climate

MDPI

Communication

Large-Scale Effects of Aridity on Leaf Nitrogen and Phosphorus Concentrations of Terrestrial Plants

De-Juan Xie [1], Chun-Jing Wang [1,2] and Ji-Zhong Wan [2,*]

[1] College of Agriculture and Animal Husbandry, Qinghai University, Xining 810016, China
[2] State Key Laboratory of Plateau Ecology and Agriculture, Qinghai University, Xining 810016, China
* Correspondence: wan1276@qhu.edu.cn; Tel.: +971-520-1533

Abstract: The leaf nitrogen (N) and phosphorus (P) concentrations of terrestrial plants make large contributions to ecosystem function and dynamics. The relationship between aridity and leaf N and P has been established through experimental studies. However, few studies have focused on the large-scale effects of aridity on the leaf N and P of terrestrial plants. In this paper, we used linear regression models to test the effects of aridity on terrestrial plant leaf N and P and the N:P ratio based on global datasets. We found that aridity had significant effects on the leaf N and P and the N:P ratio of terrestrial plants. The strongest relationships were between fern leaf P, the fern N:P ratio, tree leaf P, the tree N:P ratio, vine leaf N, and the tree N:P ratio. Aridity could be used to predict the P and N:P ratio of terrestrial plants, particularly those of ferns and trees, on large scales in arid environments. Our study contributes to maintaining ecosystem functioning and services in arid environments under climate change.

Keywords: arid environment; globe; life form; leaf trait; N:P ratio; terrestrial plant species

check for updates

Citation: Xie, D.-J.; Wang, C.-J.; Wan, J.-Z. Large-Scale Effects of Aridity on Leaf Nitrogen and Phosphorus Concentrations of Terrestrial Plants. *Climate* **2022**, *10*, 171. https://doi.org/10.3390/cli10110171

Academic Editor: Anouschka Hof

Received: 15 September 2022
Accepted: 3 November 2022
Published: 7 November 2022

1. Introduction

The leaf nitrogen (N) and phosphorus (P) concentrations of terrestrial plants play important roles in ecosystem function and dynamics [1–5]. Leaf N has significant effects on ecosystem processes, for example, photosynthetic rate, litter decomposition, and plant production [3,6–8]. Phosphorus is a vital element for the genetic material, energy storage, and cell structure of terrestrial plant species [9–11]. The leaf N:P ratio is an indicator of the nutrient condition limited to plant species growth and living [12,13]. Previous studies [3,10,13] have explored the drivers of the leaf N and P of terrestrial plants on a large scale. For example, Chen et al. found that the leaf N and P of woody plants vary, depending on different environmental conditions (i.e., climates and soils) and growth forms [10]. Therefore, leaf N and P are directly related to the physiological and ecological processes of plants.

Aridity is characterized by a severe lack of available water to the extent of hindering the physiology and ecology of plant life [3,14–17]. Experimental studies [18–21] have demonstrated that aridity can regulate changes in the leaf N and P of terrestrial plants. Aridity can affect growth rate and energy metabolism in leaves; on a small scale, aridity can affect productivity, such as net primary production and net ecosystem production [22,23]. Furthermore, increased aridity may lead to the loss of ecosystem multifunctionality [24]. Leaf N and P may reduce the negative effects of aridity on ecosystem functions and services as their key functional traits [23,24]. Large-scale studies [10,25–28] have shown that climatic factors are the drivers of the leaf nitrogen and phosphorus concentrations of terrestrial plants on a large scale. Reich and Oleksyn showed that the global patterns of plant leaf N and P are related to temperature and latitude [29]. However, few studies have indicated whether aridity could affect the leaf N and P of terrestrial plants on a large scale.

The main objective of our study was to explore the effects of aridity on the leaf N and P of terrestrial plants on a large scale. Here, we proposed two hypotheses: (1) large-scale aridity affects leaf N and P, and (2) life forms regulate the effects of large-scale aridity on the leaf N and P of terrestrial plants. Based on the testing of these two hypotheses, we aimed to provide references for ecosystem services and biodiversity management. We obtained global data on leaf N and P from Tian et al. [4] and global aridity data from Zomer et al. [30]. We used linear regression models to explore the effects of aridity on the leaf N and P of terrestrial plants across different life forms.

2. Materials and Methods

We obtained a global dataset on the leaf N and P of terrestrial plants from Tian et al. [4]. This dataset includes leaf N and P and the N:P ratio belonging to 11,354 individual records based on 1291 field sites; the dataset incorporates records from 201 families, 1265 genera, and 3227 species on a global scale [4]. The species belong to five life forms, namely, ferns, herbs, shrubs, trees, and vines [4]. We averaged the values of leaf N and P and the N:P ratio across different plant species at each investigation site based on ferns, herbs, shrubs, trees, and vines. Then, we used log10 transformation for leaf N and P and the N:P ratio for further analysis. The distribution of the studied sites is shown in Figure 1.

Figure 1. The distribution of studied sites [4]. Red plots represent the study locations for the leaf N and P and the N:P ratio.

The global aridity data (Global-AI_ET0) were downloaded from the Global Aridity Index and the Potential Evapotranspiration (ET0) Climate Database v3 [30] (https://doi.org/10.6084/m9.figshare.7504448.v3; (accessed on 15 Octorber 2022)). Global-AI_ET0 is available annually as one grid layer over the period from 1970 to 2000 [30]. This dataset shows moisture availability for the potential growth of reference vegetation and excludes the impact of soil-mediating water runoff events [30]. The spatial resolution of the aridity index is 30 arc seconds (~1 km at the square). The aridity index ranges from 0 (arid) to 1 (humid) [30]. Furthermore, we selected the bioclimatic variables, including the annual mean temperature, temperature seasonality (standard deviation $\times$ 100), annual precipitation, and precipitation seasonality (Coefficient of Variation; https://www.worldclim.org/data/index.html; (accessed on 15 Octorber 2022)).

We used linear mixed-effects models to explore the effects of aridity on the leaf N and P of terrestrial plants [31]. The leaf N and P and the N:P ratio were the response variables, the aridity index was the exploratory variable, and the species group was the fixed factor [31]. The simple and mixed regression models defined the relationships between aridity and leaf N and P and the N:P ratio with log10 transformation across different life forms (i.e., ferns, herbs, shrubs, trees, and vines). We ran the mixed and linear regression models (unitary regression models or bivariate regression models) in JMP 11 (SAS Institute, Cary, NC, USA). We used a high R^2 to quantify the large-scale effects of aridity on the leaf nitrogen and phosphorus concentrations of terrestrial plants. We used unitary regression models to explore the effects of other environmental factors (i.e., bioclimatic variables) on leaf nitrogen and phosphorus concentrations.

3. Results

There were significant relationships between aridity and leaf N and P and the N:P ratio on a large scale based on the linear mixed-effects models ($p < 0.1$). Furthermore, these relationships were significant for ferns, herbs, subshrubs, shrubs, trees, and vines ($p < 0.1$; Table 1). The R^2 values were higher based on the bivariate regression models than the unitary regression models (Table S1). Based on the bivariate regression models, we found that the significant relationships ($p < 0.1$; Table 1) between aridity and leaf N and P and the N:P ratio depend on different life forms (Figure 2 and Table 1).

Table 1. The R^2 of relationships between aridity and leaf N and P and N:P ratio based on bivariate regression models.

Life Form	Leaf N		Leaf P		N:P Ratio	
	R^2	p-Value	R^2	p-Value	R^2	p-Value
Fern	0.062	0.725	0.371	0.099	0.562	0.016
Herb	0.004	0.427	0.016	0.026	0.008	0.140
Shrub	0.010	0.032	0.071	0.000	0.082	0.000
Tree	0.030	0.065	0.110	0.000	0.117	0.000
Vine	0.173	0.071	0.031	0.648	0.218	0.032

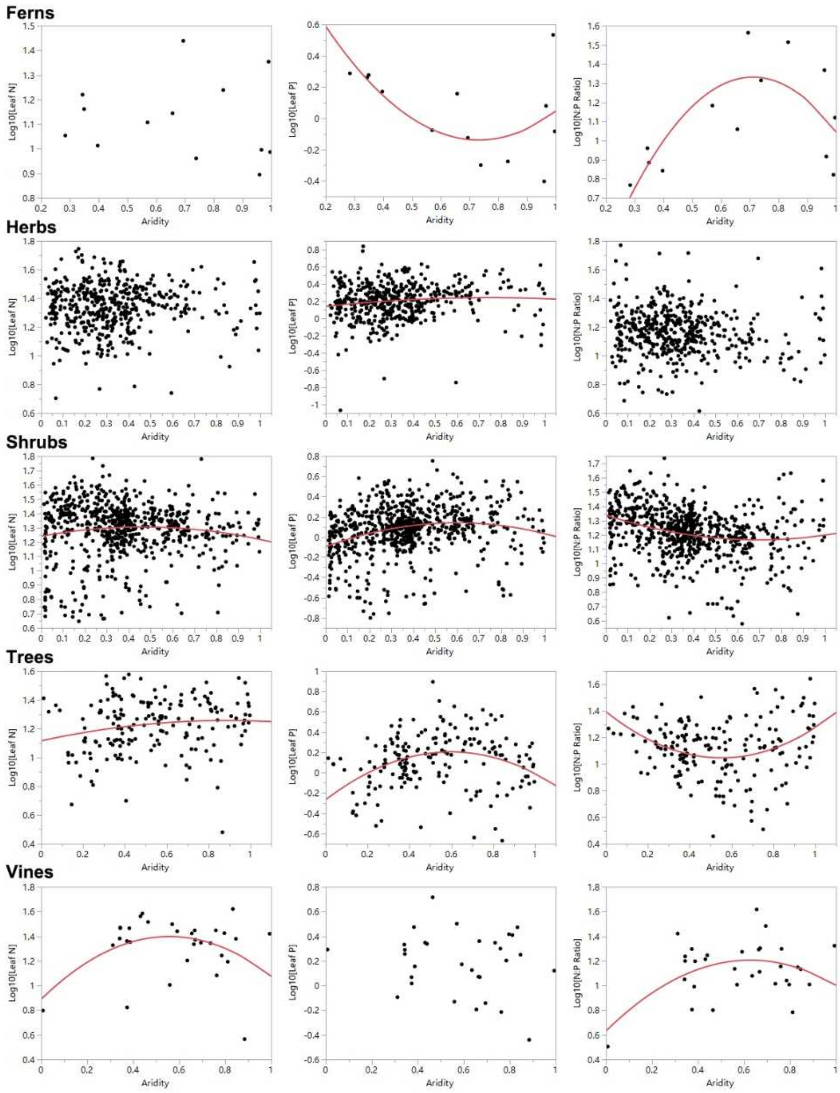

Figure 2. Relationships between aridity and leaf N and P and N:P ratio based on bivariate regression models. Aridity index values increase for more humid conditions and decrease with more arid conditions. We used log10 transformation for leaf N and P and the N:P ratio in the analysis.

Leaf N was positively related to aridity for shrubs, trees, and vines ($p < 0.1$; Figure 1 and Table 1). There were significant relationships between leaf P and aridity for shrubs, trees, and vines (i.e., increasing and then decreasing), but the relationships were the opposite for ferns ($p < 0.1$; Figure 2 and Table 1). Aridity had significant effects on the leaf N:P ratio of ferns, shrubs, trees, and vines ($p < 0.05$; Figure 2 and Table 1). Positive and then negative effects exist in ferns and vines, and the opposite effects exist for shrubs and trees (Figure 2). The largest relationships for aridity were between fern leaf P ($R^2 = 0.154$; $p < 0.1$; Table 1), the fern N:P ratio ($R^2 = 0.562$; $p < 0.05$; Table 1), tree leaf P ($R^2 = 0.148$; $p < 0.05$; Table 1), the tree N:P ratio ($R^2 = 0.140$; $p < 0.05$; Table 1), vine leaf N ($R^2 = 0.173$; $p < 0.1$; Table 1), and the tree N:P ratio ($R^2 = 0.218$; $p < 0.05$; Table 1). We found that bioclimatic variables had larger effects on leaf N, leaf P, and the N:P ratio for ferns, shrubs, trees, and vines ($p < 0.1$; Table S1). Annual mean temperature had the largest effects on vine N ($R^2 = 0.312$; $p < 0.05$; Table S1); temperature seasonality had the largest effects on tree P ($R^2 = 0.234$; $p < 0.05$; Table S1); and annual precipitation had the largest effects on fern P ($R^2 = 0.280$; $p < 0.1$; Table S1), followed by precipitation seasonality ($R^2 = 0.239$; $p < 0.1$; Table S1).

4. Discussion

The significant relationships between aridity and leaf N and P and the N:P ratio indicate that aridity has large-scale effects on nutrient acquisition. Furthermore, these relationships depend on different life forms. The effects of aridity on leaf P and the N:P ratio could widely exist across different life forms (e.g., ferns and trees), but such effects may be weak for leaf N on a large scale. Numerous experimental and field analysis studies [18–23] have shown that aridity may affect leaf N and P and the N:P ratio. Our study provides modeled analysis evidence for the relationships between aridity and leaf N and P for terrestrial plants on a large scale. Berdugo et al. indicated that aridity could drive global ecosystem thresholds [32]. Hence, our study could support the assessment of ecosystem functioning and services on a large scale under climate change.

Although we found that the effects of aridity on leaf N were weak on a large scale, aridity can play an important role in the regulation of the leaf N of terrestrial plants on a large scale. Berdugo et al. showed that drastic reductions in leaf N concentration may occur at levels of aridity lower than 0.65 [32]. Hence, we should pay attention to the changes in leaf N in the drying lands around the world. Our results show that there were significant relationships between aridity and leaf N for terrestrial plants on large scales. Hence, the changes in leaf N have a large potential to affect ecosystem functioning and services (e.g., climate regulation, nutrient cycling, and livestock production) in drying regions [24,32–34]. To maintain the stability of ecosystem functioning and services, we should monitor aridity levels, as per the suggestions of Berdugo et al. [32].

Our results demonstrate that there were significant relationships between aridity and leaf P and the N:P ratio across different life forms on a large scale. Leaf P is directly related to the physiology of terrestrial plant species and can affect the ability of terrestrial plant species to adapt to aridity [9–13]. Nitrogen and phosphorus are widely recognized as the most important limiting nutrients controlling plant growth, ecosystem functioning, and terrestrial ecosystems dynamics [1,35,36]. Both leaf P and the N:P ratio are effective indicators of nutrient limitations for terrestrial plant species along the aridity gradient [1,14,17,23]. Furthermore, these two leaf indicators could be used to monitor the stability of ecosystem functioning and services [24]. For example, Reich et al. showed that leaf P can play an important role in the relationships between photosynthesis and nitrogen based on a cross-biome analysis on numerous species [37]. The relationship between photosynthetic capacity and nutrients may be constrained by low P in drying environments (Figure 2). Hence, the detection of leaf P and the N:P ratio is important for modeling vegetation nutrient stocks and cycling in arid environments. Leaf nitrogen concentration (LNC) is a key parameter of vegetation photosynthetic efficiency and yields, and it can be applied for scientific guidance in nitrogen (N) fertilization management [37–42]. A fast and accurate estimation of crops' LNC is vital to indirectly understand crops' growth status. Similarly, nitrogen is also a component of the chlorophyll molecule, which enables a plant to capture sunlight energy by photosynthesis, driving plant growth and grain yield [40]. Nitrogen plays a critical role within a plant to ensure energy is available when and where the plant needs it to optimize yield [37,40–42]. In contrast, phosphorus promotes early root growth, winter hardiness, and seed formation; stimulates tillering; and increases water use efficiency [40].

Furthermore, we found that the largest relationships existed between aridity and fern leaf P, the fern N:P ratio, tree leaf P, the tree N:P ratio, vine leaf N, and the tree N:P ratio; this indicates that aridity can affect leaf P and the N:P ratio for ferns, trees, and vines. The photosynthetic capacity and nutrient content of ferns depend on climatic changes at temporal and spatial scales [43,44]. Based on our results, the effects of climatic factors (e.g., annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality) on the photosynthetic capacity and nutrient content of ferns were due to the limitation of leaf P caused by aridity. Furthermore, leaf P and the N:P ratio could affect the photosynthetic capacity and nutrient limitation of trees in arid environments [43–45].

Aridity is an important indicator of climate change [30]. Our results provide important references for the impacts of climate change on species and ecosystems at a global scale. Although temperature and precipitation are the drivers of plant functional trait distribution under climate change, aridity could be applied as an assessment of the effects of climate change on plant functions, closely associated with ecosystem functions and services, and biodiversity management [26,27,30,43–46]. Therefore, aridity monitoring should be widely used to evaluate ecosystem functions and services benefiting human beings under climate change.

5. Conclusions

Aridity significantly affects the leaf N and P and the N:P ratio of terrestrial plants on large scales. However, the effects are weak for leaf N and strong for leaf P and the N:P ratio. Aridity could be used to model P and the N:P ratio of terrestrial plants, particularly for ferns and trees on large scales in arid environments. Our study provides new evidence for the relationships between aridity and leaf N and P and the N:P ratio for terrestrial plants on large scales. These results contribute to monitoring ecosystem functioning and services under climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/cli10110171/s1, Table S1: The R^2 of relationships between environmental variables and leaf N and P and N:P ratio based on unitary regression models.

Author Contributions: Conceptualization, J.-Z.W. and C.-J.W.; methodology, J.-Z.W.; software, J.-Z.W.; validation, D.-J.X., J.-Z.W. and C.-J.W.; formal analysis, C.-J.W.; investigation, J.-Z.W.; resources, J.-Z.W.; data curation, J.-Z.W. and C.-J.W.; writing—original draft preparation, D.-J.X., J.-Z.W. and C.-J.W.; writing—review and editing, D.-J.X., J.-Z.W. and C.-J.W.; visualization, J.-Z.W.; supervision, D.-J.X.; project administration, D.-J.X. and C.-J.W.; funding acquisition, D.-J.X. All authors have read and agreed to the published version of the manuscript.

Funding: This work has been supported by the Scientific and Technological Achievements Transformation Project of Qinghai Science and Technology Department (No. 2021-SF-152), the Youth Project Research Foundation of Qinghai University, China (No. 2019-QNY-1), and the First Subsidy Funds for Forestry Development and Reform in 2022 (No. 2022-358): Wetland Conservation and Restoration Project for Beichuan River Source Region National Nature Reserve in Datong County, Qinghai Province, China.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Feng Xiao from Wetland Conservation Center of Qinghai Province and Chun-Hui Zhang for the comments on plant functional traits.

Conflicts of Interest: The authors declare that they have no conflict of interest.

References

1. Niklas, K.J.; Owens, T.; Reich, P.B.; Cobb, E.D. Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth. *Ecol. Lett.* **2005**, *8*, 636–642. [CrossRef]
2. Li, Y.; Niu, S.; Yu, G. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: A meta-analysis. *Glob. Chang. Biol.* **2015**, *22*, 934–943. [CrossRef] [PubMed]
3. Tang, Z.; Xu, W.; Zhou, G.; Bai, Y.; Li, J.; Tang, X.; Chen, D.; Liu, Q.; Ma, W.; Xiong, G.; et al. Patterns of plant carbon, nitrogen, and phosphorus concentration in relation to productivity in China's terrestrial ecosystems. *Proc. Natl. Acad. Sci. USA* **2018**, *115*, 4033–4038. [CrossRef] [PubMed]
4. Tian, D.; Kattge, J.; Chen, Y.; Han, W.; Luo, Y.; He, J.; Hu, H.; Tang, Z.; Ma, S.; Yan, Z.; et al. A global database of paired leaf nitrogen and phosphorus concentrations of terrestrial plants. *Ecology* **2019**, *100*, e02812. [CrossRef] [PubMed]
5. Peñuelas, J.; Poulter, B.; Sardans, J.; Ciais, P.; Van Der Velde, M.; Bopp, L.; Boucher, O.; Godderis, Y.; Hinsinger, P.; Llusia, J.; et al. Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. *Nat. Commun.* **2013**, *4*, 2934. [CrossRef]
6. Bakker, M.A.; Carreño-Rocabado, G.; Poorter, L. Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Funct. Ecol.* **2010**, *25*, 473–483. [CrossRef]
7. Adams, M.A.; Turnbull, T.L.; Sprent, J.I.; Buchmann, N. Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 4098–4103. [CrossRef]
8. Mu, X.; Chen, Q.; Chen, F.; Yuan, L.; Mi, G. Dynamic remobilization of leaf nitrogen components in relation to photosynthetic rate during grain filling in maize. *Plant Physiol. Biochem.* **2018**, *129*, 27–34. [CrossRef]
9. Liu, C.; Muchhal, U.S.; Uthappa, M.; Kononowicz, A.K.; Raghothama, K.G. Tomato Phosphate Transporter Genes Are Differentially Regulated in Plant Tissues by Phosphorus. *Plant Physiol.* **1998**, *116*, 91–99. [CrossRef]
10. Chen, Y.; Han, W.; Tang, L.; Tang, Z.; Fang, J. Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form. *Ecography* **2011**, *36*, 178–184. [CrossRef]
11. Carstensen, A.; Herdean, A.; Schmidt, S.B.; Sharma, A.; Spetea, C.; Pribil, M.; Husted, S. The Impacts of Phosphorus Deficiency on the Photosynthetic Electron Transport Chain. *Plant Physiol.* **2018**, *177*, 271–284. [CrossRef]
12. Gusewell, S.; Freeman, C. Nutrient limitation and enzyme activities during litter decomposition of nine wetland species in relation to litter N: P ratios. *Funct. Ecol.* **2005**, *19*, 582–593. [CrossRef]
13. Du, E.; Terrer, C.; Pellegrini, A.; Ahlström, A.; Van Lissa, C.J.; Zhao, X.; Xia, N.; Wu, X.; Jackson, R.B. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* **2020**, *13*, 221–226. [CrossRef]
14. Tieleman, B.I.; Williams, J.B.; Bloomer, P. Adaptation of metabolism and evaporative water loss along an aridity gradient. *Proc. R. Soc. B Boil. Sci.* **2003**, *270*, 207–214. [CrossRef]
15. Petrů, M.; Tielbörger, K.; Belkin, R.; Sternberg, M.; Jeltsch, F. Life history variation in an annual plant under two opposing environmental constraints along an aridity gradient. *Ecography* **2005**, *29*, 66–74. [CrossRef]
16. Martínez-Cabrera, H.; Jones, C.S.; Espino, S.; Schenk, H.J. Wood anatomy and wood density in shrubs: Responses to varying aridity along transcontinental transects. *Am. J. Bot.* **2009**, *96*, 1388–1398. [CrossRef]
17. Carlson, J.E.; Adams, C.A.; Holsinger, K. Intraspecific variation in stomatal traits, leaf traits and physiology reflects adaptation along aridity gradients in a South African shrub. *Ann. Bot.* **2015**, *117*, 195–207. [CrossRef]
18. Bull-Hereñu, K.; Arroyo, M.T.K. Phenological and morphological differentiation in annual Chaetanthera moenchioides (Asteraceae) over an aridity gradient. *Oesterreichische Bot. Z.* **2009**, *278*, 159–167. [CrossRef]
19. Quiroga, R.E.; Golluscio, R.A.; Blanco, L.J.; Fernández, R.J. Aridity and grazing as convergent selective forces: An experiment with an Arid Chaco bunchgrass. *Ecol. Appl.* **2010**, *20*, 1876–1889. [CrossRef]
20. Armas, C.; Rodríguez-Echeverría, S.; Pugnaire, F.I. A field test of the stress-gradient hypothesis along an aridity gradient. *J. Veg. Sci.* **2011**, *22*, 818–827. [CrossRef]
21. Quiroga, R.E.; Fernandez, R.; Golluscio, R.A.; Blanco, L.J. Differential water-use strategies and drought resistance in Trichloris crinita plants from contrasting aridity origins. *Plant Ecol.* **2013**, *214*, 1027–1035. [CrossRef]
22. Delgado-Baquerizo, M.; Maestre, F.T.; Gallardo, A.; Quero, J.L.; Ochoa, V.; García-Gómez, M.; Escolar, C.; García-Palacios, P.; Berdugo, M.; Valencia, E.; et al. Aridity Modulates N Availability in Arid and Semiarid Mediterranean Grasslands. *PLoS ONE* **2013**, *8*, e59807. [CrossRef] [PubMed]
23. Nunes, A.; Köbel, M.; Pinho, P.; Matos, P.; de Bello, F.; Correia, O.; Branquinho, C. Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. *Agric. For. Meteorol.* **2017**, *239*, 176–184. [CrossRef]
24. Gross, N.; Le Bagousse-Pinguet, Y.; Liancourt, P.; Berdugo, M.; Gotelli, N.J.; Maestre, F.T. Functional trait diversity maximizes ecosystem multifunctionality. *Nat. Ecol. Evol.* **2017**, *1*, 1–9. [CrossRef] [PubMed]
25. Han, W.X.; Fang, J.Y.; Guo, D.L.; Zhang, Y. Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China. *New Phytol.* **2005**, *168*, 377–385. [CrossRef]
26. He, M.; Dijkstra, F.A.; Zhang, K.; Li, X.; Tan, H.; Gao, Y.; Li, G. Leaf nitrogen and phosphorus of temperate desert plants in response to climate and soil nutrient availability. *Sci. Rep.* **2014**, *4*, 6932. [CrossRef]
27. Blanke, J.H.; Lindeskog, M.; Lindström, J.; Lehsten, V. Effect of climate data on simulated carbon and nitrogen balances for Europe. *J. Geophys. Res. Biogeosci.* **2016**, *121*, 1352–1371. [CrossRef]

28. Fan, J.; Harris, W.; Zhong, H. Stoichiometry of leaf nitrogen and phosphorus of grasslands of the Inner Mongolian and Qinghai-Tibet Plateaus in relation to climatic variables and vegetation organization levels. *Ecol. Res.* **2016**, *31*, 821–829. [CrossRef]
29. Reich, P.B.; Oleksyn, J. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* **2004**, *101*, 11001–11006. [CrossRef]
30. Zomer, R.J.; Xu, J.; Trabucco, A. Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. *Sci. Data* **2022**, *9*, 409. [CrossRef]
31. Harrison, X.A.; Donaldson, L.; Correa-Cano, M.E.; Evans, J.; Fisher, D.N.; Goodwin, C.E.D.; Robinson, B.S.; Hodgson, D.J.; Inger, R. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* **2018**, *6*, e4794. [CrossRef]
32. Berdugo, M.; Delgado-Baquerizo, M.; Soliveres, S.; Hernández-Clemente, R.; Zhao, Y.; Gaitán, J.J.; Gross, N.; Saiz, H.; Maire, V.; Lehmann, A.; et al. Global ecosystem thresholds driven by aridity. *Science* **2020**, *367*, 787–790. [CrossRef]
33. Soussana, J.-F.; Lemaire, G. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. *Agric. Ecosyst. Environ.* **2014**, *190*, 9–17. [CrossRef]
34. Tully, K.; Ryals, R. Nutrient cycling in agroecosystems: Balancing food and environmental objectives. *Agroecol. Sustain. Food Syst.* **2017**, *41*, 761–798. [CrossRef]
35. He, J.-S.; Wang, L.; Flynn, D.; Wang, X.; Ma, W.; Fang, J. Leaf nitrogen:phosphorus stoichiometry across Chinese grassland biomes. *Oecologia* **2007**, *155*, 301–310. [CrossRef]
36. Vitousek, P.M.; Porder, S.; Houlton, B.Z.; Chadwick, O.A. Terrestrial phosphorus limitation: Mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* **2010**, *20*, 5–15. [CrossRef]
37. Reich, P.B.; Oleksyn, J.; Wright, I.J. Leaf phosphorus influences the photosynthesis–nitrogen relation: A cross-biome analysis of 314 species. *Oecologia* **2009**, *160*, 207–212. [CrossRef]
38. Gago, J.; Coopman, R.E.; Cabrera, H.M.; Hermida-Carrera, C.; Molins, A.; Conesa, M.; Galmés, J.; Ribas-Carbó, M.; Flexas, J. Photosynthesis limitations in three fern species. *Physiol. Plant.* **2013**, *149*, 599–611. [CrossRef]
39. Tosens, T.; Nishida, K.; Gago, J.; Coopman, R.E.; Cabrera, H.M.; Carriquí, M.; Laanisto, L.; Morales, L.; Nadal, M.; Rojas, R.; et al. The photosynthetic capacity in 35 ferns and fern allies: Mesophyll CO2 diffusion as a key trait. *New Phytol.* **2016**, *209*, 1576–1590. [CrossRef]
40. Sihvonen, M.; Jussi, M.; Elena, L.; Kari Hyytiäinen, V. Management of legacy nutrient stores through nitrogen and phosphorus fertilization, catch crops, and gypsum treatment. *Nat. Resour. Model.* **2020**, *33*, e12289. [CrossRef]
41. Mueller, N.D.; Gerber, J.S.; Johnston, M.; Ray, D.K.; Ramankutty, N.; Foley, J.A. Closing yield gaps through nutrient and water management. *Nature* **2012**, *490*, 254–257. [CrossRef] [PubMed]
42. Ray, D.K.; Gerber, J.S.; MacDonald, G.K.; West, P.C. Climate variation explains a third of global crop yield variability. *Nat. Commun.* **2015**, *6*, 5989. [CrossRef] [PubMed]
43. Liao, W.; Menge, D.; Lichstein, J.W.; Ángeles-Pérez, G. Global climate change will increase the abundance of symbiotic nitrogen-fixing trees in much of North America. *Glob. Chang. Biol.* **2017**, *23*, 4777–4787. [CrossRef] [PubMed]
44. Ibáñez, I.; Zak, D.R.; Burton, A.J.; Pregitzer, K.S. Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. *Ecology* **2018**, *99*, 411–420. [CrossRef]
45. Reich, P.B.; Sendall, K.M.; Stefanski, A.; Rich, R.L.; Hobbie, S.E.; Montgomery, R.A. Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature* **2018**, *562*, 263–267. [CrossRef]
46. Wang, C.J.; Zhang, Z.X.; Wan, J.Z. Relationship between gross primary productivity and plant species richness at geographical scales: Evidence from protected area data in China. *Environ. Earth Sci.* **2021**, *80*, 189. [CrossRef]