic tissues is thus key for the functioning of terrestrial ecosystems, C cycling, and for their response to current global changes, and can be further improved by the inclusion of other vegetation types in future studies.

The latitude-temperature theory supports a monotonic variation in foliar N and P concentrations with latitude due to latitude-induced shifts in temperature and precipitation. Nevertheless, this relationship remains unclear and sometimes opposite patterns have been reported (McGroddy et al., 2004; Reich & Oleksyn, 2004; Kerkhoff et al., 2005; Ordonez et al., 2009; Yuan & Chen, 2009; Elser et al., 2010). The substrate age hypothesis, however, claims that older soils may be more N-abundant and P- limited than relatively younger soils (Walker & Syers, 1976). Due to sustained P losses over geological timescales, P availability is expected to decrease with increasing soil age, implying a transition from N to P limitation when going from younger soils to older soils (Walker & Syers, 1976; Chadwick et al., 1999; Vitousek et al., 2010). Although these global patterns might hold, foliar element concentrations can be highly heterogeneous on a regional scale. As such, foliar N and P concentrations have been shown to vary with mean annual precipitation within the tropics (Santiago et al., 2004) and within the temperate forest zone (Han et al., 2005). Additionally, soil type, temperature, water availability and even light intensity affect foliar nutrient concentrations (Huxman et al., 2004; Voesenek & Pierik, 2008; Ordonez et al., 2009; Wang et al., 2012). This suggests that climatic and edaphic factors should be included when trying to con- strain variability in foliar nutrient concentrations. However, the consistency of these relations on a larger scale remains to be tested.

Most studies quantifying foliar elemental composition focus predominantly on foliar N and P, leaving foliar K largely under- studied. Contrastingly, K is the most abundant nutrient in leaves after N and is considerably more abundant than P (Sardans et al., 2006; Zheng & Shangguan, 2007). Being a rock-derived nutrient, as P, its availability is mainly dependent on the parent material and weathering state (Catmak, 2005). Foliar K is important for water-use efficiency regulations in dry environments (Egilla et al., 2005; Graciano et al., 2005; Sardans et al., 2012a,b) via its effects on stomatal function, cellular osmotic equilibrium and water fluxes (Babita et al., 2010; Laus et al., 2011; Sardans & Penuelas, 2015, 2021). Importantly, K-limitation has been reported across forests from different biomes (Olde Venterink et al., 2001; Tripler et al., 2006; Wright et al., 2011; Sardans & Penuelas, 2015, 2021), which further stresses the importance of including foliar K when trying to constrain foliar nutrient concentrations globally.

Evolutionary history effects are a long-term and complex pro- duct of the evolutionary processes resulting from a species' natural selection. This species adaptation to biotic and abiotic interactions with soil, climate and other species coexistence play a key role in determining the elemental foliar composition at continental (Sardans et al., 2015; Penuelas et al., 2019) and global (Sardans et al., 2021) scales.

Bayesian models allow for the disentanglement of the species/taxonomical effects linked to long-term evolution (phylogeny) from those due to species/taxonomy linked to more recent convergent evolutionary processes, including strong selection within the phylogeny and recent epigenetic changes that are not directly due to and thus detected by strict use of phylogenetic distance matrix as covariable (Sardans et al., 2021). Apart from the evolutionary history effects, other abiotic (climate, soil type) and biotic (competition) factors play a significant role in explaining the foliar elemental composition variability found in large data sets of thousands of woody species growing in all continents (Sardans et al., 2015, 2021; Penuelas et al., 2019).

Despite the important role of N, P and K in terrestrial ecosystems and their contribution to the global C-cycle models precision, only few studies have provided a global map approach to predict foliar N and P concentrations (Butler et al., 2017; Moreno-Martınez et al., 2018). In the case of K, no gridded global map is available (Sardans et al., 2012a; Sardans & Penuelas, 2015). Furthermore, a good understanding of the links between foliar nutrient concentrations and soil, climate and atmospheric deposition remains elusive while that evolutionary history effects on tree foliar nutrient concentrations at spatial scale remain unexplored as a whole.

Our first two aims were to (1) provide high resolution (1 km2) grid maps of woody plants foliar N, P and K concentrations in woody communities at a global scale and (2) identify global N, P and K patterns. We built models for foliar nutrient concentrations based only on environmental variables, without including the likely dominant evolutionary history effects, to provide relationships with the climate variables and thus allow to project changes of foliar composition in response to climate change. Our third aim was (3) to investigate the evolutionary history effects in interaction with the effects of soil, climate and atmospheric deposition.

Material and Methods

The methods summary is in figure 1.

Database generation

We combined 24 631 inputs for N foliar concentrations in dry weight (DW), 23 726 for P foliar concentrations in DW and 18 988 for K foliar concentrations in DW corresponding to woody plants around the world (Fig. 2). The data were obtained from 257 published articles (Supporting Information Table S1), the TRY database (http://www.try-db.org/TryWeb/dp.php), the ICP Forest database (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests, http://icp-forests.net/page/data-requests), the Tundra Trait Team (https://tundratraitteam.github.io/) and the Catalan Forest Inventory (Gracia et al., 2004). All foliar data were obtained using comparable analytical methods, mostly based on elemental analysers for N, and on acid digestion coupled to optical spectrometry detection (in the majority of cases inductively coupled plasma to optical emission spectroscopy (ICP-OES) for P and K). All foliar samples were mature leaves collected between 1990 and 2016. We only used data from georeferenced plots. The samples with values more than two times SD were considered outliers and removed in order to avoid analytical or transcription data errors. Final sample sizes (number of data points) and elements used in each model are shown in Table S2.

Data for soil, climate and N and P deposition were added to foliar concentrations using the RASTER (Hijmans, 2019) and SF (Pebesma, 2018) packages in R. Thirty-four soil variables from the Land-Atmosphere Interaction Research Group at Sun Yat-sen University (Guangzhou, China) were initially considered, at resolutions of 1 km at the equator (Shangguan et al., 2014). We initially considered 26 climatic variables, which were the standard bioclimatic variables from the WorldClim v.2 database (Fick & Hijmans, 2017; Table S3), an aridity index and data for evapotranspiration from the CGIAR-CSI v.2 database (Trabucco & Zomer, 2019) also at a resolution of 1 km2 at the equator. These climatic data have been estimated from long-term meteorological time series (1970–2000), based on interpolated climatic data pro- vided by meteorological stations around the globe and adjusted to topography. Twelve variables of N deposition were extracted from Ackerman et al. (2018) (Table S3), which provided data for organic, inorganic, oxidate and reduced forms of N deposition at a resolution of 25 km at the equator. The downscaling to 1 km was done with res function in RASTER R package (Hijmans, 2019). Data for P deposition were from Wang et al. (2017) at a resolution of 1 km and as a mean for 1997–2013 (Table S3).

This database of the foliar N, P and K concentrations and information for soil, climate and N and P deposition was classified in six morphoclimatic types of forest by geographical location and species morphology. Those are tropical evergreen, tropical deciduous, temperate coniferous, temperate broadleaved evergreen, and temperate broadleaved deciduous and boreal. The tropical, temperate and boreal assignations were based on the World Wide Fund for Nature (WWF) ecoregion map (Olson et al., 2001), where 'Tundra' and 'Boreal Forest/Taiga' account for boreal forests; 'Temperate Broadleaf and Mixed forests', 'Temperate grasslands, Savanas and Scrublands', 'Montane grasslands and Scrublands', 'Mediterranean Forests, woodlands and Scrub', 'Temperate Conifer Forests' and 'Deserts and xeric scrublands' higher than 30° latitude account for the temperate forests and 'Tropical and subtropical Moist Broadleaved Forest', 'Tropical and subtropical Dry Broadleaved Forest', 'Tropical and subtropical grasslands, Savanas and Scrublands', 'Tropical and subtropical Coniferous forests', 'Mangroves', 'Flooded Grasslands and Savannas' and 'Deserts and xeric scrublands' lower than 30° latitude account for tropical forests. The evergreen, deciduous, coniferous and broadleaved designation was not assigned by map category but has been assigned by species characteristics according literature and specialist criterion in order to be more specific. In case some species could be deciduous or evergreen this species would be considered in both categories. Thus, the latitudinal designation is complemented by the foliar morphology in the different morpho- climatic type assignation. After, each morphoclimatic subset is the database used for each model training.

Neural networks and global maps of elemental composition

We built a total of 18 models, i.e. 6 groups of morphoclimatic types × 3 foliar variables (N, P and K concentrations), using neural networks in R with the package *keras* (Allaire & Chollet, 2019). The Kaiser-Meyer-Olkin method was applied to each subset of data for the 73 variables of soil, climate and deposition to automatically exclude the most strongly autocorrelated variables and avoid coliniality. We set the correlation threshold between 0.6 and 0.9 to obtain a set of the 19 remaining variables (Table S4). The datasets with remaining variables were then randomly divided into training, test and validation subsets, at a ratio of 60%, 20% and 20% (Lever et al., 2016), respectively and standardizing the data. A ponderation system based on weighting the samples by Europe and the rest of the World has been included to level the data origin and smooth the possible unbalancing effect from massive sampling in Europe. A neural network was constructed with one input layer, two hidden layers of 128 densely connected neurons and one output layer with one neuron, so we built independent networks for each nutrient and morpho-climatic forest type. The models were trained by optimizing mean squared errors on the test set. The validation data were used to cross-validate the accuracy of the model following the k-fold methodology and the root mean squared error (RMSE), the mean, the standard deviation, the coefficient of variation and R^2 was calculated for each model. Each model, was trained and calculated several times until stabilize the variation due to the random splitting of the data set. The mean of those values resulting of each repetition was calculated to obtain a final stable value with its corresponding standard error.

The variable importance function in the *Dalex* R package (Biececk, 2018) was used to identify the most influential predictor variables in the predicted outcome. This function calculates the loss function using the squared error of the model (_full_model_), randomizes each variable, calculates the loss in the absence of a predictive signal and calculates the loss with all variables randomized (_baseline_). We repeated this process 100 times per iteration in each model, for a mean total of 10 000 randomizations.

The land-cover map from ESA-CCI v2.0.7b at a resolution of 300 m was used to set up the model predictions for the six morphoclimatic forest types by element in three global raster maps. The resolution was modified to 1000 m using the aggregate function of the *raster* package with the mode as a gathering parameter. The land-cover map was then reclassified (Table S5) to our six morphoclimatic types to match the land-cover map with our prediction and use it to mask the vegetation for determining the distribution of each vegetation group. For mixed forests in the land cover map we calculated and plotted the corresponding mean values of each forests predictions for that region in order to better assess the reality. The neural network predictions were then plotted in three raster longitude/latitude WGS84 projection at a resolution of 1 km with the predicted percentages of foliar N, P and K concentrations in mature leaves of woody species. Uncertainty maps were also provided for each element using the mean standard error of the mean (SEM).

Generalized linear models

We selected the 10 most important variables based on their importance in the neural-network model to identify significant correlations with N, P, K concentrations. We then created a subset of the six least strongly correlated variables and built saturated glm models using these six variables and their first-degree interactions following gamma family distribution with an inverse link. We then applied the dredge function in the MuMIn R package (Barton, 2019) to select the final model based on the lowest Akaike information criterion and a maximum of six variables and interactions per model. We also determined the proportion of deviance explained by the glm or a pseudo-R^2 value with the Dsquared function into modEvA (Barbosa et al., 2015) R package.

Generalized linear mixed models

We used Bayesian generalized linear mixed models in the *MCMCglmm* R package (Hadfield 2010) to understand the combined role of phylogeny and species compared to the predictors used for the neural network (variables for soil, climate and deposition). We again selected the 10 most important variables for each biome and element based on the importance of the neural-network variables and also created a subset of the six least strongly correlated fixed variables for running the models. We also used the phylogenetic tree provided by Qian and Jin, 2015 which matches with 1580 of our species. Those corresponding species conformed to the random part of the model as "phylogeny" and the species group as "species". We ultimately built 6 × 3 models with the form: element~var1+var2+var3+var4+var5+var6, random=phylogeny+species. The random variance explained by phylogeny and by species was thus also specified.

Soil age

We used the USDA classification of soil taxonomy when no map of soil age was available for determining whether and how the age of the substrate also influenced the foliar elemental compositions. The USDA classification partially and categorically considers soil age in their order divisions and allowed us to infer the effect of the soil age into elemental composition. We grouped our predicted N, P and K concentrations by their corresponding soil orders. Then we compared the orders using an ANOVA and a Tukey's post hoc test with the HSD.test from *agricolae* (Mendiburu, 2020) R package. Finally, we represented the results in violin plots by soil order.

Results

High resolution (1 km^2) global maps of foliar N, P and K concentrations in woody communities based on environmental variables

The estimations of foliar N, P and K concentrations by neural network models showed precisions of 0.337, 0.040 and 0.181 normalized root mean squared error (RMSE) respectively and 0.63, 0.31 and 0.32 R^2 respectively in predicted vs observed regressions (Figure 3).

Foliar N concentrations were predicted to be lowest in northwestern Eurasia and the north of North America. Foliar N concentrations were notably high in eastern Russia, central Africa, some regions in the Rocky Mountains and the Andes (Figure 4a) so to follow a latitudinal pattern at a glance is difficult. The map showing the standard error of the mean (SEM) estimation among replicates indicated that the predicted uncertainties were highest in mountainous areas, some regions in Siberia, the Labrador Peninsula, the Somali Peninsula and some sparse points (Figure S1a). The coefficient of variation (CV) for N in the neural-network models by morphoclimatic group ranged from 9.97 % in temperate coniferous to 33.46 % in Temperate coniferous, with a mean of 18.94 % CV for all forest types (Table S6).

The latitudinal pattern of foliar P concentrations is not clear either at a glance but lower levels are common in the tropical fringe. Foliar P concentrations were lowest in Northern Latitudes of North America, Florida, central Amazonia, some zones in central Africa, some zones in East Siberia, south-east of Asia and some zones in southern Australia. There were high foliar P concentrations in the Rocky Mountains and North America, the south of the Andes, central Europe, central parts of southern Africa and some spots in Siberia (Figure 4b). The high foliar P concentration in Siberia match with an uncertainty spot into the standard error of the mean map and also Labrador's Peninsula in an uncertain P zone. Other zones of uncertainty were in some parts of North America and in some isolated pixels in central Asia (Figure S1b). The CV for foliar P concentrations in the neural-network models ranged from 64.76% in temperate deciduous broadleaved to 109.30 % CV in tropical evergreen forests, with a mean of 98.26 % CV for all forest types (Table S6).

The predicted foliar K concentrations did not follow a global latitudinal pattern either. Some zones such as the Rocky Mountains, the southern Andes, the Somali Peninsula, and the North of Australia were predicted to have high foliar K concentrations. Foliar K concentrations were lowest at the mouth of the Amazonian River, in the Labrador Peninsula and central and west of Russia (Figure 4c). The zones with higher SEM are the south-east of Siberia, the south of Africa and the Rocky Mountains. The CV for K in the neural-network models ranged from 3.81 % in Temperate evergreen broadleaved forests to 27.64 % in Tropical evergreen, with a mean of 15.42 % CV for all forest types (Table S6).

Soil types

Spodosols and Histosols were the soil orders with lowest foliar N concentrations while Oxisols and Vertisols had the highest foliar N concentrations. The soil orders with the lowest foliar P concentrations were Oxisols and Ultisols, being Vertisols and Mollisols those with the highest foliar P concentrations. The lowest foliar K concentrations were found in Spodosols and Gelisols and the highest in Vertisols and Aridisols (Figure 5 and Table S7).

The environmental (climate and soil) versus the evolutionary history (phylogeny and species) effects in the different morphoclimatic types.

Nitrogen

The generalized linear models (glm) only with environmental variables conducted for each biome only explained from 5.5 % of the variability for temperate broadleaved evergreen to 38.8 % of the variability in N for boreal forests (Table S8). Soil pH, aridity index and solar radiation and precipitation seasonality correlated positively with foliar N concentrations in tropical evergreen forests. Soil gravel and evapotranspiration seasonality were positively correlated with foliar N concentrations while soil base saturation was negatively correlated in tropical deciduous forests. For temperate coniferous forest, foliar N concentrations correlated positively with soil pH and precipitation of the warmest quarter while soil base saturation evapotranspiration and soil pH were negatively correlated. In turn, foliar N concentrations in temperate broadleaved evergreens were correlated positively with aridity index, evapotranspiration and soil pH. In temperate broadleaved deciduous forests foliar N concentrations were correlated positively with annual precipitation and negatively with aridity index, soil pH and precipitation of the driest quarter. Finally, foliar N concentrations were positively correlated with minimum June, July and August precipitation and negatively correlated with maximum June, July and August precipitation and maximum temperature of the warmest month in boreal forests (Table S8).

The generalized mixed models (glmm), which besides environmental variables included the evolutionary history effects that comprise phylogeny and species, explained much more variance than glm. Evolutionary history effects (random variables in this case), also known as Pagel's lambda, explained 42-81% of the variability in foliar N concentrations while the exclusively environmental fixed variables explained only 1-58% (Table S9b). Phylogeny explained most of the variance in tropical evergreen, temperate coniferous, temperate broadleaved evergreen and boreal forests.

Phosphorus

The glm models built entirely with environmental variables only explained from 5% of the total variance for tropical deciduous to 18% in temperate coniferous forests (Table S8), including: a positive relation of foliar P concentrations with evapotranspiration seasonality and a negative relation with inorganic N deposition, soil pH, isothermality and mean temperature of the driest quarter, in tropical evergreen forests; a positive relation of foliar P with exchangeable soil Ca and a negative relation with soil base saturation, soil pH and isothermality in tropical deciduous forests. Foliar P concentrations were positively related with aridity index and exchangeable soil K and negatively related with soil pH in temperate coniferous forests. In temperate broadleaved evergreen forests foliar P concentrations were negatively correlated with annual evapotranspiration, daily mean solar radiation, precipitation of the driest month and mean diurnal range. In temperate broadleaved deciduous forests a positive relation between evapotranspiration seasonality, solar radiation and precipitation of the driest month and foliar P concentrations has been found with also a negative relation with precipitation of the coldest quarter. Moreover, there was a positive relation between foliar P concentrations and maximum June, July and August precipitation and mean annual temperature and a negative relation between foliar P concentrations and wet oxidate N deposition in boreal forest.

The glmm models, which besides environmental variables included the evolutionary history effects that comprise phylogeny and species, showed that these legacy effects explained most of the variance of foliar P concentrations, similar than in foliar N concentrations. The overall legacy effects thus explained 39-99% of total foliar P concentration variance in these biomes (Table S9b). Phylogeny explained most of the variance in tropical evergreen, temperate coniferous and boreal forests.

Potassium

The glm models built entirely with environmental variables explained total foliar K concentrations variance only between 3% for temperate broadleaved evergreen and temperate broadleaved deciduous and 97% for boreal forest types (Table S8). There was a positive relation between foliar K concentrations and soil exchangeable acidity and mean annual precipitation and a negative relation with dry N deposition in tropical evergreen. There was a negative relation between foliar K concentrations and evapotranspiration and wet reduced N deposition in tropical deciduous forests. Positive relationships between foliar K concentrations and aridity index, evapotranspiration seasonality, maximum June, July and August precipitation and mean annual temperature were found in temperate coniferous forest. There was a negative relation with solar radiation and precipitation of the driest quarter in temperate broadleaved evergreen forests. A positive relation between foliar K concentrations and soil pH and precipitation of the coldest quarter has been seen in temperate broadleaved deciduous. Finally, there was a positive relation between foliar K concentrations and mean temperature of coldest quarter, minimum temperature of the coldest month while there was a negative relation with dry N deposition and mean annual precipitation in boreal forests.

The glmm models, which besides environmental variables included the evolutionary history effects showed that these legacy effects explained most of the variance of the foliar K concentrations data, similar to foliar N and P concentrations. Legacy explained 22-98% of the variance, and the environmental fixed variables only explained from <1 to 8% of the variance (Table S9b).

The predictive power of the models for the whole dataset considering all the morpho-climatic types together increased highly when including evolutionary history effects in comparison with the models without them. The R^2 of the relationship between observed and predicted values increased from 46% to 68% for N, from 21% to 43% for P, and from 22% to 33% for K comparing the glm models with environmental variables against the glmm models considering also the evolutionary history (Figure 6).

Discussion

Global maps

We have produced raster maps with predicted foliar N, P and K concentrations with 1 km spatial resolution, by only considering environmental factors and no ecophysiological traits. Avoiding ecophysiological traits will allow for models to be easily adapted to future climate change scenarios, applying only the predicted environmental abiotic conditions. The addition of functional traits obtained by satellite remote sensing may offer slightly better performance (Moreno-Martínez et al. 2018), but these traits are difficult to predict and map for future scenarios. Our maps thus constitute the most reliable current proxy of global forest foliar elemental composition and can be easily used for modeling studies by providing the amount of foliar N, P and K concentrations in dry weight for each terrestrial location just from environmental variables.

The uncertainty of the predicted foliar concentrations was highest in zones with strong gradients of environmental variation and/or in zones with a low density of sampling points, such as the Rocky Mountains, the Himalayas and the Andes. Some of them also coincide with sparse vegetation points or big land extensions without experimental data available, like the Asian part of the boreal morphoclimatic type. The relationships between the observed foliar N, P and K concentrations and the expected concentrations in function of the neural network models used to build the maps have, however, proved to have reasonable goodness of fit and precision (Figure 3).

Environmental factors

The environmental drivers of foliar elemental composition were different across the six morphoclimatic types. This lack of common and consistent environmental global drivers is coherent with the divergence in results of more regional studies on foliar nutrients (e.g. Sandel et al., 2010 and Santiago et al., 2004). These diverging responses to the selected predictors reveal that plant sensitivity and determinant factors are dependent on morphoclimatic type emphasizing the differential pressures between latitudes and foliar type.

The correlations between foliar P concentrations and climatic variables seem to be partially ruled by instability of the system. In Tropical evergreen, Tropical deciduous and in Temperate broadleaved deciduous a higher seasonality or less isothermality is related with higher P levels. Foliar K concentrations were associated with water-dependent variables in Temperate coniferous, Temperate broadleaved evergreen and boreal, having higher K values in more arid conditions. These results are consistent with the narrow link between plant water-use efficiency and K concentrations (Sardans and Peñuelas, 2015) which acknowledges the osmotic use of K in water retention.

Foliar N and P concentrations under different soil types were consistent with the soil-age hypothesis at global scales, which describe young soils as N-limited and P-rich and old soils as N- rich and P -limited. Oxisols, which generally represent the oldest and more weathered surface soils, were sustaining woody plant communities with relatively more N and less P in their leaves, followed closely by Ultisoils which exhibited a similar pattern (Figure 6). This pattern, however, did not apply to forest communities on '*younger*' soils, where more P and less N is to be expected. Our corresponding explanation is at the level of the order of soil taxonomy's classification, and we must take into account that there is no family covering all the young soils.
Vertisols is the soil order with simultaneously high levels of N, P and K . Those soils are characterized by high content of expansive clay and high cation exchange capacity (Soil Survey Staff. 1999).

Evolutionary history effects

The evolutionary history effects were found to explain most of the variability in foliar N, P and K concentrations, thus complementing and extending the prediction capacity of environmental factors. Most of the variance explained by the environmental factors in glm, was explained by evolutionary history effects in glmm. Species are associated with particular soil and climatic traits, so phylogeny incorporates climatic and soil conditions to some extent. This strong evolutionary history signal in foliar elemental composition has recently been reported in studies at local, regional and global scales (Castellanos et al., 2018; Peñuelas et al 2009, 2010, 2019; de la Riva et al., 2017; Hu et al., 2018; Reimann et al., 2018; Sardans and Peñuelas, 2015, Sardans et al, 2015, 2016b, 2020). For example, specific families with singular nutrient levels such as Fabaceae which are N-fixer have foliar N concentrations of 2.08 %, i.e. higher than the mean 1.62 % , whereas Proteaceae, which are typically from low-P environments (Hayes et al., 2021) have a mean of 0.066 % P, i.e. lower than the mean 0.126 %. Consequently, this key role of evolutionary history is important in order to determine the foliar elemental composition and is the most consistent explanation behind the lack of strong effect of climatic variables in similar studies of this topic (Reich and Oleksyn 2004; McGroddy et al. 2004; Kerkhoff et al. 2005; Yuan and Chen 2009; Ordoñez et al. 2009; Elser et al., 2010) that did not take evolutionary history effects into account.

Our results strongly resonate with the biogeochemical niche hypothesis (Peñuelas et al., 2008, 2019; Sardans et al., 2021), which predicts that different species, as evolutionary products, would have different optimal elemental compositions (elementomes). Phylogeny and species, as proxies of overall evolutionary history, explained on average more than 2/3 of the variability of the foliar concentrations of N, P and K. Phylogeny represents long-term evolutionary information, while species represent more short-term evolution, which underlie more recent evolution and coevolution of different and distant taxonomical clades by coinciding under similar environmental (climate, soil, competition) conditions. Several recent evolutionary events such as climate warming, species migration, shifts in species interactions (e.g. with herbivorous or parasitic species) and climatic convergence can all increase the rate of evolutionary convergence among species from different clades or the evolutionary divergence within the same clade, and thus can also differentially increase the rate of evolution as observed in several characters in different species (Wright et al., 2006; Gillman et al., 2010; Kellner et al., 2011; Puurtinen et al., 2016; Jwa et al., 2017; Molina-Montenegro et al., 2018). All these factors cannot be "detected" by phylogeny but can be detected by taxonomy, in this case by the current species factor inside the evolutionary history effects.

The rate of species turnover in woody vegetation along spatial gradients, however, is expected to be outpaced by environmental change in short- and medium-term, as evidenced by projections of climatic, socio-economic and C-cycle models for the coming decades. The use of algorithms to predict foliar N, P and K concentrations in the near future has thus to be based on models including only climate, N deposition and soil traits that can effectively change in short time intervals of decades. Our study, though, identified the crucial explanatory role of evolutionary history effects as independent variables in global-scale models of foliar N, P and K concentrations. Evolutionary history effects were the main drivers controlling the foliar elemental composition under each environmental condition. Species is thus an important factor for plant functional traits present throughout the plant kingdom, for predicting the use of bioelements and thus for the biological control of biogeochemical cycles. The strong effects of evolutionary history suggest that the incorporation of dominant species into models, although difficult, would largely improve its predicting power. Species and their phylogeny, that represent long-term information stored in genes, together with more recent phenotypic/epigenetic shifts, determine the elemental composition of current plant cover.

The coexistence of species is another factor determining elemental composition. Considering coexistence in addition to environmental conditions and genetic legacies will favor even more the identification of the whole pool of variability of foliar elemental composition (Peñuelas et al. 2019). A possible approach with this purpose could come from combining our maps with GBIF (Global Biodiversity Information Facility) occurrences or improving the classification capacity of satellite imagery.

Final remarks and conclusions

We generated global maps for foliar N, P and K concentrations at resolutions of 1 km using neural-network machine learning, with mean R^2 values of 0.63, 0.32 and 0.32, and RMSE values of 0.34, 0.04 and 0.18 respectively, providing the best maps to date based only on environmental variables and without functional traits. The distribution of foliar N and P concentrations was consistent with the soil-age hypothesis. The pattern of foliar N, P and K concentrations and their relationships with environmental variables differed depending on the forest morphoclimatic type emphasizing different environmental pressures. Thus, the separation of global forest in the main morphoclimatic types is thus necessary to model forest canopy elemental composition. More than that, adding evolutionary history effects through general linear mixed models to environmental variables largely increased the amount of explained variance emphasizing the role of evolutionary history in controlling foliar elemental composition, and encouraging the use of species in future models of foliar elemental composition.

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Author contributions

'JS, PC, MO, IAJ and JP designed the research and got the funds. HV, JS, JM and PZ performed the research. HV, JS, JM, MFM, MB, DSG, PC and JP interpreted the result. HV, JS and JP wrote the manuscript.'

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Figure Legends

Figure 1: Summary of the methodology followed in this paper

Figure 2: Sampling points for N, P and K. Colors corresponding to different morphoclimatic groups and their combinations in mixed forests. TempC = Temperate coniferous. TempBE= Temperate evergreen broadleaved. TempBD=Temperate broadleaved deciduous. TropE= Tropical evergreen. TropD= Tropical deciduous.

Figure 3: Observed versus predicted values for neural networks models predicting foliar N, P and K concentrations. Black line = fitted linear model between observed and predicted values. Red line = 1:1 line. RMSE = root mean squared error.

Figure 4: Neural Network predicted maps of foliar a) N, b) P and c) K concentration for woody plants. White areas indicate no woody vegetation.

Figure 5: Violin plots of predicted values of foliar N, P and K concentrations grouped by soil order (USDA soil taxonomy). The predicted values of foliar N, P and K concentrations differ significantly among soil types ($P<0.05$).

Figure 6: Observed versus predicted values for the generalized linear models (without legacy factors) and the generalized linear mixed models (with legacy factors) models predicting foliar N, P and K concentrations. Black line = fitted linear model between observed and predicted values. Red line = 1:1 line. Equation describing the black line. RMSE = root mean squared error.