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Drought conditions could exacerbate nitrogen and phosphorus imbalances in important European forest tree species

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Abstract

Key message A large European forest monitoring dataset reveals a pattern of reduced foliar nitrogen (N) and phosphorus (P) concentrations following drought conditions in spruce and pine, and, in the case of P, beech and oak, often exhibiting N:P imbalances. Gradual nutritional imbalance and nutrient deficiency during droughts raise concern for tree vitality and forest carbon sequestration under climate change.

Context Nitrogen (N) and phosphorus (P) are essential nutrients for tree metabolism, forest growth, and carbon sequestration, yet the drivers of their availability to trees are often complex to untangle.

Aims and methods In this study, we investigated environmental controls of foliar N, P, and N:P based on > 4100 N and P measurements in foliage samples of main tree species (beech, oak, spruce, and pine) across 279 European monitoring sites by applying mixed regression models.

Results We found overall nutritional declines over the past three decades that ranged from – 1.8% to – 2.7% and from – 3.5% to – 4.2% per 10 years for foliar N and P concentrations respectively. At around two-thirds of monitoring sites, where foliar N:P significantly increased over the examined time span, these increases were dominated by declines in foliar P. Foliar sampling years with summer droughts (standardized precipitation evapotranspiration index < – 1.2) were associated with lower standardized foliar P concentrations in all tree species compared to average years.

Conclusion We concluded that variations in drought conditions drive foliar N and P on a short-term, mostly annual basis, while throughfall deposition of N impacted foliar N over larger time spans of several decades depending on tree species.

Keywords Forest nutrition, Drought, Foliage, Deposition, Phosphorus, Nitrogen

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1 Introduction

Nitrogen (N) and phosphorus (P) are critical macronutrients that most frequently limit ecosystem primary production (Vitousek et al. 2010). In forest monitoring programs, foliar nutrient measurements are a common tool to assess tree nutritional status of N and P, and help to identify potential problems with regard to nutritional deficiencies and imbalances (Rautio and Fürst 2013). For European forests, recent studies documented declines in foliar N and P over the past three decades (Jonard et al. 2015; Talkner et al. 2015; Braun et al. 2020; Prietzel et al. 2020; Peñuelas et al. 2020; Du et al. 2021). This trend of foliar N and P raises concern about adverse effects on forest vitality, since N and P availability to trees modulates drought response (Gessler et al. 2017), influences tree growth rates (Braun et al. 2010, 2020; Sardans and Peñuelas 2013; Etzold et al. 2020; Körner 2022), and ultimately the magnitude of the global forest carbon (C) sink (Fernández-Martínez et al. 2014; Peñuelas et al. 2017; Schulte-Uebbing and de Vries 2018; Schulte-Uebbing et al. 2022).

Determining the primary environmental drivers of trends in foliar N and P status is challenging. Key factors under investigation are N and sulfur (S) deposition rates, soil properties, climate, and atmospheric CO_2 levels (Sardans et al. 2017; Talkner et al. 2019; Braun et al. 2020; Peñuelas et al. 2020; Krüger et al. 2021). The complexity of disentangling the relative effects of these factors on nutrient levels arises from their potentially non-linear dynamics and interactions (Sardans and Peñuelas 2012; Yuan and Chen 2015). Additionally, biogeochemical cycles of different nutrients may diverge in profound ways, adding complexity to assessing drivers of nutrient imbalances as represented by relative contents of nutrients to each other (such as foliar N:P) (Du et al. 2021).

Since the 1950 s and with a peak in the 1980 s, large areas of Europe have been subjected to excess deposition loads of reactive inorganic N as a result of anthropogenic emissions from industry and agriculture (Waldner et al. 2015; Engardt et al. 2017). Due to N emission abatement measures, atmospheric N deposition to forests has decreased in the past decades (Waldner et al. 2014), although it remains at relatively high levels in parts of Central Europe (Michel et al. 2024). Depending on deposition history and site-specific environmental factors, N availability to forest trees is spatially diverse across Europe and ranges from high levels to progressively N-limiting oligotrophic conditions (Schmitz et al. 2019; Du et al. 2019, 2021). In contrast, background atmospheric deposition of P is generally considered small (Jönsson Belyazid and Belyazid 2012) or, at most, locally elevated due to short-distance agricultural sources (Tipping et al. 2014). European forest soils originating from carbonate- or silicate-rich parent material are often low in tree-available P (Prietzel et al. 2022). Since soil P is usually not replenished through atmospheric deposition, forest trees have developed adaptative strategies to handle varying degrees of soil P supply (Lang et al. 2016). Lang et al. (2017) identified distinct P cycling regimes in beech forests: In P-acquiring forest systems, P is sufficiently available from primary minerals to be introduced into the reactive forest nutrient cycle by soil microbes and mycorrhizas. In P-recycling forests in contrast, mineral soil P is depleted, so trees shift to P recycling from soil organic matter for maintaining sufficient P nutrition (Lang et al. 2016, 2017; Prietzel et al. 2022). In these systems, P uptake by trees from forest floors is favored through active mineralization and root colonization, while P remains low in mineral soil solution (Jonard et al. 2009, 2010).

Deposition of reactive N is suggested to increase foliar N contents (de Vries et al. 2003; Sardans et al. 2016; Talkner et al. 2019). Its impact on soil P bioavailability and ultimately foliar P, on the other hand, is less straightforward and might depend on its acidifying effect of soil pH. In calcareous soils (relatively high pH), P is mostly present as sparsely soluble calcium (Ca)-bound P (Prietzel et al. 2016), hence soil acidification due to N deposition could potentially increase bioavailable P (Bueis et al. 2019). With progressing acidification (soil pH < 6), however, P tends to form insoluble compounds by reaction with aluminum (Al) or iron (Fe) oxides (Vincent et al. 2012; Bueis et al. 2019). Consequently, plant-extractable P in forest soils is usually considered most abundant between pH 6 and 7 as a rule of thumb (Jönsson Belyazid and Belyazid 2012) with most mineral forest topsoils in Europe falling below this pH range (Cools and De Vos 2011).

In contrast to declining N deposition (Waldner et al. 2014), atmospheric CO_2 levels are continuously increasing. Forest field experiments have provided insight into impacts of experimentally elevated ambient CO_2 on tree nutrient status: in a majority of studies, concentrations of foliar N and P were lower in foliage and aboveground plant biomass under elevated CO_2 (Sardans and Peñuelas 2012; Deng et al. 2015), which could be the result of a nutrient dilution effect in thickening foliage biomass due to CO_2 fertilization (Peñuelas et al. 2020; Krüger et al. 2021; Norby et al. 2024), even though Bader et al. (2013) did not find CO_2 fertilization effects on leaf mass per area in an experimental forest setting. In European forest monitoring, the increase in atmospheric CO_2 correlated with a decrease in foliar N and P, and an increase in N:P (Peñuelas et al. 2020). However, such correlations were not found in a global dataset (Sardans et al. 2017).

Some studies empirically analyzed the effects of climate on forest N and P dynamics. Krüger et al. (2021) found relationships of foliar N and P with temperature and precipitation, which are either negative or positive depending on tree species. Findings of climate effects on foliar P concentrations from other empirical studies are not conclusive (Yuan and Chen 2015; Sardans et al. 2017; Braun et al. 2020). In an experimental setting, however, drought was found to reduce foliar N concentrations in beech and oak (Joseph et al. 2021; Marušić et al. 2023), as well as in a Mediterranean forest (Sardans et al. 2008). Likewise, foliar P concentrations in beech were lower after drought treatments (Peuke and Rennenberg 2004; Marušić et al. 2023).

In this study, we take on the issue of identifying drivers of temporal trends of foliar N, P, and N:P in different tree species by making use of a large harmonized data set of foliar N and P, inorganic N and S throughfall deposition, and drought indicators across European forests over a time period of the last three to four decades. Specifically, we tested the relative impact of N and S deposition and drought on foliar nutrient status, in order to highlight possibly emerging problems under changing deposition and climate regimes.

2 Material and methods

2.1 Description of data sets

2.1.1 Foliar N and P values

We made use of a large European data set of > 4100 measurements of foliar N and P originating from various biogeographic regions (alpine, Atlantic, boreal, continental, and Mediterranean). Sampling and analysis of tree leaves and needles for N and P were performed by members of the International Co-operative Programme (ICP) Forests Level II biomonitoring network (Schwärzel et al. 2022) in accordance with harmonized methods as specified by Rautio et al. (2020). Measurements performed in ICP Forests laboratories include concentrations of N and P in foliage dry weight, as well as dry mass of 100 leaves or 1000 needles. Consequently, foliar N and P in the dataset are available as concentration values (mg $g^{-1}_{d.w.}$) and contents (mg in 100 leaves/1000 needles). In this study, we based part of our temporal analysis (Sect. 3.1 and Sect. 3.3) on foliar contents to avoid concentration dilution effects of nutrients in potentially thickening foliage over time due to CO_2 fertilization (Krüger et al. 2021). Investigated tree species were common beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), and sessile and pedunculate oak (*Quercus petraea* and *robur*, aggregated as *Quercus* sp.). All spruce and pine values originate from current-season needles that had sprouted in the year of sampling. For quality assurance of foliar chemical measurements, ICP Forests laboratories participate in annual mandatory ring tests. Sampling of tree canopies is performed at the 279 forest monitoring sites of this study mostly every second year during peak season in summer for deciduous trees or dormant season in fall/winter for coniferous trees. Multiple (usually 5–10) trees are sampled at most monitoring sites per tree species during each survey year. In order to obtain one foliar *N* or *P* value respectively per site and year, we either used measurements from samples pooled over multiple trees or we averaged values for sites, of which individual tree data was available. Across the whole dataset, the mean inter-tree coefficient of variation of N and P concentrations of foliage sampled from five or more trees per monitoring site and year ranged between 0.22 and 0.25 depending on tree species. For comparison of foliar values from different years and monitoring sites among classes of standardized precipitation evapotranspiration index (SPEI)/relative extractable soil water (REW) (Sect. 3.2), we standardized each foliage value by calculating its deviation from the long-term median of the corresponding time series at each site divided by the standard deviation of the corresponding time series at each site.

For the analysis of site-specific time series of foliar N and P (Sect. 3.1), we exclusively considered data from sites with ≥ 7 foliar survey years. The average (± standard deviation) time series length in the dataset is 14 ± 5 years and the medium calendar year is 2007. The longest time series includes 28 foliar survey years from 1994 to 2022. A geographic overview of forest monitoring sites, where foliar time series were analyzed, is presented in Fig. 1. For the analysis on drought impacts (Sect. 3.2), we calculated standardized (i.e., long-term deviation from site-median divided by site-standard deviation; ltd.) foliar values to make data comparable among sites. For the analysis on foliar deficiencies (Sect. 3.4), we classified foliar concentrations according to threshold values per tree species listed in Mellert and Göttlein (2012) and Göttlein (2015).

2.1.2 SPEI

The SPEI represents a multiscalar drought indicator based on an aggregated climatic water balance, i.e., the difference between precipitation and potential evapotranspiration over the considered time period at a given site (Vicente-Serrano et al. 2010). Daily potential evapotranspiration at each monitoring site was calculated using the FAO Penman–Monteith equation (Allen et al. 1998) implemented in the R package *Evapotranspiration* (Guo et al. 2016). Meteorological input data (open field air temperature, relative humidity, solar radiation, wind speed, and precipitation) to compute potential evapotranspiration and subsequently the climatic water balance were measured on-site (Raspe et al. 2020) and

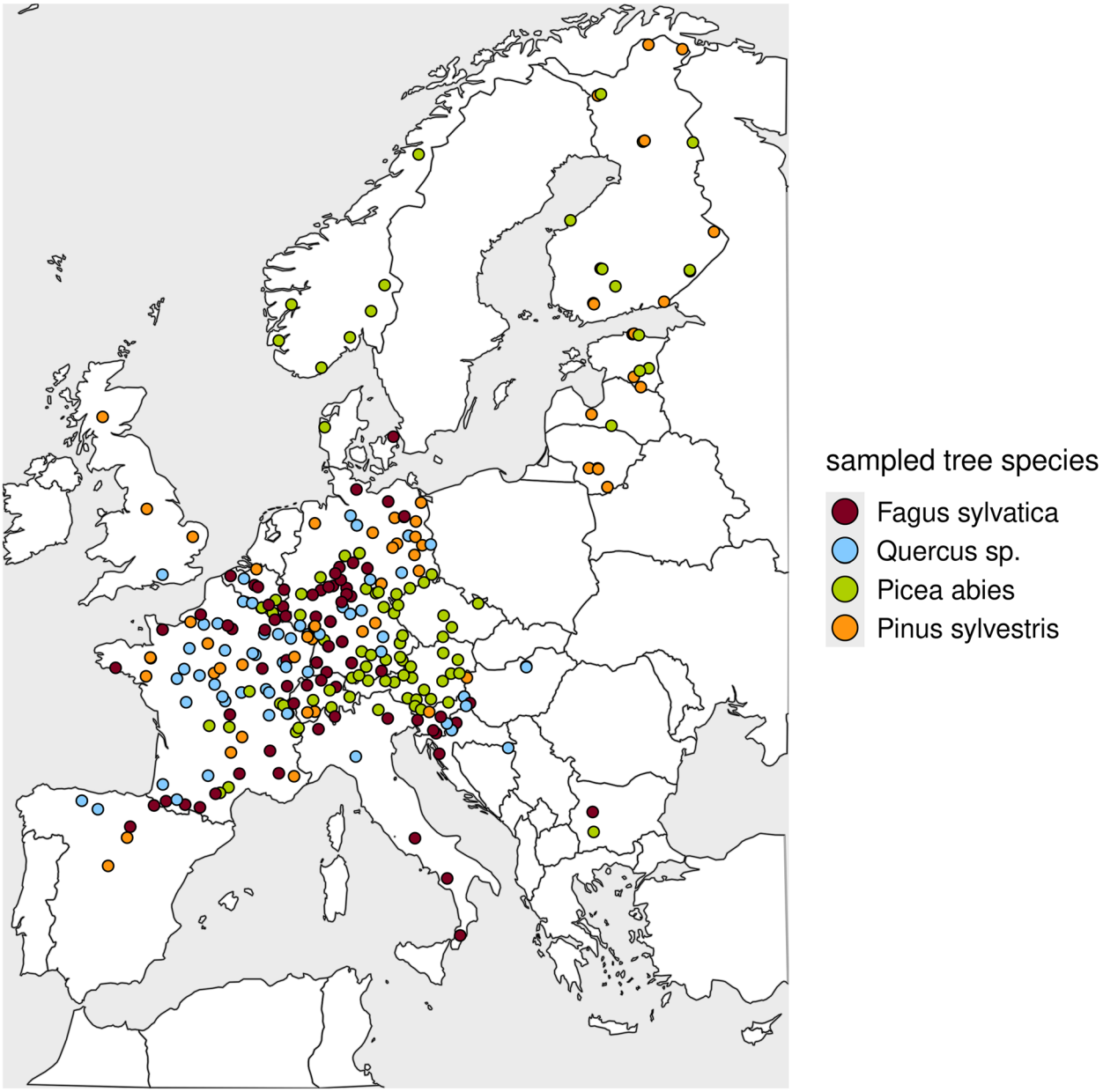

Fig. 1 Map of Europe displaying geographic locations of 279 forest monitoring sites, from which we used temporal data on foliar N and P of sampled tree species

subsequently gap-filled and harmonized with values from ERA-5 on a daily resolution (Muñoz Sabater 2019; Muñoz-Sabater et al. 2021). Final SPEI values were calculated by 12- and 3-month accumulation of the climatic water balance using the R package *SPEI* (Beguería and Vicente-Serrano 2023). Time periods for examining foliar differences among SPEI classes (Sect. 3.2) were spring (3 months: April–June) and summer (3 months: July–September) of the respective foliage sampling year, and the calendar year prior to foliage sampling (12 months: January–December).

2.1.3 Relative extractable soil water

We obtained values of relative extractable soil water (REW) in the root zone by performing water budget modeling using the soil vegetation atmosphere

transport model LWF-Brook90 (Hammel and Kemmel 2001; Schmidt-Walter et al. 2020). Like this, we made use of a modeled drought indicator based on parameters that are (partly) derived from actual on-site measurements, particularly related to soil properties as an alternative to SPEI. For more information on method and model parameters, refer to the Appendix Sect. 6.1 and Sect. 6.2.

2.1.4 Total inorganic N and S deposition

Atmospheric deposition below canopy (throughfall, TF) and outside the forest (bulk deposition) was continuously sampled with typically weekly to monthly intervals. Chemical composition was analyzed in laboratories according to the ICP Forests Manual (Clarke et al. 2022). Annual amounts of throughfall were calculated according to Waldner et al. (2014) and total deposition (TD) of inorganic N estimated using the approach of Braun et al. (2022). Deposition of S represents sulfate (SO_4^{2-}). For multiple linear regression analysis (Tables 2 and 3), we summed up the deposition value of each year with the deposition value of the previous year in order to evaluate short-term deposition impacts on investigated foliar nutrients.

Gap-filling was applied to impute missing N deposition data (single plot-years or entire plots) for the analysis on classes of N deposition and foliage values (Fig. 5). The gap-filling was performed using the random forest approach as implemented by the R package *ranger* (Wright and Ziegler 2017) and EMEP MSC-W model output as predictor variables (Simpson et al. 2012) (see Appendix Sect. 6.3 for further details).

2.2 Statistical analysis

For a tabulated overview of regression models used in this study, refer to Table 1.

2.2.1 Linear mixed-effects model (LMM)

To identify species-specific temporal trends of foliar N, P contents and concentrations, and N:P across the ICP Forests monitoring sites, we applied a linear mixed model with time as the fixed effect and site as random factor (random intercept and slope) using the lmer-function from the *lme4* package (Bates et al. 2015) in R. Foliage data was standardized prior to model application to make intercept and slope independent from each other. Time data on foliage sampling years was centered around the medium monitoring year 2007, such that the intercept of the LMM represents an estimate of the mean foliar value in 2007. From the LMM output, we calculated the relative percent change in 10 years by dividing the LMM slope by the LMM intercept and multiplying with 10. For more details on this approach, refer to Jonard et al. (2015).

2.2.2 Linear regression trends

In order to compare the magnitude of temporal trends of foliar N with foliar P (Sect. 3.1), we calculated respective linear regression slopes per tree species for each monitoring site relative to the respective regression intercept in 2007.

2.2.3 Multiple linear regression

Data on deposition of inorganic N and of S (Sect. 2.1) to forest monitoring sites were available for a subset of sites (211 out of 279) of the total dataset of foliar N or P, such that the relative impact of N and S

Table 1 Overview of statistical methods and their motivation to achieve targeted goals of analysis

Goal of analysis	Method	Reason for method
Identification of global temporal trends across the whole foliar dataset	Linear mixed models (LMM) with monitoring site as random effect	Output from LMM provides information on a linear relationship between two variables (here: foliar nutrient and time) while controlling for the variation from different groups that data-points fall into (here: monitoring sites)
Assessing the importance of foliar N vs. foliar P for progressing foliar N:P imbalances over time	Simple linear regression	Comparison of the magnitude of significant linear regression slopes derived from site-data independent of overall temporal trends
Relative short-term impact of N deposition, S deposition, and summer SPEI on foliar N and P contents	Multiple linear regression, detrended values	Data detrending focusing on short-term effects by restricting spurious regression due to concurrent but possibly unrelated trends
Relative long-term impact of N deposition, S deposition, and summer SPEI on foliar N and P contents	Multiple linear regression, absolute (non-detrended) values	Multiple regression of absolute values evaluates concurrent long-term temporal trends and spatial patterns

deposition vs. SPEI on foliar N and P can be evaluated for these sites. To do this, we performed multiple linear regression of foliar P and N contents respectively to summer (July–September) SPEI of the corresponding foliage sampling year and to N and S deposition. We ran the multiple linear regression analysis for deposition aggregated over a time period of 2 years (deposition value during foliage sampling year + during the previous year). Since foliar and deposition values follow temporal trends (Sect. 3.1, Waldner et al. 2014), we compared output from multiple linear regression for two separate model runs using (a) linear detrended and standardized foliar and deposition data per monitoring site to investigate short-term impacts independent of monitoring site, and (b) data without prior detrending to investigate coinciding long-term deposition and foliar trends as well as spatial patterns. Summer SPEI did not exhibit any detectable significant linear trends, except on seven sites, which we excluded from the dataset prior to regression analysis.

2.2.4 Wilcoxon test

We used the Wilcoxon test to assess foliar differences among classes of drought indicators.

3 Results

3.1 Overview of foliar N and P trends across monitoring sites

Results from linear mixed-effects models indicate statistically significant temporal declines in foliar N and P concentrations in all examined tree species across the overall dataset. Over 10 years, relative to the baseline year 2007, overall percent reduction rates ranged from −1.7% to −2.6% and from −3.5% to −4.1% for foliar N and P concentrations respectively (Fig. 2, leftmost bars). Contents of N in 100 leaves/1000 needles exhibit statistically significant and negative temporal trends exclusively in pine. Corresponding trends of P contents are statistically significant and negative for oak, spruce, and pine, but not for beech (Fig. 2, rightmost bars). The percent change of the foliar ratio N:P is positive and significant for all species except beech (Fig. 2, middle bar).

The increase of the N:P ratio can be due to (1) an increase in N with no existing trend in P, (2) a decrease in P with no existing trend in N, (3) concurrently an increase in N and a decrease in P, (4) an increase in N that is of higher magnitude than a concurrent increase in P, or (5) a decrease in P that is of higher magnitude than a concurrent decrease in N. We compared the magnitude of linear regression slopes of foliar N and P concentrations at all 82 monitoring sites with a significantly increasing linear temporal trend in foliar N:P. At around two-thirds (54 sites: 44 sites of case 2, 10 sites of case 5, no sites of case 3 or 5) of the 82 sites, increasing foliar N:P was primarily driven by declining foliar P, highlighting the critical role of P in emerging N:P imbalances. At only 7 out of 82 sites (~ 9%) with significantly increasing foliar N:P, the respective increase in foliar N:P was dominated by an increase in N with no existing trend in P (case 1). This result suggests that N plays a minor role in temporally progressing nutrient imbalances derived from increasing foliar N:P. The rest (21 sites) of the 82 sites of increasing foliar N:P could not be classified as dominated by either foliar P or foliar N.

At 20 sites, foliar N:P decreased significantly over the respective time periods. Of these 20 sites, 10 sites were dominated by declines in foliar N, either because foliar N was decreasing by magnitude more than foliar P (2 out of 10 sites) or because there was no significant trend in foliar P, but in foliar N (8 out of 10 sites). Trends at 4 out of the 20 sites with significantly decreasing foliar N:P were P-driven as a result of significantly increasing foliar P, the remaining 6 sites could not be attributed to either N or P dominance.

3.2 Relationship of foliar N:P, foliar N and P with SPEI

Across the dataset, standardized ltd. (long-term deviation from site-median divided by site-standard deviation) foliar N:P values exhibited significant distinguishability when partitioned into classes of associated environmental conditions defined by SPEI as dry (represented by low SPEI; here: SPEI < −1.2), medium, and wet (represented by high SPEI; here: SPEI > 0.5). As a dataset-wide pattern, foliar N:P was higher after dry conditions (low SPEI) compared to wet conditions (high SPEI). This difference of ltd. foliar N:P between low and high SPEI class, however, varied among tree species and SPEI time periods: all tree species, except spruce, exhibited significantly higher ltd. foliar N:P following dry summer conditions (Fig. 3). For spring SPEI, the difference in ltd. foliar N:P between wet and dry conditions was significant for the two deciduous species (beech and oak), but not for spruce and pine (Appendix Fig. 9). For previous year SPEI, ltd. foliar N:P was significantly different between low and high SPEI exclusively for beech (Appendix Fig. 7).

Depending on environmental conditions, foliar N and P concentrations may have a different relative impact on foliar N:P. For all investigated tree species, ltd. foliar

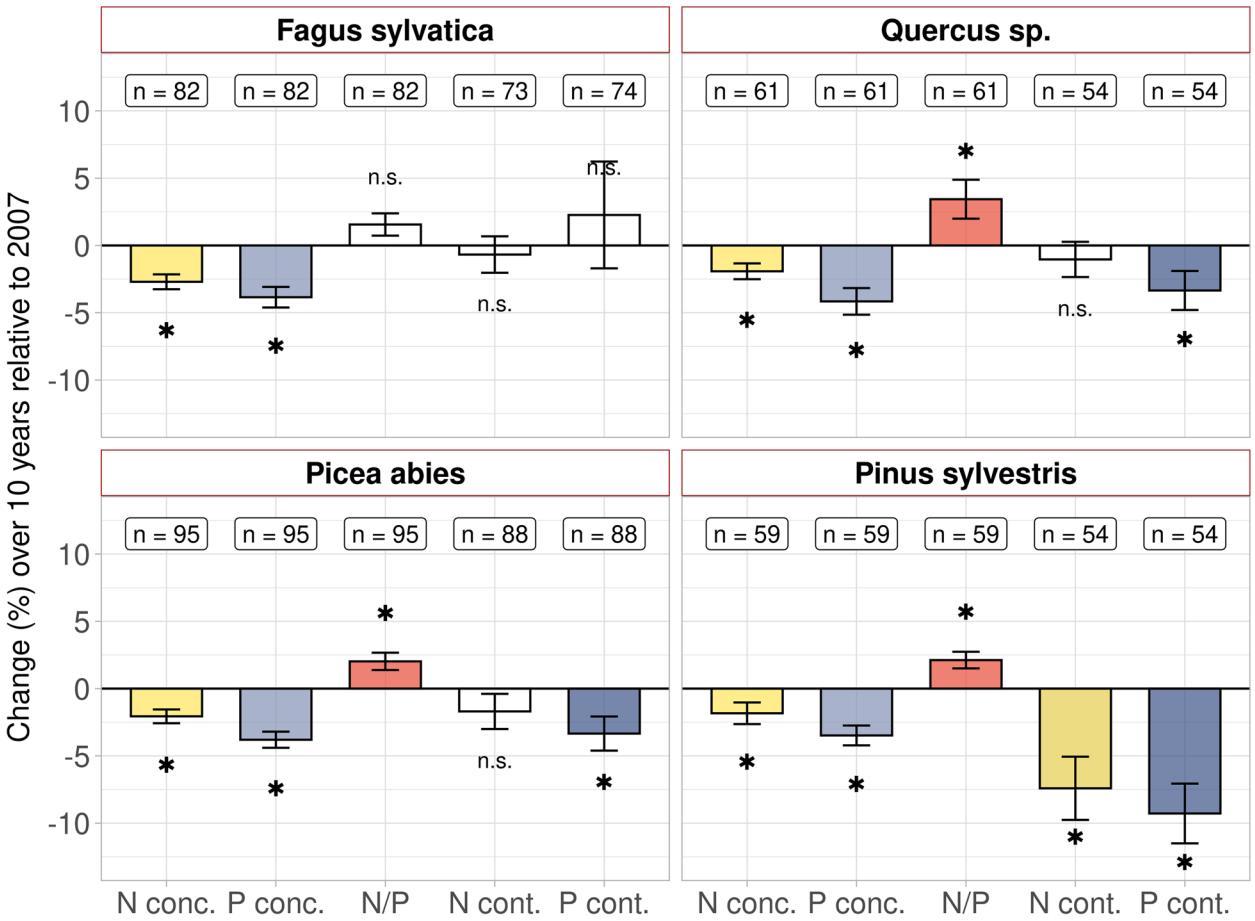

Fig. 2 Respective percent temporal change of foliar nitrogen (N) and phosphorus (P) concentrations (conc., leftmost bars) and contents (cont., rightmost bars), and foliar N:P ratio (middle bar) over 10 years relative to the medium calendar year 2007 across time series of all monitoring sites. Values are derived from linear mixed-effects models using ICP Forests measurements of foliage samples from common beech (*Fagus sylvatica*), sessile and pedunculate oak (aggregated as *Quercus* sp.), Norway spruce (*Picea abies*), and Scots pine (*Pinus sylvestris*) with foliar sampling sites as a random factor. Asterisks (*) denote statistical significance on a 0.95 confidence interval (n.s. = not significant) and *n* denotes number of sites. Foliar measurements of spruce and pine were performed in current-season needles

P concentrations were significantly lower after dry summer periods of SPEI < −1.2 than after wet periods of SPEI > 0.5 (Fig. 4). Ltd. foliar N concentrations were lower after dry relative to wet summer periods in oak and pine, but not in beech and spruce (Appendix Fig. 16). Therefore, for beech and spruce, this sensitivity of ltd. foliar P concentrations to environmental conditions in summer, but not of ltd. foliar N concentrations suggests that higher ltd. foliar N:P after a dry than after a wet summer (Fig. 3) is driven by P.

With some minor differences, results on relationships of foliar N, P, and N:P with SPEI classes were equivalent for REW classes, suggesting that both drought indicators are suitable for evaluating drought impacts on foliar N, P, and N:P. For the corresponding REW assessment, refer to Appendix Sect. 6.4.

3.3 Relative impact of SPEI, N, and S deposition on foliar P and N contents

We find summer SPEI to be a significant and positive explanatory variable of ltd. foliar N and P contents respectively for all tree species—except beech ltd. foliar N—in multiple linear regression of standardized and detrended data (i.e., no consideration of temporal trends over the past three decades) (see Table 2). Thus, decreasing summer SPEI values (i.e., relatively drier conditions) are related to more negative deviations of foliar N contents (except beech) and foliar P contents from long-term median at varying detrended (i.e., short-term) loads of N and S deposition.

In a comparative regression run using absolute foliar contents (mg N or P in 100 leaves/1000 needles) and spatiotemporally associated deposition of total inorganic N

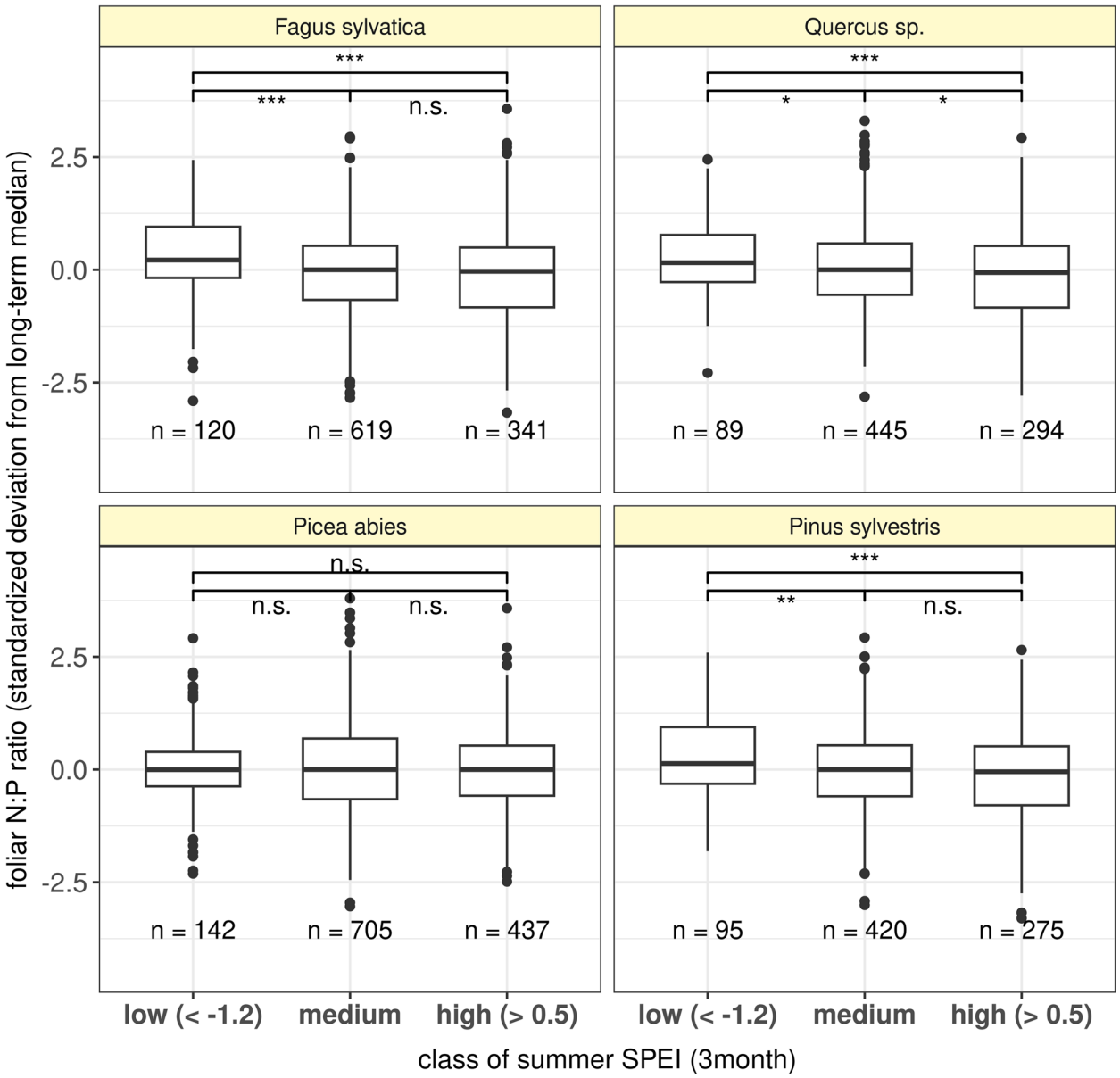

Fig. 3 Standardized values of foliar N:P (deviation from long-term median per forest site) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of low, medium, and high summer (July–September) SPEI. Low SPEI values < − 1.2 represent dry environmental conditions (integrated precipitation deficit and atmospheric evaporative demand), while high SPEI values > 0.5 represent relatively wet environmental conditions at each site and summer period. Asterisks denote significance level for differences of standardized foliar N:P among SPEI classes determined by Wilcoxon test (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant) and *n* denotes number of site-years

and S without prior data detrending or standardization, we evaluated significantly positive relationships of foliar N contents with N deposition for spruce and pine and of foliar P contents for pine (Table 3). Hence, spatiotemporal absolute levels of N deposition were associated with absolute levels of foliar N contents for spruce and pine.

As an illustrative example, Fig. 5 visualizes spatial patterns of co-occurring relatively low/high N deposition levels with low/high foliar N contents of spruce and pine of three different time periods until 2020 (see Appendix Sect. 6.5 for method details). In Central Europe, historically high N deposition loads (Waldner et al. 2014; Michel et al. 2024) co-occur with relatively high needle N contents at multiple forest monitoring sites, while in Northern Europe, relatively low N deposition and N contents co-occur at multiple sites (Fig. 5). Figure 5 illustrates that

these spatial patterns are stable over several decades. Therefore, we conclude that significant effects of N deposition on foliar N or P contents in Europe are primarily long-term, spatial and tree species-specific, e.g., regions with historically high N deposition loads are associated with higher foliar N contents at multiple forest monitoring sites. Summer SPEI, on the other hand, impacts foliar N and P contents at forest monitoring sites on a short-term annual basis (detrended standardized data).

Please note, however, that while regression relationships of foliar N and P contents with summer SPEI, N, and S deposition are significant across the dataset depending on tree species and variables, they otherwise explain little variation of foliar values (see R^2 values in

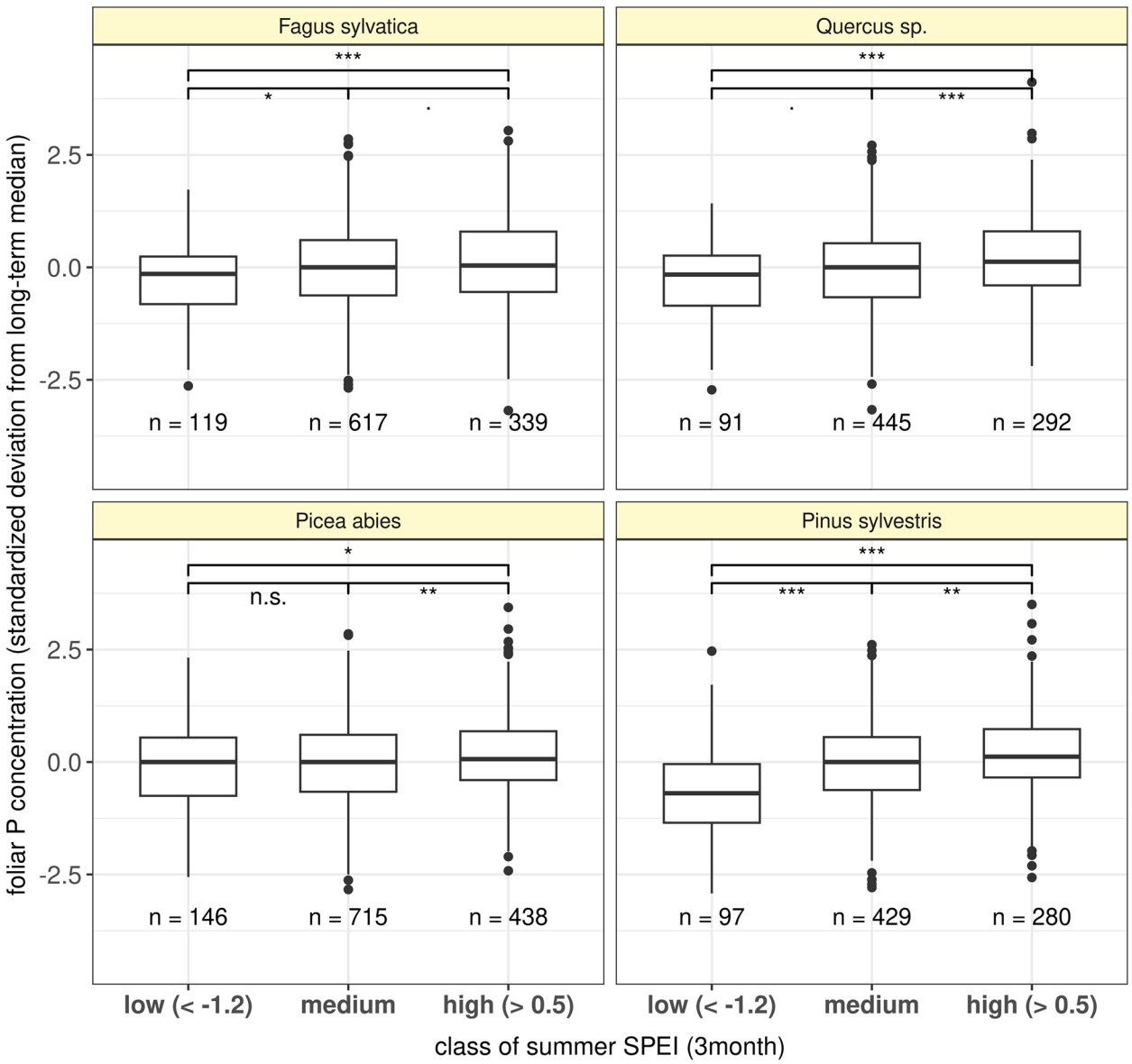

Fig. 4 Standardized values of foliar P concentrations (deviation from long-term median per forest site) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of low, medium, and high summer (July–September) SPEI. Low SPEI values < − 1.2 represent dry environmental conditions (integrated precipitation deficit and atmospheric evaporative demand), while high SPEI values > 0.5 represent relatively wet environmental conditions at each site and summer period. Asterisks denote significance level for differences of standardized foliar P contents among SPEI classes determined by Wilcoxon test (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant). The number of site-years, *n*, is given below each box

Tables 2 and 3). We therefore caution that at an individual forest site other unaccounted factors might be more relevant to foliar N and P than, e.g., N deposition (see Sect. 4.2).

3.4 SPEI associated with foliar N and P deficiencies

We investigated SPEI effects on tree vitality as represented by foliar N and P deficiency status. Foliage samples classified as P-deficient were associated with significantly lower summer SPEI (except oak) than non-P-deficient foliage samples (Fig. 6). Equivalent evaluation of N deficiency status revealed that summer SPEI values were significantly lower associated with N-deficient than non-N-deficient pine needles but no significant difference for spruce needles was found (Appendix Fig. 23, lower pane). For beech and oak, assessment of N deficiency was not meaningful because only 1% or less of total available leaf N concentrations in the European ICP Forests dataset exhibit N deficiencies.

We examined co-occurrences of summer SPEI < −1.2 (dry conditions) with P-deficient foliage samples at the respective monitoring site and foliage sampling year (site-year) with the goal to test if these co-occurrences happen at higher rates than if the two events were independent from each other. Site-years with summer SPEI < −1.2 represented 11% of total site-years, and 28% of these site-years with summer SPEI < −1.2 were associated with foliage samples exhibiting P deficiency. Under the premise that summer SPEI < −1.2 and foliar P deficiency were two independent events, the binominal probability of the evaluated percentage of co-occurrences of foliar P deficiency and summer SPEI < −1.2 equates to 0.1% across the total dataset (see Appendix Sect. 6.6 for details on probability assessment). Broken down to tree species, the respective probability of independent co-occurrences is 2.6% for beech, 21.3% for oak, 18% for spruce, and 1.2% for pine. We therefore suggest that summer SPEI < −1.2 and foliar P deficiency are very likely not independent in the case of beech and pine, and moderately likely not independent in the case of oak and spruce. The equivalent probability of observed co-occurrences of foliar N deficiency and summer SPEI < −1.2 under the assumption of independence is 58.2% for spruce and 2.5% for pine, thus prevalence of N deficiency after dry summer conditions is very likely elevated in pine needles. Based on this probability assessment, we therefore hypothesize that dry environmental conditions during summer have the potential to jeopardize P nutritional status of beech and pine, and potentially oak and spruce, and N nutritional status of pine.

4 Discussion

4.1 Drought indicator impacts on foliar N, P, and N:P per tree species

Where we found significant differences among classes of SPEI (or REW, see Appendix Sect. 6.7), drier than usual environmental conditions were consistently associated with lower ltd. foliar N and P concentrations, and higher ltd. foliar N:P (see Sect. 3.2). Specifically in the case of P, we attribute lower foliar P associated with dry conditions to decreased P uptake from soils, because phosphate transport from soils to roots occurs mainly via

Table 2 Output from multiple linear regression of ltd. foliar N contents (detrended) or ltd. foliar P contents (detrended) respectively to ltd. N deposition (detrended) + ltd. S deposition (detrended) + summer SPEI. Statistically significant coefficients are marked in bold font with asterisks denoting significance level (***: 0.001; **: 0.01; *: 0.05)

Species	Independent variables	Dependent variables					
		ltd. foliar N contents (detrended)			ltd. foliar P contents (detrended)		
		Slope (s.e.)	R^2	*n*	Slope (s.e.)	R^2	*n*
Beech	ltd. N depo. (detrended)	0.07 (0.05)			−0.02 (0.05)		
	ltd. S depo. (detrended)	**0.11 (0.05)***	0.03	436	0.17 (0.05)	0.02	442
	Summer SPEI	0.06 (0.05)			**0.09 (0.04)***		
Oak	ltd. N depo. (detrended)	−0.12 (0.08)			−0.09 (0.08)		
	ltd. S depo. (detrended)	0.01 (0.08)	0.04	222	−0.03 (0.08)	0.04	222
	Summer SPEI	**0.19 (0.07)****			**0.18 (0.07)***		
Spruce	ltd. N depo. (detrended)	−0.01 (0.04)			−0.03 (0.04)		
	ltd. S depo. (detrended)	−0.03 (0.04)	0.04	685	−0.04 (0.04)	0.04	692
	Summer SPEI	**0.20 (0.04)*****			**0.19 (0.04)*****		
Pine	ltd. N depo. (detrended)	−0.10 (0.06)			−0.05 (0.06)		
	ltd. S depo. (detrended)	−0.08 (0.05)	0.03	390	−0.05 (0.05)	0.04	399
	Summer SPEI	**0.12 (0.05)***			**0.17 (0.05)*****		

Table 3 Output from multiple linear regression of foliar N contents (non-detrended) or foliar P contents (non-detrended) respectively to N deposition (non-detrended) + S deposition (non-detrended) + summer SPEI. Statistically significant coefficients are marked in bold font with asterisks denoting significance level (***: 0.001; **: 0.01; *: 0.05)

Species	Independent variables	Dependent variables					
		Foliar N contents (non-detrended)			Foliar P contents (non-detrended)		
		slope (s.e.)	R^2	*n*	slope (s.e.)	R^2	*n*
Beech	N depo. (not-detrended)	0.42 (0.56)			−0.02 (0.03)		
	S depo. (not-detrended)	0.61 (0.56)	0.02	436	0.05 (0.03)	0.02	442
	Summer SPEI	4.85 (3.51)			**0.50 (0.21)***		
Oak	N depo. (not-detrended)	−1.10 (2.32)			−0.23 (0.15)		
	S depo. (not-detrended)	−1.30 (2.03)	0.02	222	0.06 (0.13)	0.03	222
	Summer SPEI	27.8 (16.5)			2.00 (1.07)		
Spruce	N depo. (not-detrended)	**0.45 (0.06)*****			−0.01 (0.01)		
	S depo. (not-detrended)	0.02 (0.07)	0.15	685	0.01 (0.01)	0.02	692
	Summer SPEI	**2.42 (0.63)*****			**0.30 (0.09)*****		
Pine	N depo. (not-detrended)	**5.94 (0.59)*****			**0.30 (0.06)*****		
	S depo. (not-detrended)	0.11 (0.80)	0.32	390	0.09 (0.08)	0.15	399
	Summer SPEI	**14.4 (5.32)****			**1.81 (0.53)*****		

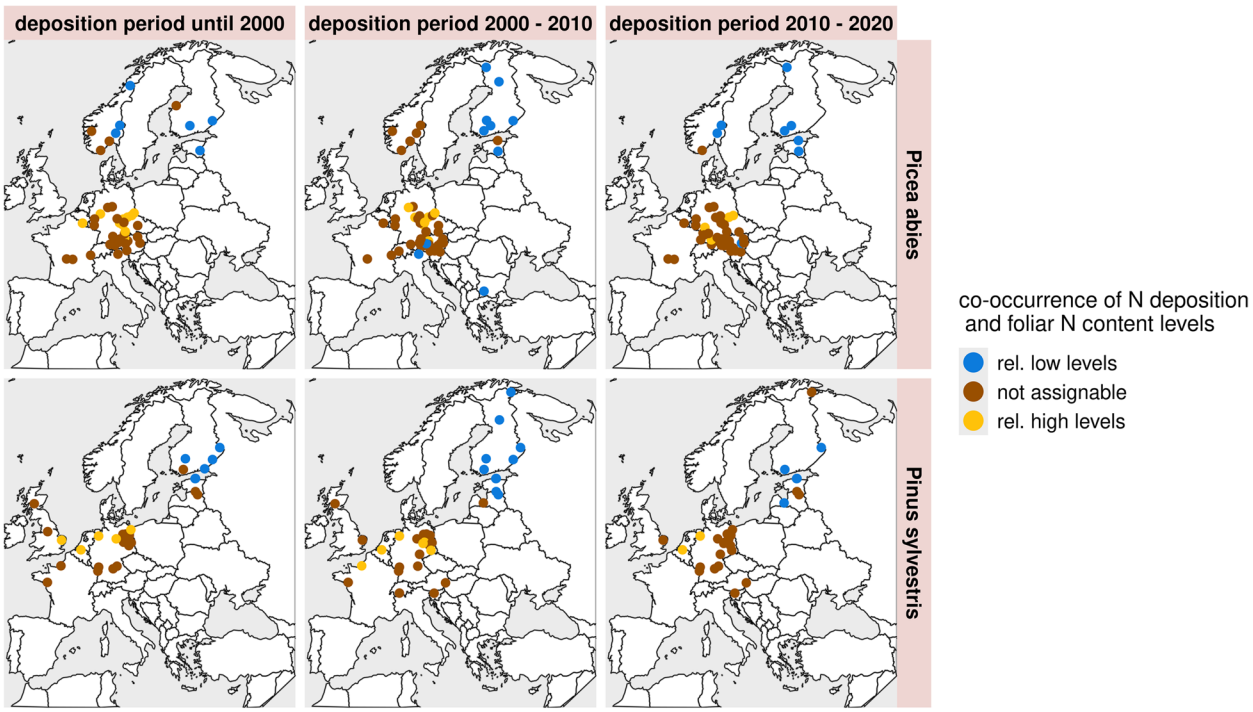

Fig. 5 Spatial co-occurrence of N deposition levels averaged over three different time periods and foliar N contents of spruce (top row) and pine (bottom row) at the end of the respective time periods at ICP Forests monitoring sites. Co-occurrence classes of rel. low/high levels represent sites, where N deposition levels and foliar N contents are both relatively low/high (i.e., both < 30th percentile/> 70.th percentile of overall dataset) related to the respective time period. The class "not assignable" denotes sites, where levels of N deposition and foliar N contents coincided with the medium range of the overall dataset or could not be consistently classified as either both relatively low or relatively high (see Appendix Sect. 6.5)

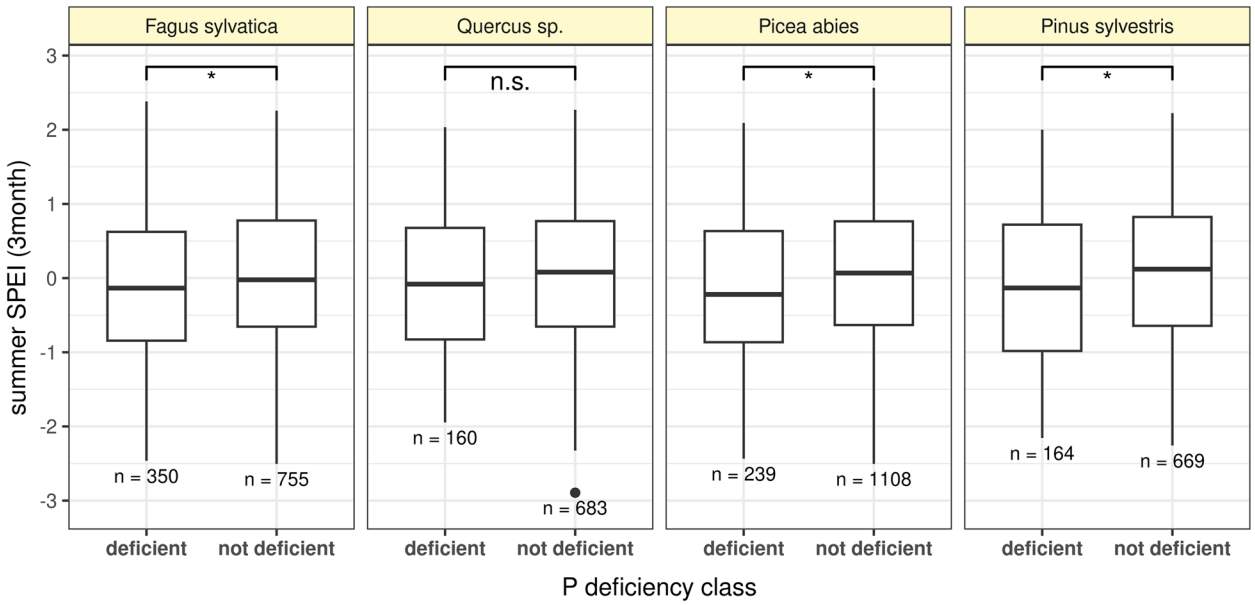

Fig. 6 Values of standardized precipitation evapotranspiration index (SPEI) during summer (July–Sept., see Sect. 2.1) grouped by P deficiency class (deficient/not deficient) of foliar P concentration per tree species from respective forest monitoring site and foliage survey year. Asterisks denote significance level for differences between foliar P deficiency classes determined by Wilcoxon test (***: 0.001; **: 0.01; *: 0.05; n.s.: not significant)

diffusion, with the diffusion coefficient in the soil being directly proportional to volumetric soil water content (Marschner and Rengel 2012). The impact of drought on ectomycorrhizal mediated P uptake, however, is currently unclear. Differences in ltd. foliar N, P, and N:P related to water balance deviated somewhat by tree species with regard to time periods, SPEI vs. REW, and nutrient. In the following, we discuss these patterns for each tree species separately.

4.1.1 Fagus sylvatica

Beech was the only tree species, for which ltd. foliar N and P concentrations, and N:P differed significantly related to classes of SPEI of the calendar year prior to the foliar sampling year (Appendix Figs. 7, 12 and 18). We speculate that this memory effect of beech to the climatic water balance of the previous year is related to beech fructification dynamics. Nussbaumer et al. (2021) found that in years of high production of fruits and seeds (so-called mast years), foliar N and P contents in beech are reduced, which was attributed to resource allocation of nutrients to generative growth. Fructification could therefore partly explain our findings of lower ltd. beech foliar N and P concentrations after dry conditions of the previous year, because masting behavior of beech was observed to be linked to weather, including dry and warm summer conditions during the year prior to the mast year (Hacket-Pain et al. 2015; Bogdziewicz et al. 2017; Nussbaumer et al. 2018). Furthermore, memory effects of previous-year temperature and precipitation on radial growth have been reported for beech in contrast to oak, which might be relevant for foliar nutrients (Di Filippo et al. 2007; Čufar et al. 2008; Hacket-Pain et al. 2016). Additionally, we note that Ognjenović et al. (2022) found a strong impact of previous year drought on defoliation change of beech in Croatia. Effects of prolonged drought on foliar P concentrations were confirmed experimentally in beech saplings (Marušić et al. 2023). Apart from SPEI during the year prior to the foliage sampling year, both classes of low spring SPEI and low summer SPEI are associated with low ltd. beech leaf P concentrations by dataset-wide tendency (Appendix Fig. 20, Fig. 4). By contrast, there was no significant difference of ltd. beech leaf N concentrations among classes of spring and summer SPEI (Appendix Figs. 14 and 16). Therefore, the relationship of ltd. foliar N:P of beech with spring and summer SPEI is likely driven by P.

4.1.2 Quercus sp

Ltd. foliar P concentrations of oak differed significantly exclusively between classes of low to high spring (Appendix Fig. 20) and summer SPEI (Fig. 4). In Central Europe, oaks are observed to be more resistant to forest drought with regard to growth and sap flow compared to tree species like beech or spruce (Scherrer et al. 2011; Vitasse et al. 2019; Vanhellemont et al. 2019), which is attributed to greater rooting depth and ring-porous wood of oak (Leuzinger et al. 2005; Neuwirth et al. 2021), albeit an

increase in oak mortality was reported after the extreme summer drought in Europe in 2018 (Schuldt et al. 2020). Although the link between oak drought resistance and foliar nutrients is not straightforward, we speculate that nutrient transport in oak is affected to a lesser extent by low water content in upper topsoils than in beech, spruce, and pine. There are almost no oak foliage samples in the whole dataset exhibiting N deficiency (Appendix Fig. 23), suggesting that differences in oak leaf N:P between dry and wet environmental conditions in spring/summer (Appendix Fig. 9, Fig. 3) are driven by P. Finally, we hypothesize that wet spring conditions (relatively high SPEI > 0.5) favor relatively high levels of foliar P in oak (Appendix Fig. 20).

4.1.3 Picea abies

For spruce, we evaluated significant differences of ltd. foliar P and N concentrations in summer among SPEI/REW classes and REW classes respectively (Fig. 4, Appendix Figs. 16 and 17). In contrast, ltd. foliar N:P of spruce did not exhibit significant differences among classes of SPEI (Fig. 3, Appendix Figs. 7 and 9), suggesting a comparable impact of environmental conditions in spring or summer on foliar N and P of spruce. We point out that all coniferous *N* and *P* values evaluated here were measured in current-season needles that had been harvested in most cases during the dormant season in fall/winter of the year of needle sprouting, thus we cannot infer the impact of dry vs. wet environmental conditions on multi year-old needles. There is some uncertainty in literature related to translocation of P from older to younger spruce needles (Khanna et al. 2007). However, a more recent study of adult spruce trees reports no targeted P translocation from 2- to 1-year-old needles to counter variation in soil P availability over time (Manghabati et al. 2019), and a possibly present nutrient translocation did not offset differences in ltd. foliar N and P concentrations among SPEI/REW classes. Both N and P have been identified as primary limiting nutrients for growth of spruce in the Bavarian Alps (Mellert and Ewald 2014). Therefore, our results on differences in ltd. foliar N and P concentrations in spruce among classes of low to high SPEI/REW draw attention to the role of dry environmental conditions in spruce N and P status that might affect spruce growth.

4.1.4 Pinus sylvestris

Similarly to spruce, pine ltd. foliar P and N concentrations differed significantly among classes of low to high spring/summer SPEI/REW (Fig. 4, Appendix Figs. 14, 15, 16, 17, 20, 21 and 22), but not among respective classes of the previous calendar year (except for REW, Appendix Figs. 12, 13, 18 and 19), indicating that dry to wet environmental conditions impact foliar pine N and P primarily during the year of needle sprouting. Differences among ltd. foliar pine N:P values (Appendix Figs. 7, 8, 9, 10 and 11) were only significant for REW classes of spring and for SPEI classes of summer (Fig. 3), and it is challenging to determine, if these N:P differences are driven by N or P. The prevalence of both foliar N and P deficiencies in pine is elevated after summer SPEI < −1.2, emphasizing the adverse effect of drought on pine nutritional status.

4.2 Unaccounted factors in regression models of this study

While output from multiple linear regression models of ltd. foliar P and N contents to summer SPEI and N and S deposition revealed multiple significant and consistent relationships (see Sect. 3.3), respective coefficients of determination (R^2) were low (Tables 2 and 3), suggesting that a high variance in foliar P and N contents cannot be explained by the respective regression models, which outputs only tendencies across the whole ICP Forests data set. We hypothesize that this unexplained variance mainly originates from (i) variation in forest soil conditions, (ii) tree internal nutrient dynamics, and (iii), to a lesser extent, from temporal variation of foliar nutrients within the growing season and measurement uncertainty:

(i) Soil characteristics like nutrient content, soil texture, soil parent material, humus form, pH, root distribution, and mycorrhiza regulate nutrient availability to plants (Marschner and Rengel 2012; Moore et al. 2022; Sandén 2024), such that the nutrient status of leaves reflects available soil nutrients like P (Fäth et al. 2019). We found significant relationships of median foliar P concentrations with topsoil total P stocks for beech, spruce, and pine (Appendix Fig. 24). For analyzing water balance impacts on foliar N and P (Sect. 3.2), we standardized all foliar values as deviations from respective long-term site-median divided by the respective site-standard deviation (Sect. 2.1), in order to improve comparability among forest sites. However, under the premise that soil nutrient availability mediates the effect of water balance conditions on foliar nutrients to an unknown extent, perfect site comparability cannot be achieved by standardization of foliar nutrient values alone. We thus speculate that the high variance of regression model output could be reduced by separately evaluating environmental impacts on foliar nutrients by soil nutrient availability levels.

(ii) An additional source of uncertainty in the linear regression model (Sect. 3.3) could be related to tree internal nutrient cycling, storage, and resource allo-

cation. Trees resorb part of their nutrients in foliage from senescing leaves into storage structures of trunk or roots, such that nutrients are readily available for tree growth the following spring in temperate latitudes (Brant and Chen 2015; Muhammad et al. 2020). Furthermore, inter-year internal nutrient investments (e.g., nutrients in leaves vs. fruits) of trees exhibiting masting behavior differ between masting and non-masting years (Nussbaumer et al. 2021; Bogdziewicz et al. 2024). In literature, there exist inconsistent reports concerning climate impacts on resorption efficiencies of N and P, as analysis of these relationships in global datasets is often confounded by latitudinal and soil nutrient effects (Brant and Chen 2015; Yan et al. 2018). Moreover, severe drought events in forests may result in early leaf senescence to avoid water loss from transpiration, which can entail nutrient loss if resorption did not occur before leaf desiccation (Marchin et al. 2010). The extent to which dry environmental conditions affect timing of leaf senescence, nutrient resorption, and evolving nutrient resource allocation due to fructification merits further research and could not be accounted for in this study.

(iii) Within the ICP Forests program, foliage sampling of deciduous trees happens during the European peak growing season before autumnal senescence (July–September depending on latitude) for deciduous trees and during the dormant season (October to February depending on latitude) for coniferous trees (Rautio et al. 2020). During these foliage sampling periods, foliar N and P concentrations are expected to be relatively stable (Kelly and Lambert 1972; Hatcher 1990; Mediavilla and Escudero 2003), yet fluctuations in foliar nutrients within the sampling periods cannot be ruled out, increasing data variation. In ICP Forests laboratory ring tests, tolerable deviation from mean test value is ± 10% for N and P concentrations (Tatzber 2024). Thus, we suggest that measurement errors of nutrient concentrations and of leaf and needle mass only contribute to a small extent to variance of regression model output.

5 Conclusion

Foliar P concentration, and, to a lesser extent, foliar N concentration in main tree species, has been decreasing at many forest monitoring sites in Europe, while foliar N:P has been increasing (Sect. 3.1). Across foliage data of this study, we found that drought conditions (SPEI < − 1.2) during summer are associated with higher negative deviations from respective site-median of foliar P concentrations in all investigated tree species (beech, oak, spruce, and pine), and of foliar N concentrations in spruce and pine compared to respective foliar values after relatively wet summer conditions (SPEI > 0.5). Depending on tree species, differences between ltd. foliar P or N concentrations were also significant for spring as aggregation time period for wet vs. dry environmental conditions (beech, spruce, and pine) or, in the case of beech, for the calendar year prior to foliage sampling (Sect. 3.2). We conclude that hydrologic conditions during summer, spring, and, in the case of beech, the previous year impact particularly foliar P concentrations, but also foliar N concentrations on a short-term annual basis. Throughfall deposition of N impacts foliar nutrition insofar as forest sites with spatiotemporally relatively high deposition rates are associated with relatively high foliar N contents in spruce and pine, thus N deposition could be a long-term driver of foliar N (Sect. 3.3).

Evolving nutritional imbalance as represented by increases in N:P could compromise tree health and vitality of future forests. Changes in P mostly dominate both temporal trends of foliar N:P of all investigated tree species (Sect. 3.1) and drought impacts on foliar N:P of beech and oak (Sect. 3.2). Since climate change is progressing and summer heatwaves are projected to become more frequent particularly in Southern and Central Europe (IPCC 2023), P nutritional status of forest trees could further decline and nutritional imbalance of N:P could exacerbate at affected forest sites. We therefore call for research on mechanisms disrupting P uptake under drying conditions by trees that are rooted in forest soils of various levels of soil P availability. Thereby, forests most at risk of current or future P deficiencies and N:P imbalance can be identified and silvicultural practices adapted (like tree species selection and association in mixed forests, harvesting intensity and methods with regard to soil disturbances and fertilization).

Appendix

Description of water budget modeling output: relative extractable soil water (REW)

We obtained values of REW in the root zone by performing water budget modeling using the soil vegetation atmosphere transport model LWF-Brook90 (Hammel and Kemmel 2001; Schmidt-Walter et al. 2020). LWF-Brook90 simulates daily transpiration and interception evaporation of a "single big leaf" canopy, along with soil and snow evaporation, and vertical

water fluxes through a soil profile by solving the Richards equation (Richards 1931). The model was run using the same meteorological dataset that was used to calculate SPEI, along with site-specific stand characteristics, including leaf area index (LAI) and stand height measured as part of ICP Forests monitoring. If no on-site measurements were available, allometric functions were used to estimate LAI from mean diameter at breast height (DBH), stand height, stand age, and stand density (spruce: Hammel and Kemmel (2001), beech: Meusburger et al. (2022), oak and pine: Weis et al. (2023)). The soil was divided into 22 model layers representing the mineral soil and a variable number of humus layers depending on the thickness of the forest floor. The model domain reached down to 300 cm soil depth. Rooting depth to derive REW was 160 cm for beech, 180 cm for oak, 120 cm for spruce, and 180 cm for pine (Czajkowski et al. 2009; Weis et al. 2023). Soil hydraulic properties were inferred from measured soil texture, bulk density, organic matter content and volumetric stone fraction (Cools and De Vos 2020) using pedotransfer functions (mineral soil: Wösten et al. (1999), forest floor: Hammel and Kemmel (2001)). The species-specific model parameters applied to represent beech, oak, spruce, and pine stands are based on Weis et al. (2023), who defined standard parameter sets for these tree species. The parameter sets were tested on sites, at which timeseries of throughfall ($n = 511$) and soil water content ($n = 133$) were available from measurements of varying intensity, and objective goodness-of-fit criteria were calculated (throughfall: mean error, root mean square error; soil water content: Nash–Sutcliffe efficiency). For a better overall agreement of simulated model outputs and observed observations, adjustments were made to the standard parameter sets concerning rainfall interception parameters and maximum stomata conductivity parameter, reducing errors in throughfall and increasing the number of plots with Nash–Sutcliffe efficiency > 0 for soil water content from 35 to 50 plots. The species-specific parameters are listed in Appendix Table 4. We aggregated REW values over three different time periods: (1) calendar year prior to foliage sampling year, (2) − 14 days to + 40 days of the beginning of the vegetation period of foliage sampling year, (3) 1 st of July to either foliage sampling or to 15th of September (if foliage sampling date was later than 15th of September as is the case for most coniferous foliage samples) of the same year. Equivalent to the standardization of foliar *N* and *P* values, we standardized each REW value per respective time period by subtracting the long-term median of each site and dividing by the standard deviation of each site. The beginning of the vegetation period was modeled based on daily temperature at each site and year using the Menzel method implemented in the R package *vegperiod* (Nuske 2022).

LWF-Brook90 parameters

Table 4 Species-specific standard parameters used in LWF-Brook90. Parameters with intra-annual variation (summer/winter) depend on phenology and refer to peak season leaf area index and minimum winter leaf area index

	Beech	Oak	Spruce	Pine
Albedo	0.18	0.18	0.14	0.14
Albedo with snow on the ground	0.23	0.23	0.14	0.14
Radiation extinction coeff	0.6	0.6	0.5	0.5
LAI[a] (m^2 m^{-2}, summer/winter)	6/0.6	4.5/0.45	5.5/4.45	3.5/2.1
Stand height[a] (m)	30	30	30	25
Rooting depth (m)	− 1.6	− 1.8	− 1.2	− 1.8
β-parameter (root distribution)	0.976	0.976	0.966	0.966
Max. leaf conductivity (mm s^{-1})	0.0042	0.0055	0.0035	0.004
Max. canopy conductance (mm s^{-1}, summer)	0.0252	0.02475	0.01925	0.014
Critical leaf water potential (MPa)	− 2	− 2.5	− 2	− 2.5
Rain interception catch rate (%, summer/winter)	46/13.6	36/11.7	43/36.4	45/31
Rain interception capacity (mm, summer/winter)	1.6/0.52	1.26/0.45	1.5/1.3	1.13/0.78
Snow interception capacity (mm, summer/winter)	4.2/0.96	3.24/0.81	3.9/3.24	2.7/1.86

[a] If available, plot-specific values were used

Gap-filling of ICP Forests N deposition data

All predictor variables for the random forest approach were based on output from the EMEP MSC-W model (Type 2 rv 5.3) (Simpson et al. 2012) downloaded on 2024–12-23 and extracted for all forest sites, where foliar N and P is monitored. The relevant predictor variables

identified based on variable importance were precipitation amount, wet and dry deposition of oxidized and reduced N as well as surface air concentration of reduced and oxidized N compounds. In addition, total N deposition calculated from the sum of EMEP wet and dry deposition was used as a predictor. Performance of the gap-filling was assessed by leave-one-out cross-validation (all years from a single plot per iteration). Results indicated that the gap-filled deposition data resulted in the same classification of deposition amount (relatively low, not assignable, relatively high) compared to the measured total deposition in 90% of the plot-years. The gap-filling performance was thus considered to be sufficient for the purpose of the main analyses.

Relationship of foliar N:P, foliar N and P to REW

Besides SPEI, we compared values of ltd. foliar N:P, N concentrations, and P concentrations among classes of standardized long-term deviations (ltd.) of relative extractable soil water (REW) from median per forest site in summer, the beginning of the vegetation period, and the previous calendar year respectively from output of water budget modeling (Sect. 6.1). For ltd. foliar N:P, there was no significant difference between classes of low (< 25th percentile of whole dataset) and high (> 75th percentile of whole dataset) ltd. REW values from previous calendar year (except beech, Appendix Fig. 8), the beginning of the vegetation period (except pine, Appendix Fig. 10), and summer (except spruce, Appendix Fig. 11). For ltd. foliar N concentrations, we found significant differences between classes of low and high ltd. REW (with lower ltd. N concentrations at lower ltd. REW) during the beginning of the vegetation period (Appendix Fig. 15) for pine, during summer (Appendix Fig. 17) for all species, and during the previous calendar year (Appendix Fig. 13) for beech and pine. Values of ltd. foliar P concentrations were significantly lower associated with low ltd. REW values at the beginning of the growing season for beech and pine compared to high ltd. REW values (Appendix Fig. 21). Ltd. foliar P concentrations of all species followed classes of low relative to high ltd. REW in summer (Appendix Fig. 22). Except for oak, there were significant differences between ltd. foliar P concentrations associated with classes of low vs. high ltd. REW of the year prior to foliage sampling (Appendix Fig. 19).

Spatiotemporal co-occurrence of N/S deposition levels with foliar nutrients

To visualize spatiotemporal co-occurrences of foliar N and P with N or S deposition on a map, we assigned all datapoints to three different time periods (calendar years ≤ 2000, decade 2000–2010, decade 2010–2020), normalized, summarized and classified values per parameter, tree species, and decade and subsequently related the classes of deposition and foliage data to each other. Prior to analysis, we excluded any deposition data from sites with less than three measurements per decade or from sites, for which deposition data within each decade respectively had a relative standard deviation > 0.8. For each tree species, we averaged deposition data per site and decade (deposition $value_{avg.}$) and subsequently rescaled deposition values via min–max-normalization to calculate normalized deposition values that are comparable among forest sites:

$$value_{normalized} = \frac{value_{avg.} - value_{min.Europe}}{value_{max.Europe} - value_{min.Europe}} \quad (1)$$

where deposition $value_{min.Europe}$ and deposition $value_{max.Europe}$ represent the minimum and maximum deposition value across all deposition values of deposition $value_{avg.}$ respectively.

Mean tree species-specific foliage values per decade were obtained by averaging all foliar measurements in samples harvested at the end (final calendar year) of each deposition decade ± 3 years, in order to investigate foliar nutrient levels after one decade of respective deposition levels. For instance, an average foliar value to the deposition decade 2000–2010 originates from samples of the foliage survey years 2007–2013. Since foliage survey years in ICP Forests usually happen in uneven years, foliage $value_{avg.}$ is based on four foliar measurements in most cases. We filtered out foliage $value_{avg.}$ based on less than three foliar measurements and/or foliar measurements with a relative standard deviation > 0.8 per site-decade. Equivalently to deposition values, all foliage $value_{avg.}$ were rescaled via min–max normalization (Eq. 1), where foliage $value_{min.Europe}$ and foliage $value_{max.Europe}$ represent the minimum and maximum value across all foliage $value_{avg.}$ respectively.

We classified normalized deposition and foliage values per tree species as relatively low, if they were smaller than the 30th percentile, and as relatively high, if they were greater than the 70th percentile of respective normalized values across all site-decades.

Any $value_{normalized}$ between the 30th and 70th percentile was classified as medium. We related classes of relatively low, medium, and high deposition values to classes of foliage values. If a class of relatively low deposition for a given site-decade coincided with relatively low foliar N or P, we labeled the respective site-decade by "rel. low levels." Conversely, if a class of relatively high deposition for a given site-decade coincided with relatively high foliar N or P, we labeled the respective site-decade by "rel. high levels."

Any other combination of deposition class with foliage class (e.g., medium deposition with low foliage value) was labeled as "not assignable." Finally, we visualized coinciding deposition and foliage classes on maps resolved by decade.

Probability assessment

The binomial probability P for at least k successes (i.e., k or more) in n trials is given by

$$P(k,n,p) = 1 - \sum_{i=0}^{k-1} \binom{n}{k} \cdot p^k \cdot (1-p)^{n-k} \quad (2)$$

where p represents the probability for one success given that trials are independent. We calculated p as the product of the probability for SPEI < -1.2 and the probability of N or P deficiency in one site-year within the total dataset of n_{tot} values, in order to obtain the annual probability for co-occurrence of low SPEI and nutrient deficiency:

$$p = \frac{n_{SPEI<-1.2}}{n_{tot}} \cdot \frac{n_{deficient}}{n_{tot}} \quad (3)$$

All values from the ICP Forests dataset that were plugged into Eqs. 2 and 3 are listed in Table 5 per tree species and nutrient (nitrogen or phosphorus), along with the resulting probability P.

Table 5 Values derived from the ICP Forests dataset used to compute probability P (rightmost column)

Nutrient	Tree species	n_{tot}	$n_{SPEI<-1.2}$	$n_{deficient}$	p	$k_{co\text{-}occur}$	P
P	*Fagus sylvatica*	1105	121	342	0.03	50	0.026
	Quercus sp.	843	92	150	0.02	20	0.213
	Picea abies	1347	151	223	0.02	30	0.180
	Pinus sylvestris	833	101	151	0.02	29	0.012
N	*Picea abies*	1335	149	476	0.04	52	0.582
	Pinus sylvestris	814	98	169	0.02	30	0.025

Graphical overview of foliar concentrations with drought parameters

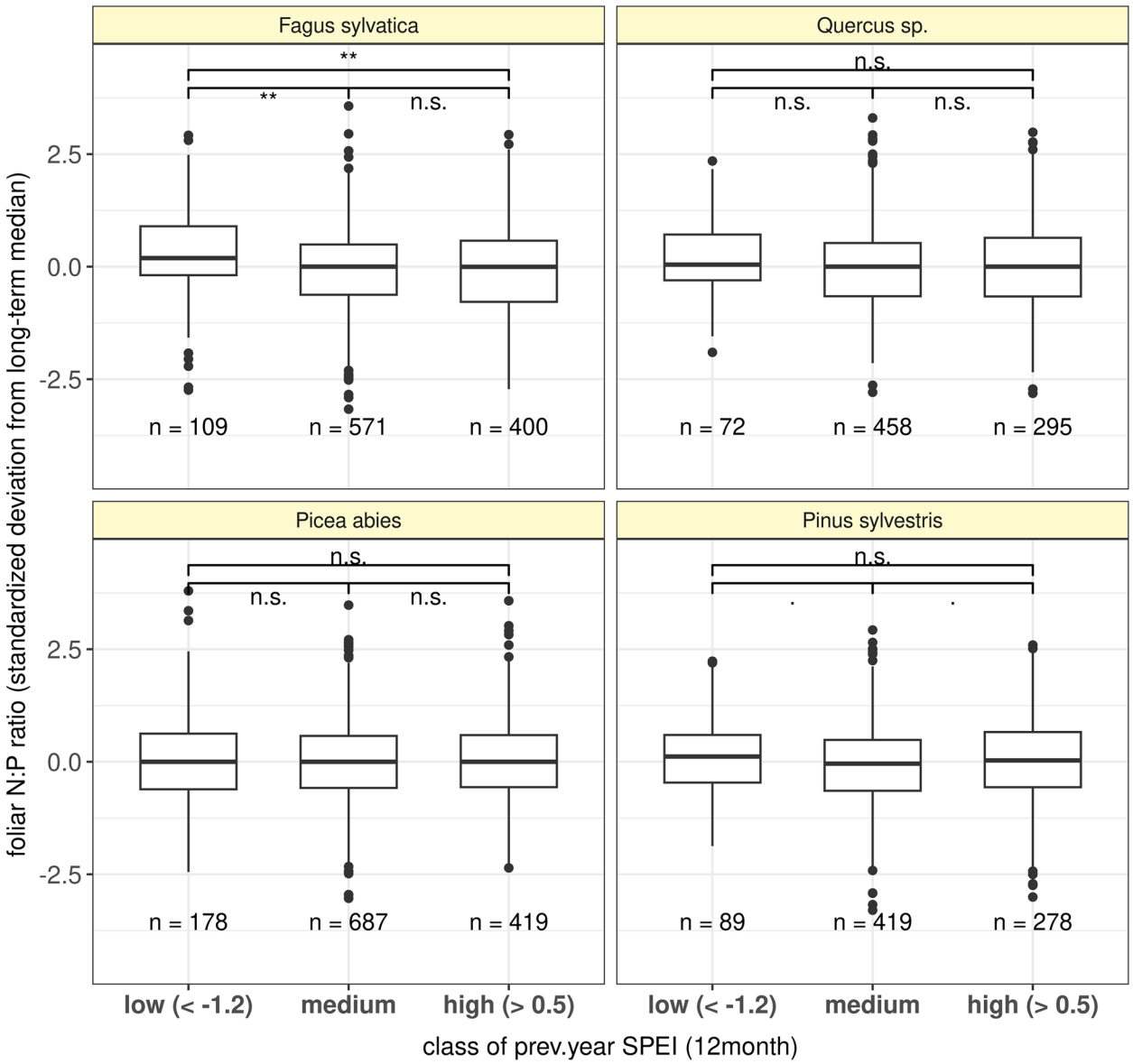

Fig. 7 Foliar N:P (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during the previous calendar year of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

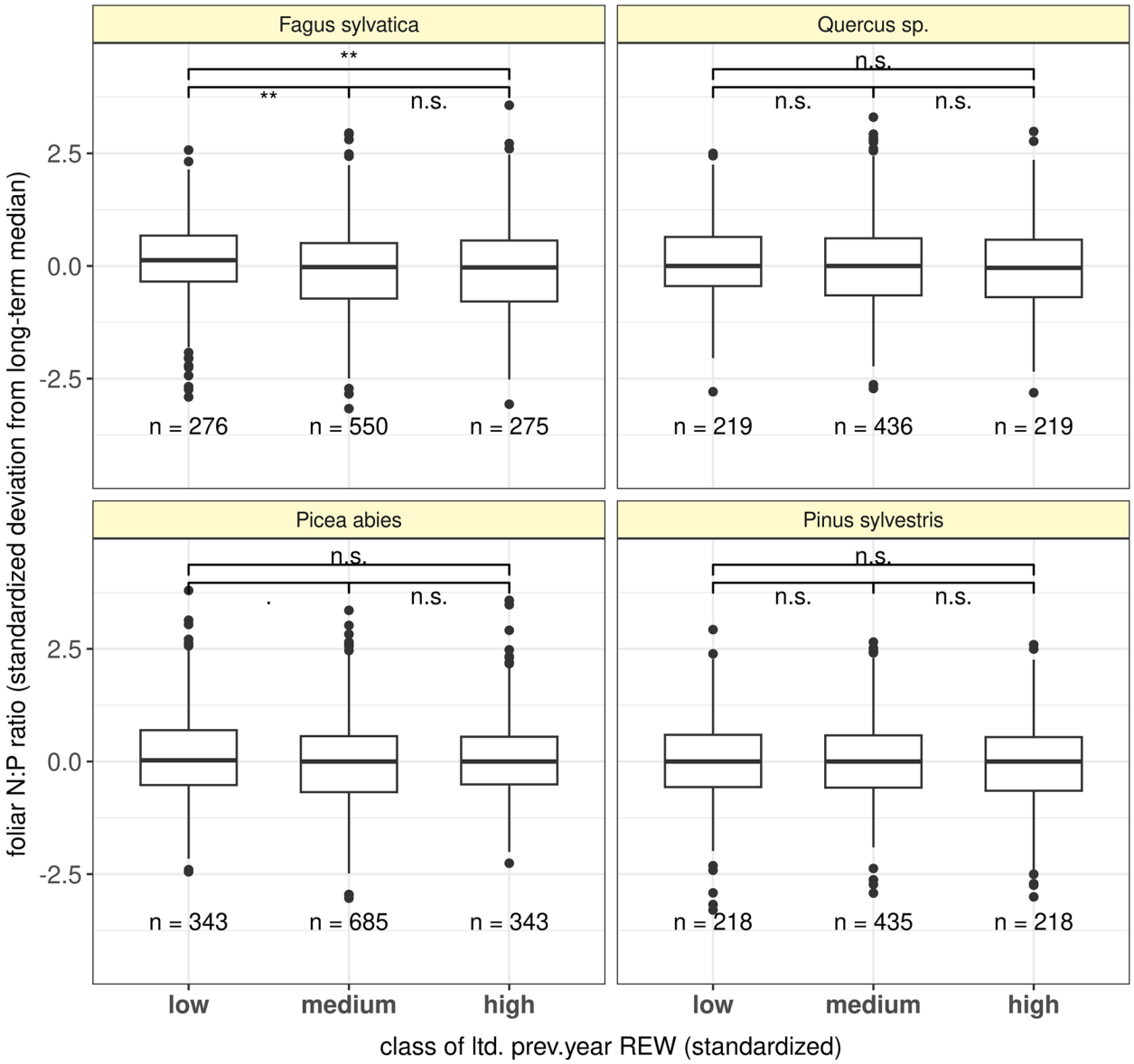

Fig. 8 Foliar N:P (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the calendar year prior to the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW previous year values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW previous year values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

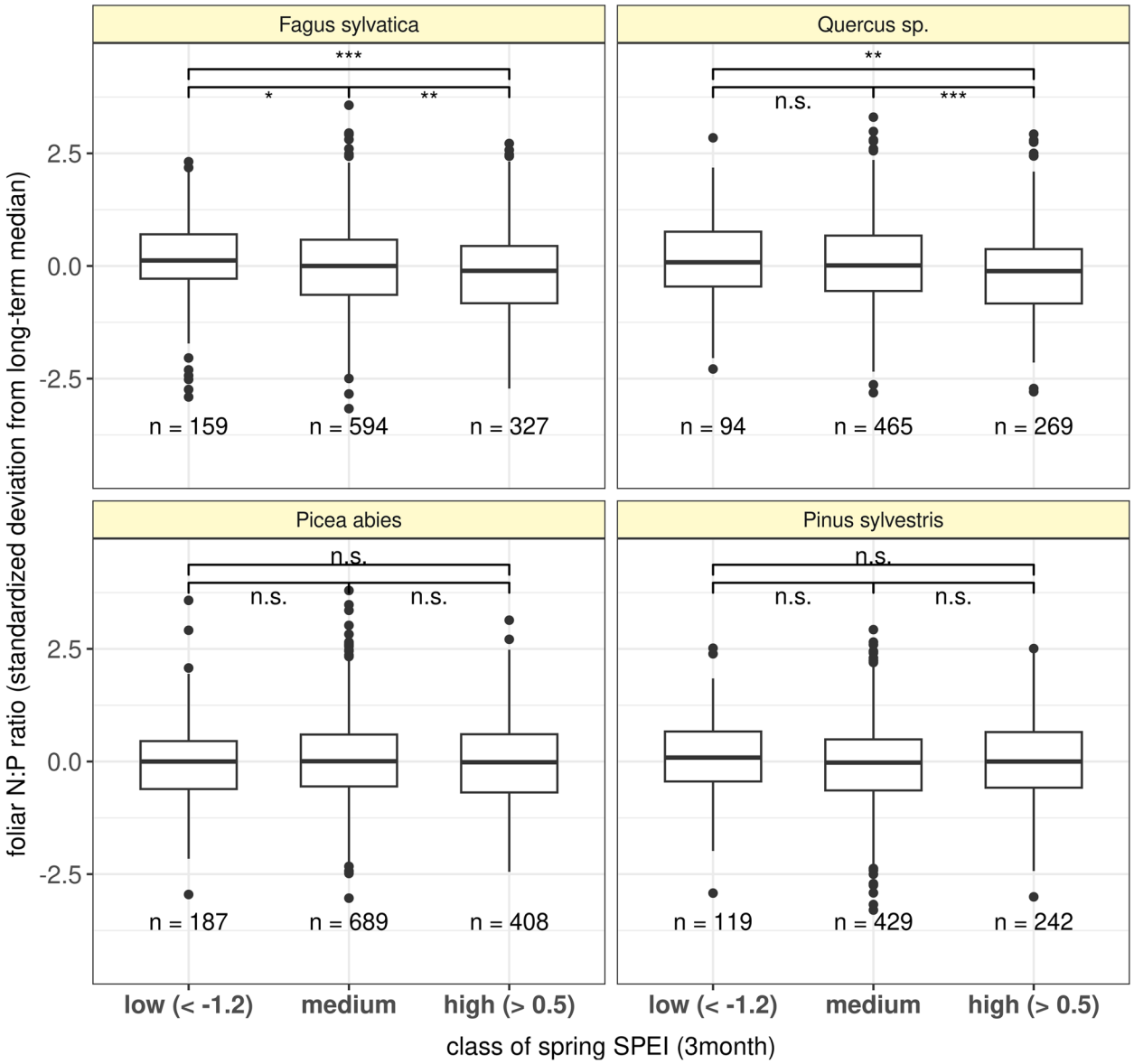

Fig. 9 Foliar N:P (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during spring (April–June) of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

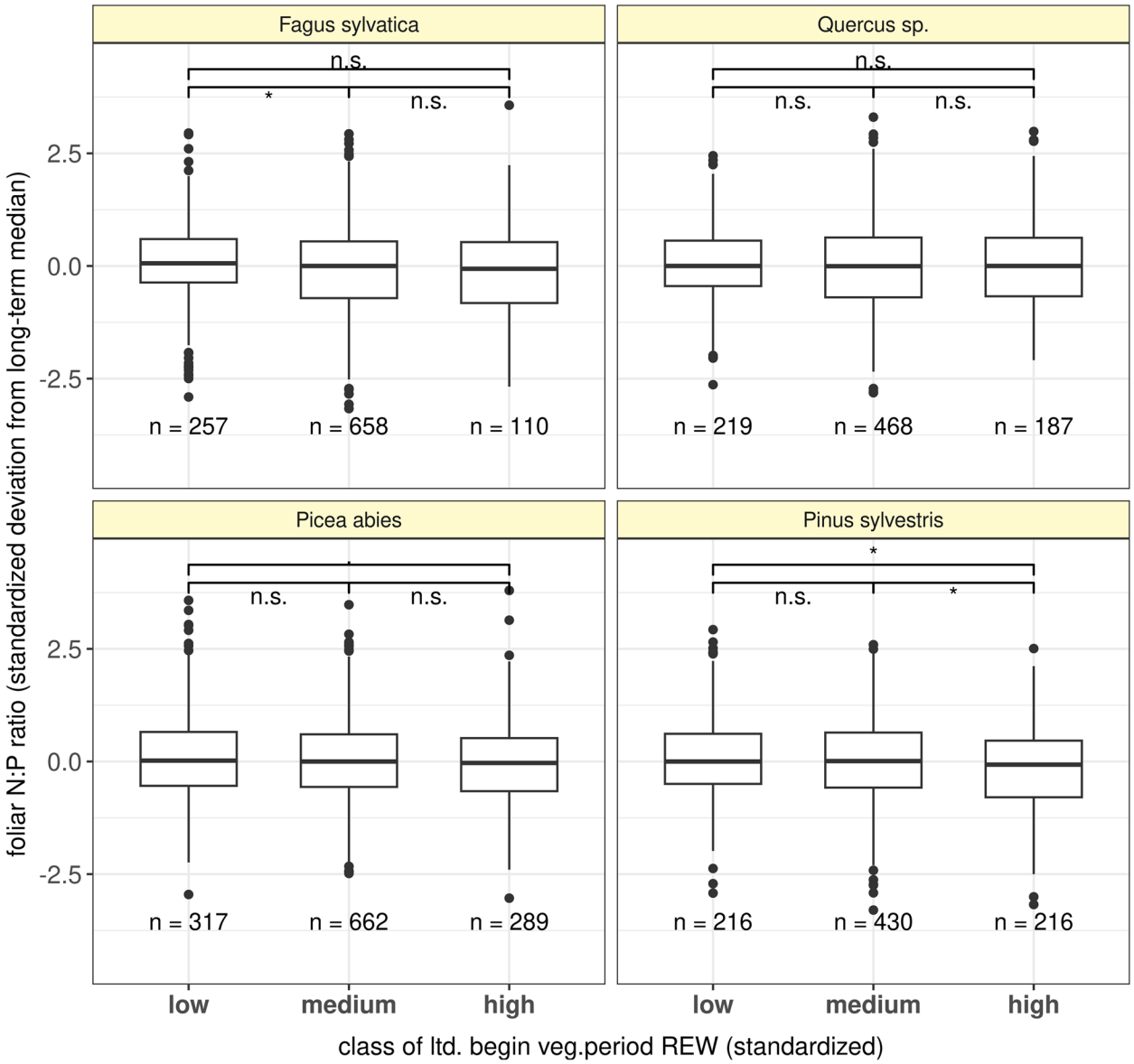

Fig. 10 Foliar N:P (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the beginning of the growing season (time span of 14 days before the beginning of the vegetation period to 40 days after the beginning of the vegetation period) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW spring values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW spring values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

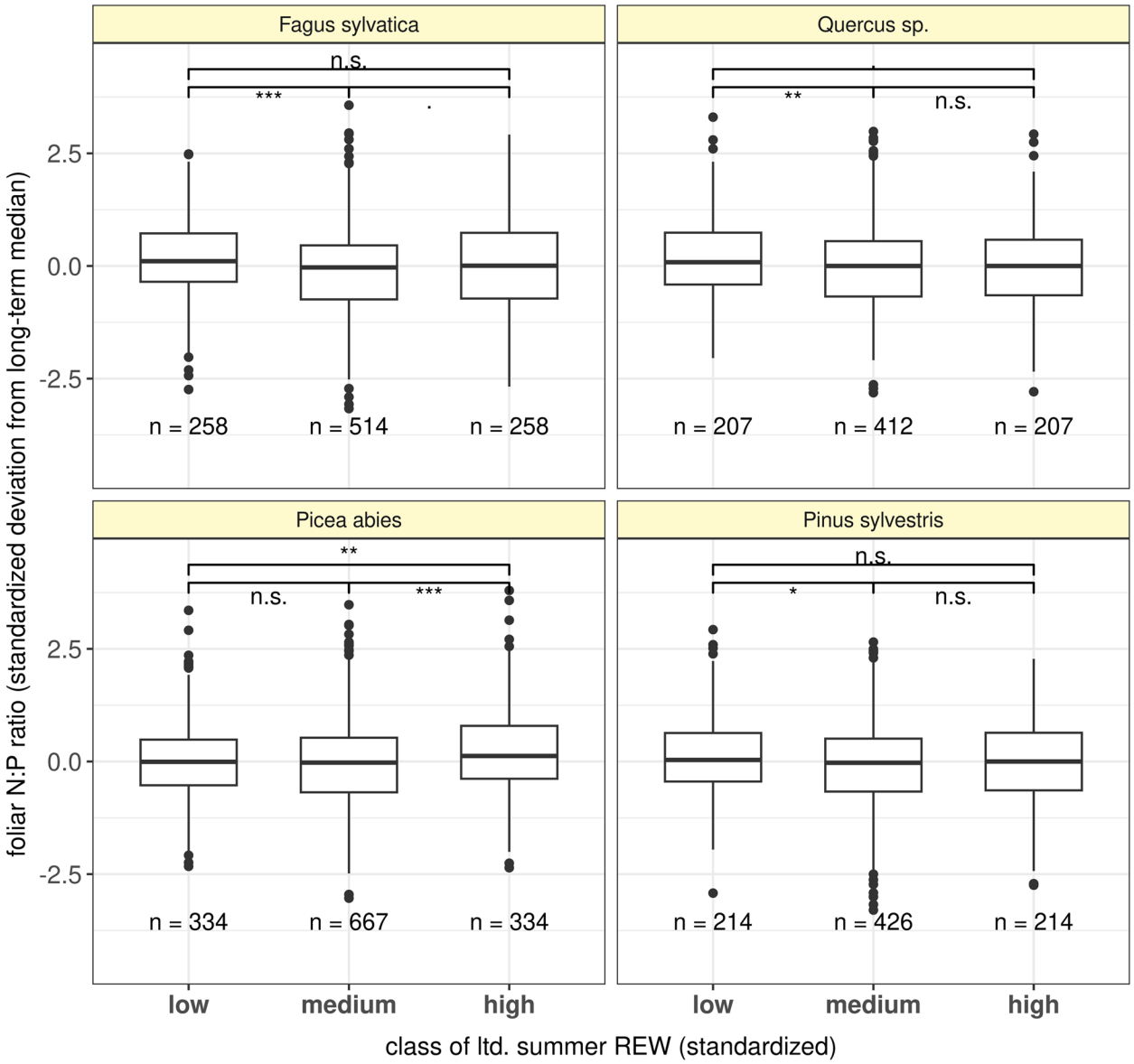

Fig. 11 Foliar N:P (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during summer (deciduous trees: 1 st July—foliage sampling date, coniferous trees: 1 st July—foliage sampling date/15th of September) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW summer values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW summer values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

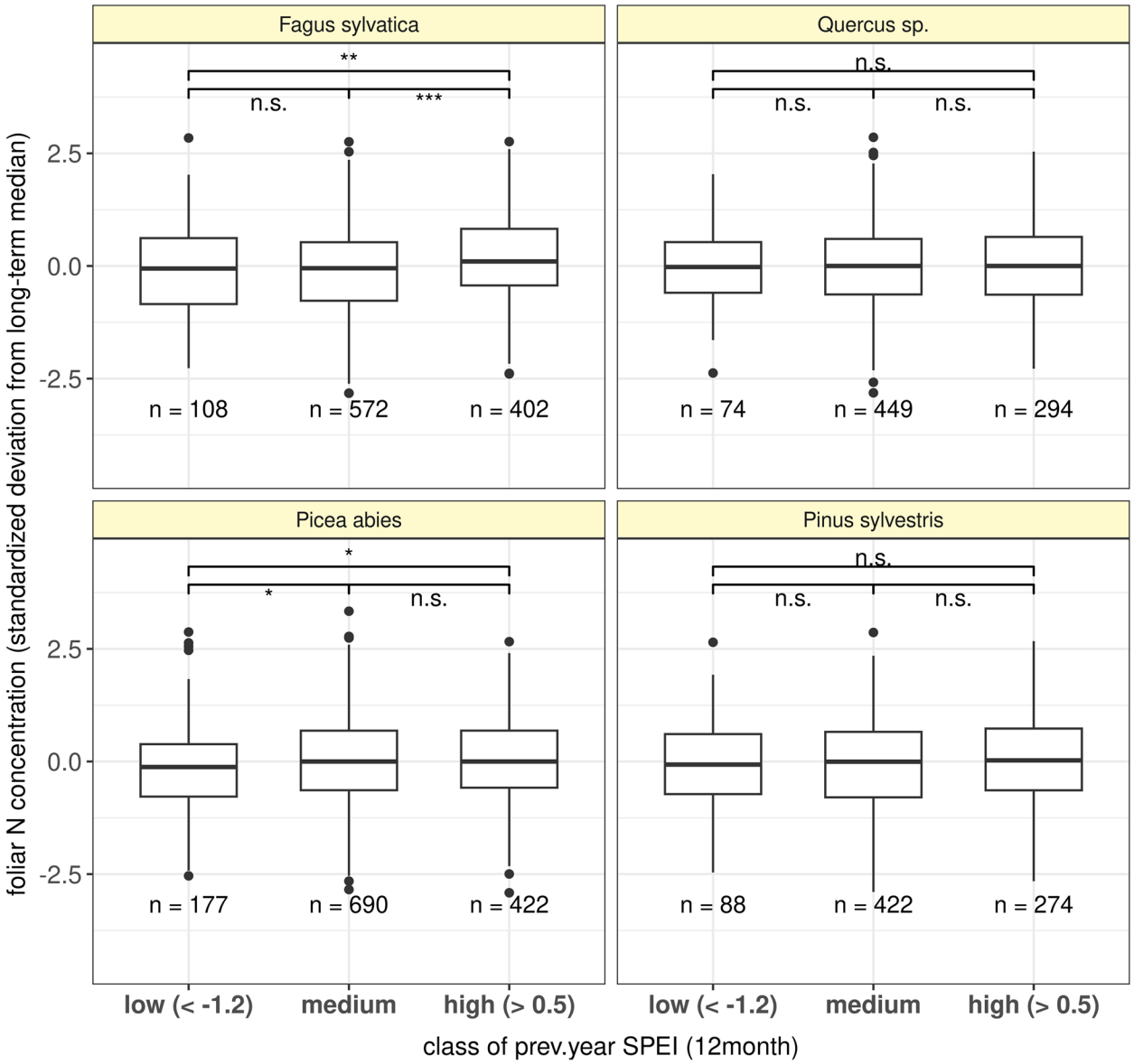

Fig. 12 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during the previous calendar year of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.:0.1; n.s.: not significant)

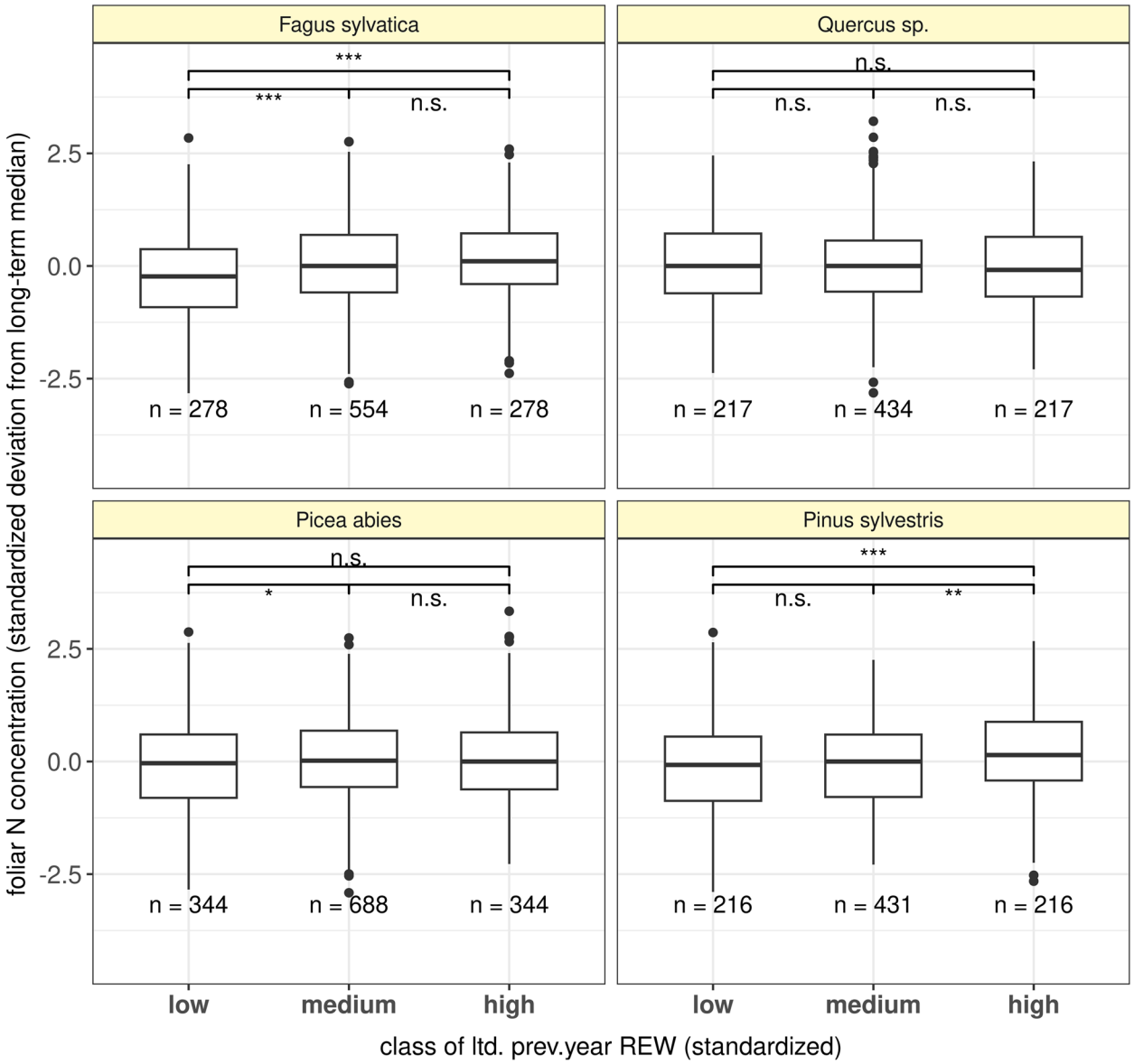

Fig. 13 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the calendar year prior to the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW previous year values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW previous year values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

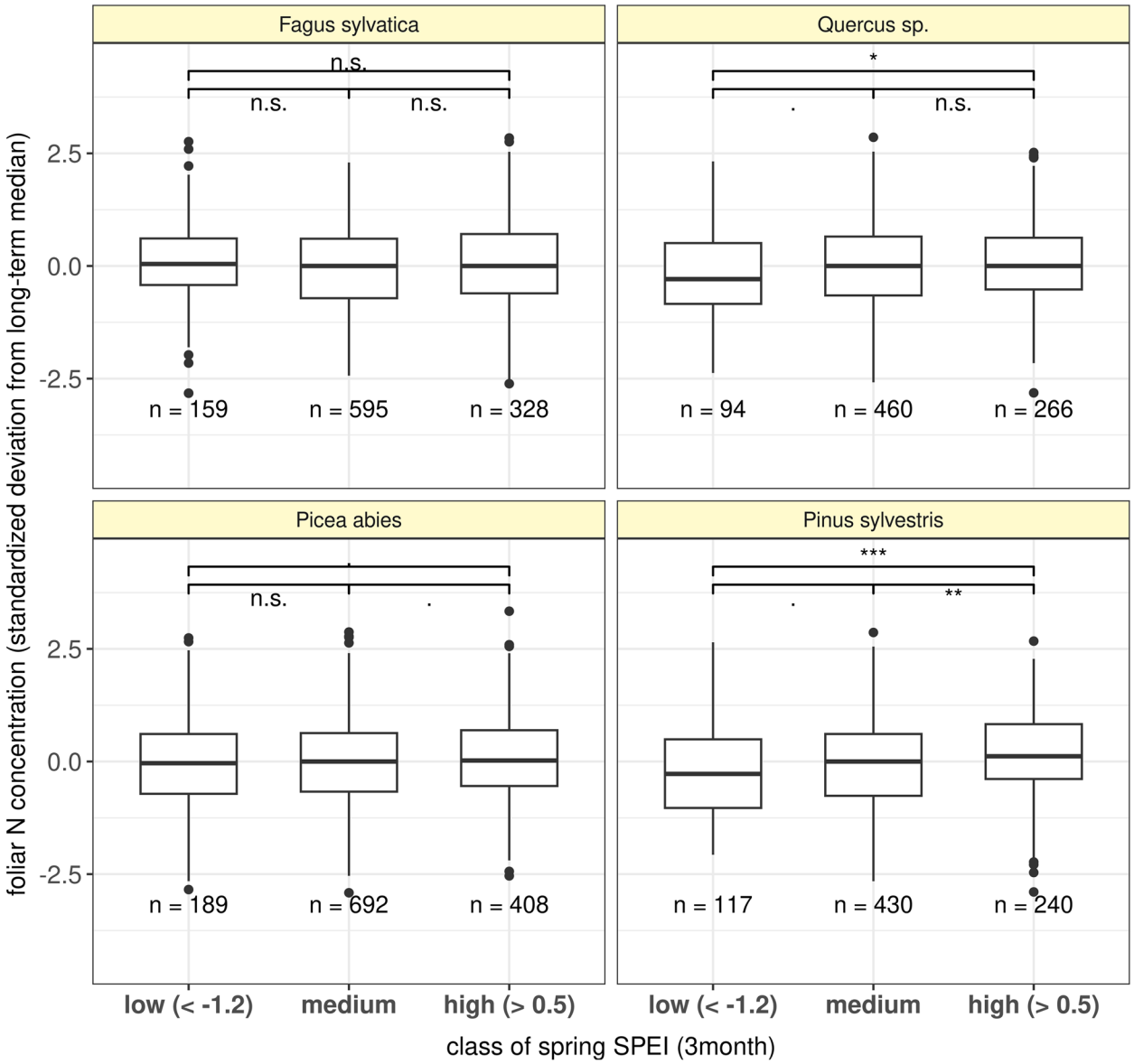

Fig. 14 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during spring (April–June) of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.:0.1; n.s.: not significant)

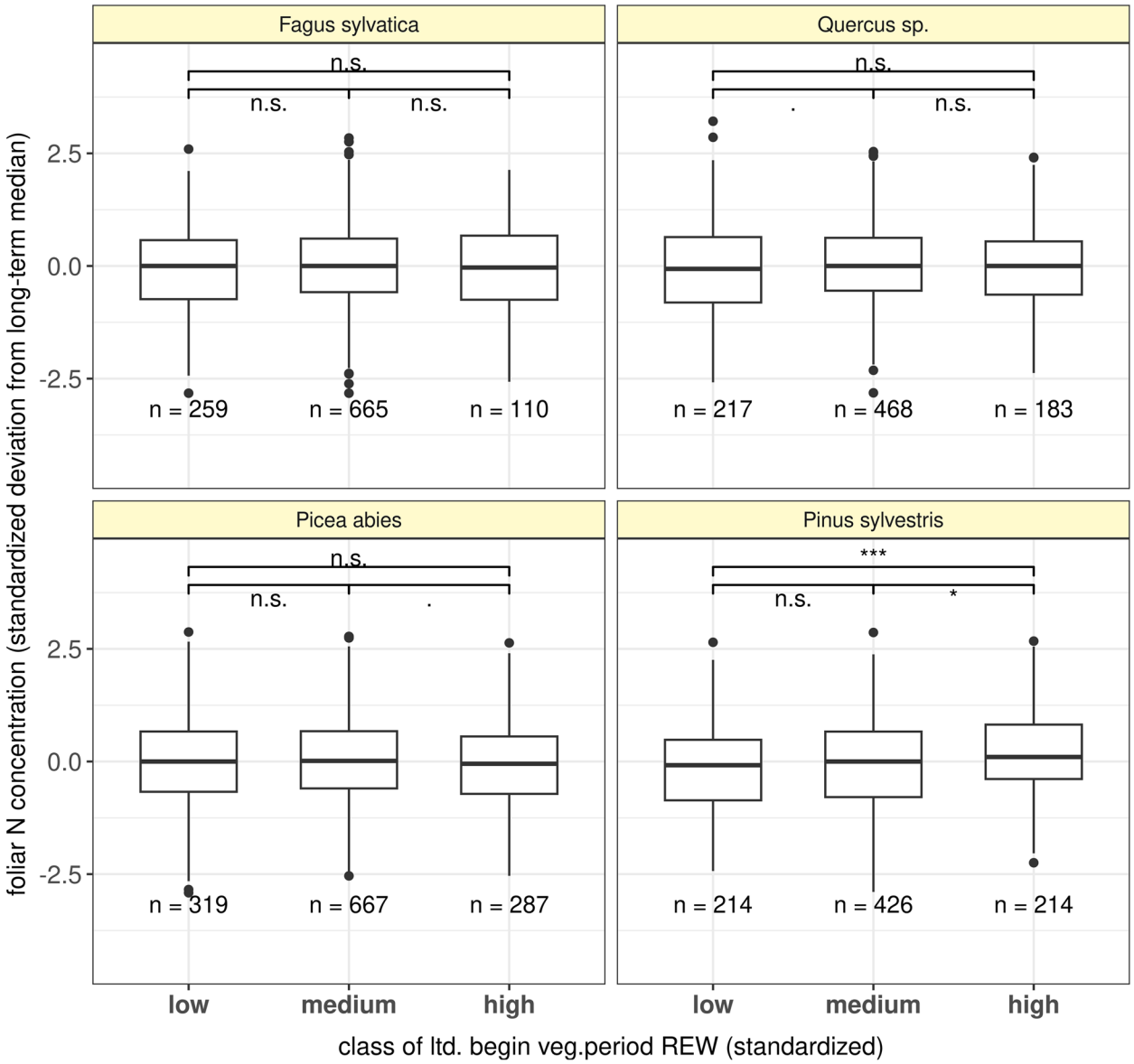

Fig. 15 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the beginning of the growing season (time span of 14 days before the beginning of the vegetation period to 40 days after the beginning of the vegetation period) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW spring values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW spring values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

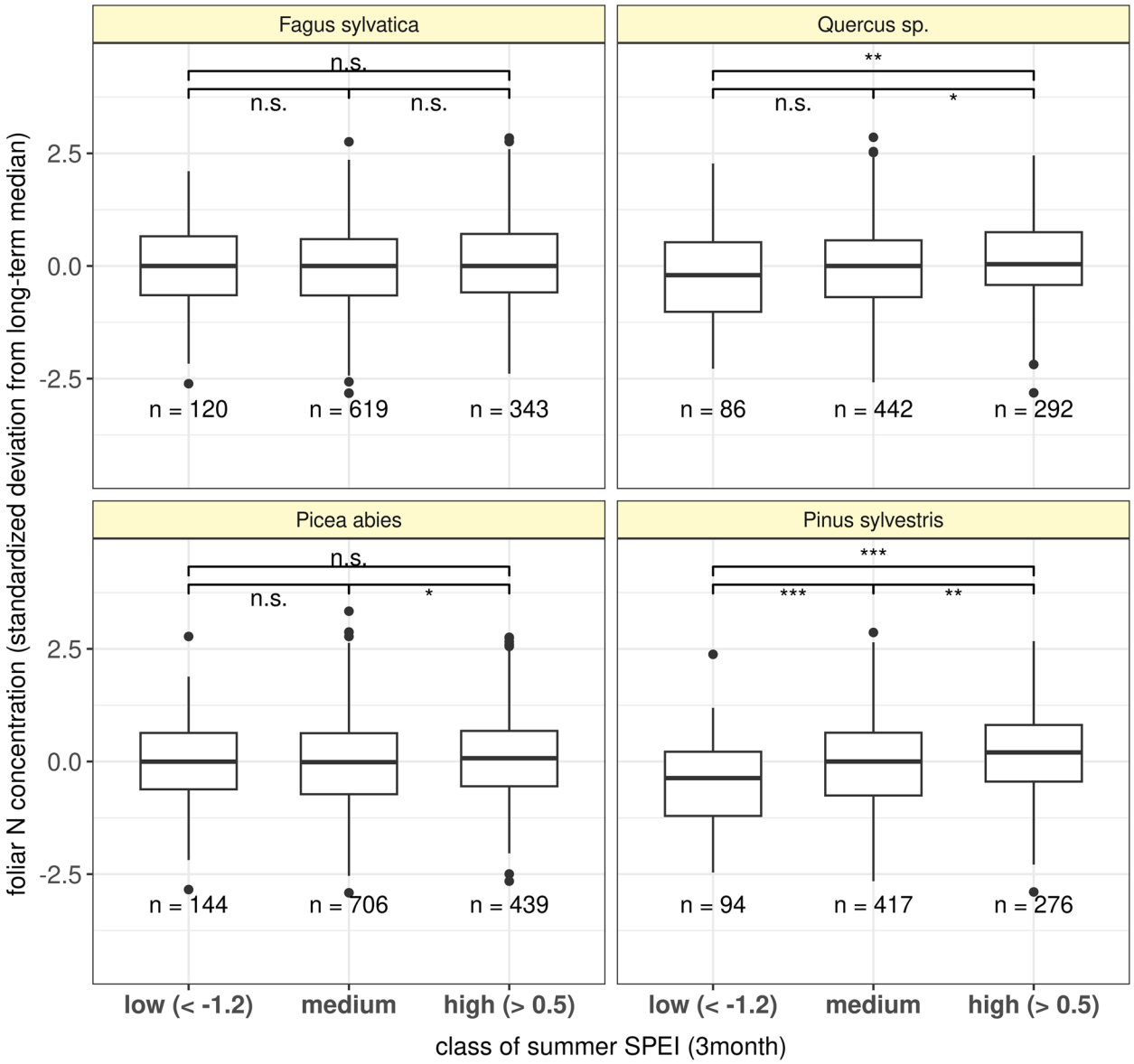

Fig. 16 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during summer (July–September) of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.:0.1; n.s.: not significant)

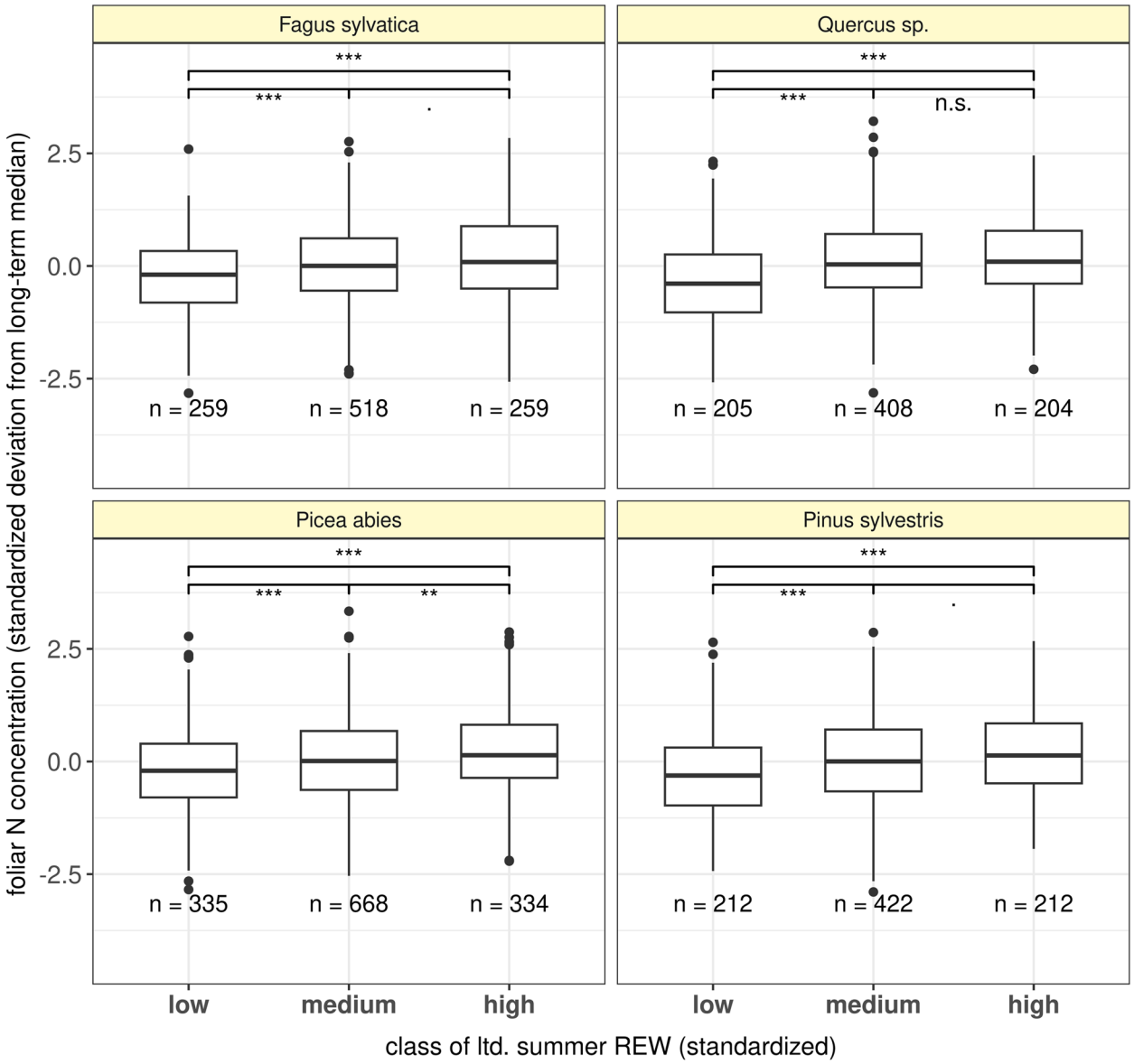

Fig. 17 Foliar N concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during summer (deciduous trees: 1 st July—foliage sampling date, coniferous trees: 1 st July—foliage sampling date/15th of September) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW summer values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW summer values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

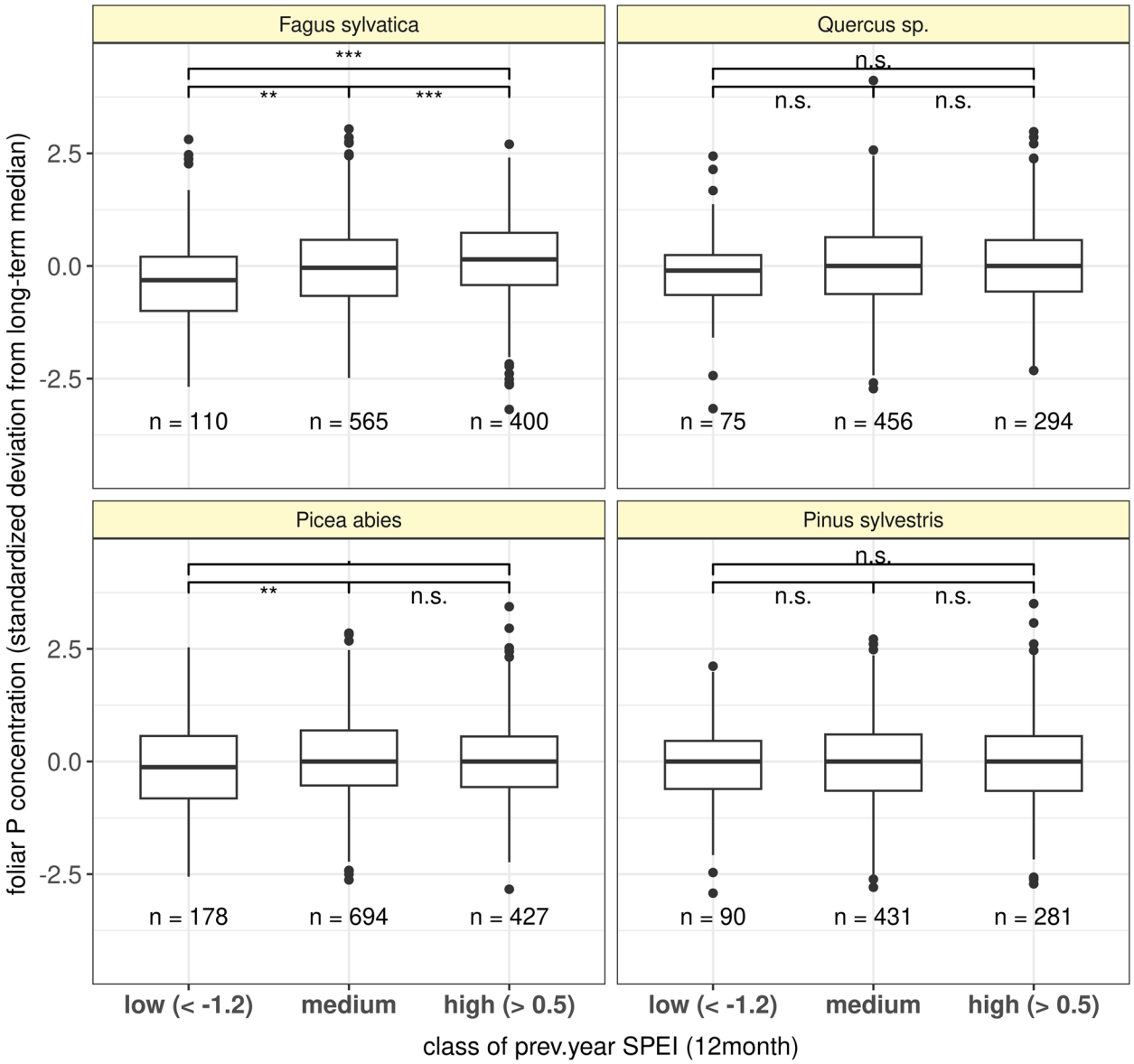

Fig. 18 Foliar P concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during the previous calendar year of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.:0.1; n.s.: not significant)

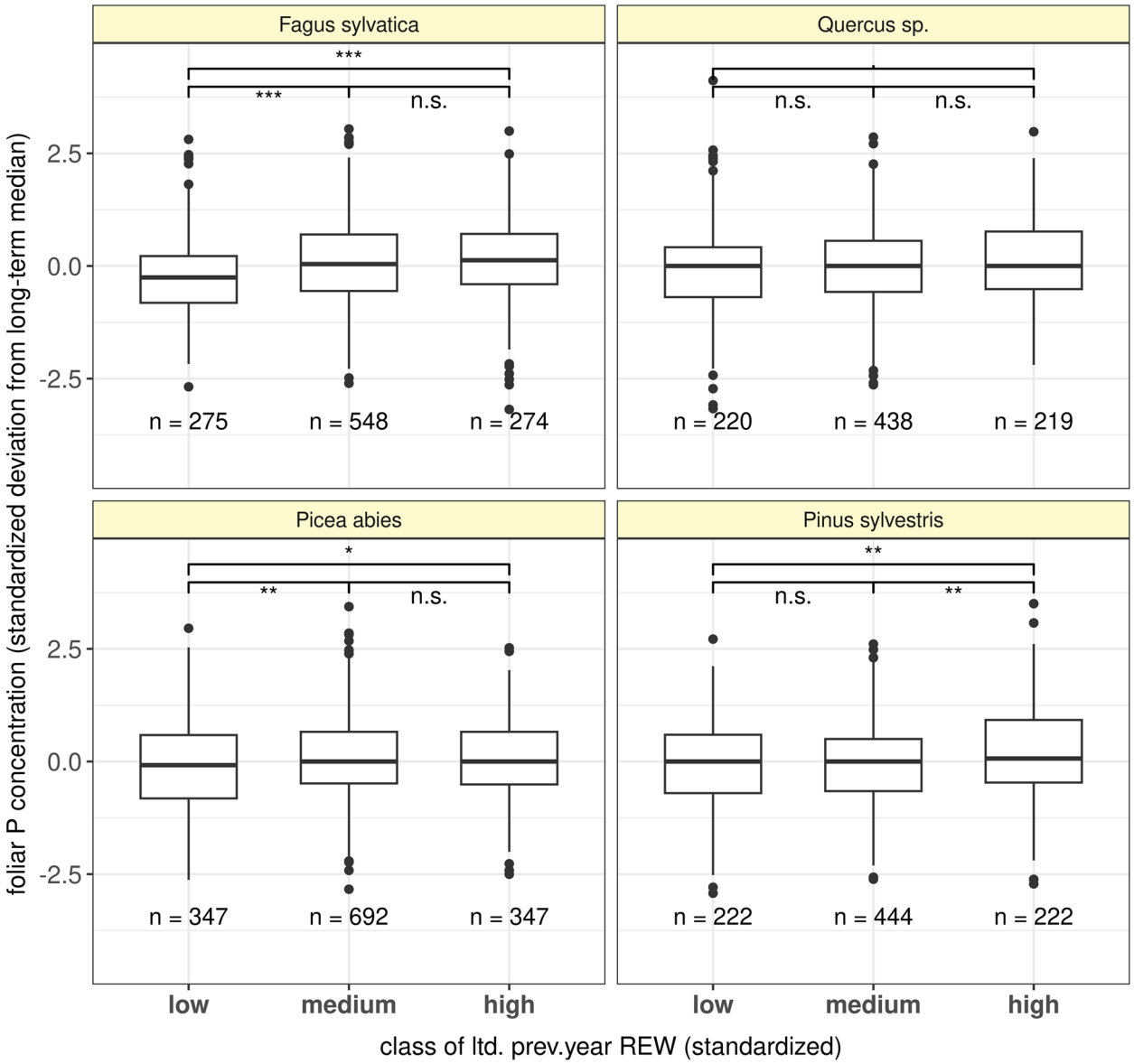

Fig. 19 Foliar P concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the calendar year prior to the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW previous year values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW previous year values. Statistically significant differences (Wilcoxon test) among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

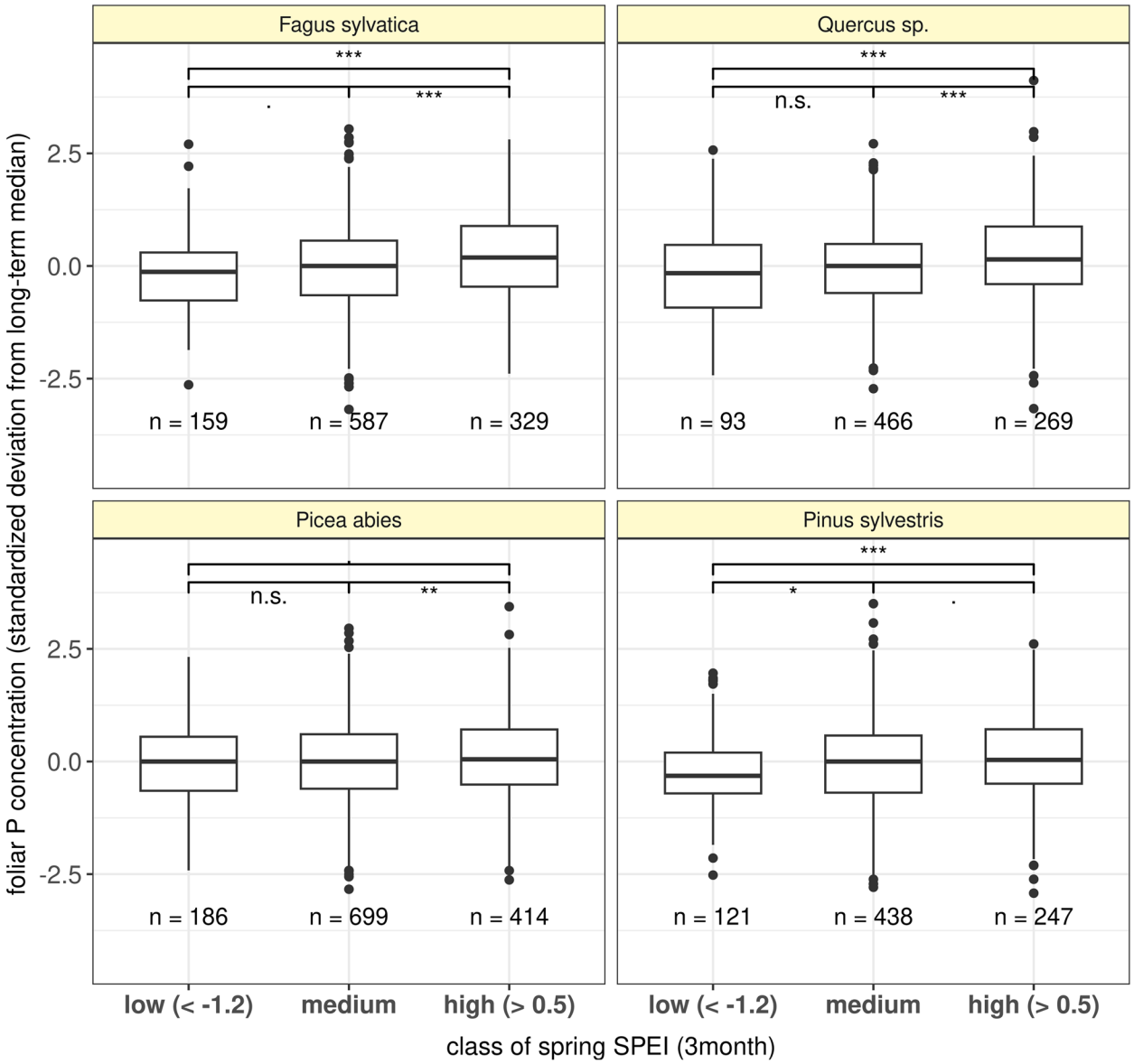

Fig. 20 Foliar P concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of SPEI values during spring (April–June) of the respective foliage sampling year. A relatively low SPEI < − 1.2 represents dry environmental conditions, while SPEI > 0.5 represents wet environmental conditions. Statistically significant differences (Wilcoxon test) among SPEI classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

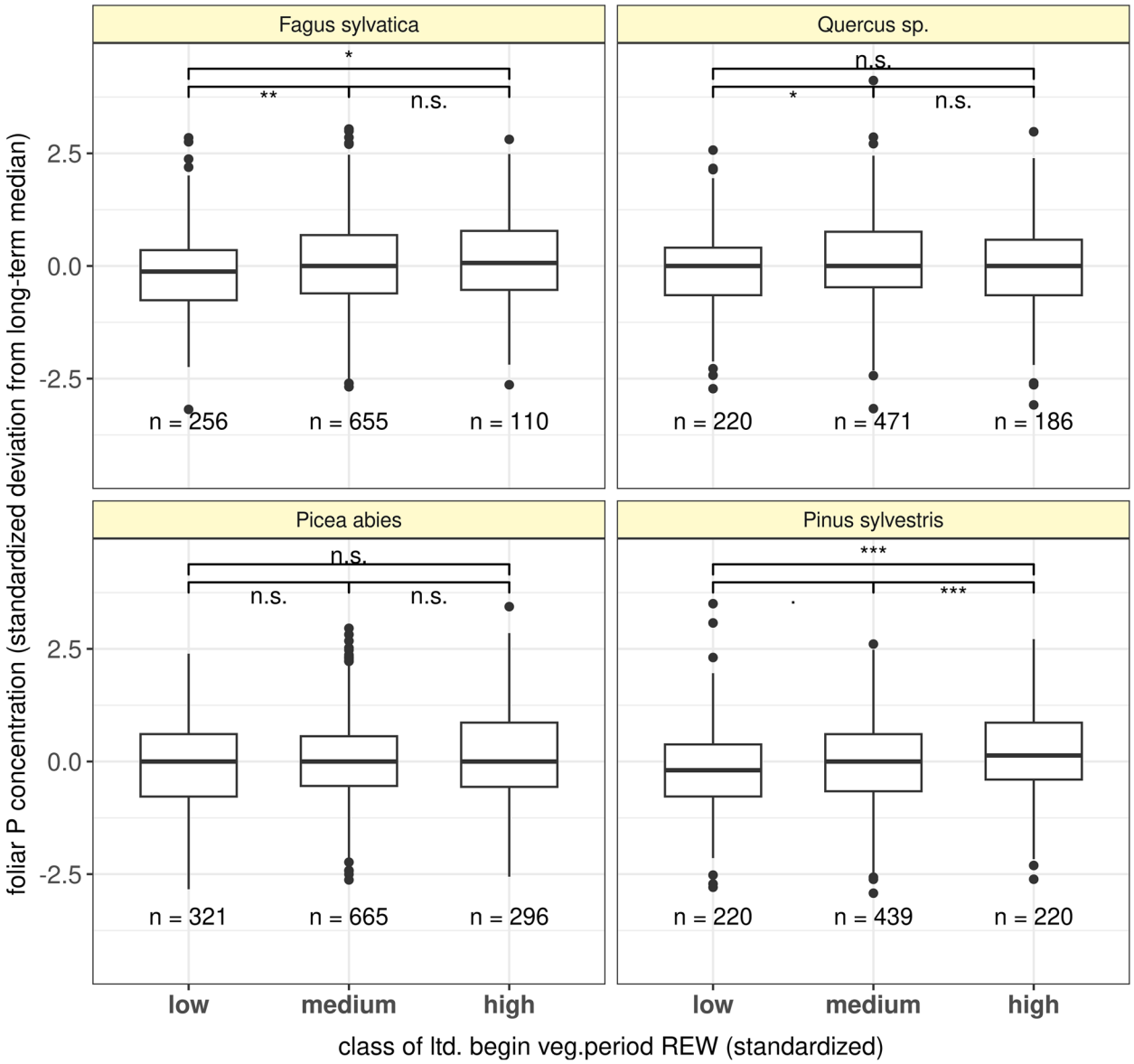

Fig. 21 Foliar P concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during the beginning of the growing season (time span of 14 days before the beginning of the vegetation period to 40 days after the beginning of the vegetation period) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW spring values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW spring values. Statistically significant differences (Wilcoxon test) of foliar P contents among ltd. REW classes are indicated by asterisks (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant)

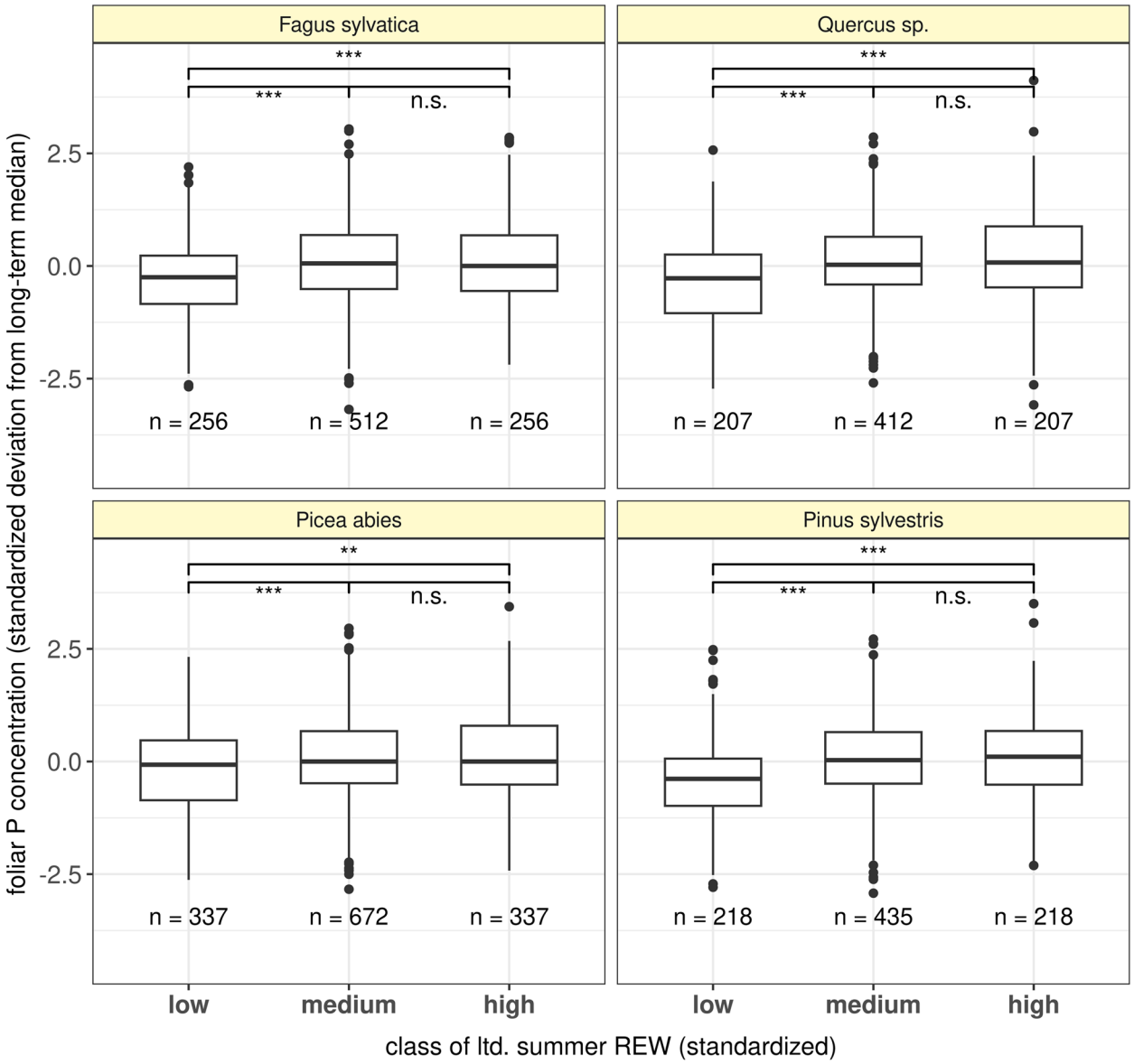

Fig. 22 Foliar P concentrations (long-term deviation from site-median, standardized) of four tree species (beech, oak, spruce, and pine) grouped by corresponding classes of relative extractable soil water (REW, long-term deviation from site median, standardized) during summer (deciduous trees: 1 st July—foliage sampling date, coniferous trees: 1 st July—foliage sampling date/15th of September) of the respective foliage sampling year. A class of low ltd. REW represents values < 25th percentile of all ltd. REW summer values, while a class of high ltd. REW represents values > 75th percentile of all ltd. REW summer values. Statistically significant differences (Wilcoxon test) of foliar P contents among ltd. REW classes are indicated by asterisks (***: 0.001; **:0.01; *: 0.05;.: 0.1; n.s.: not significant)

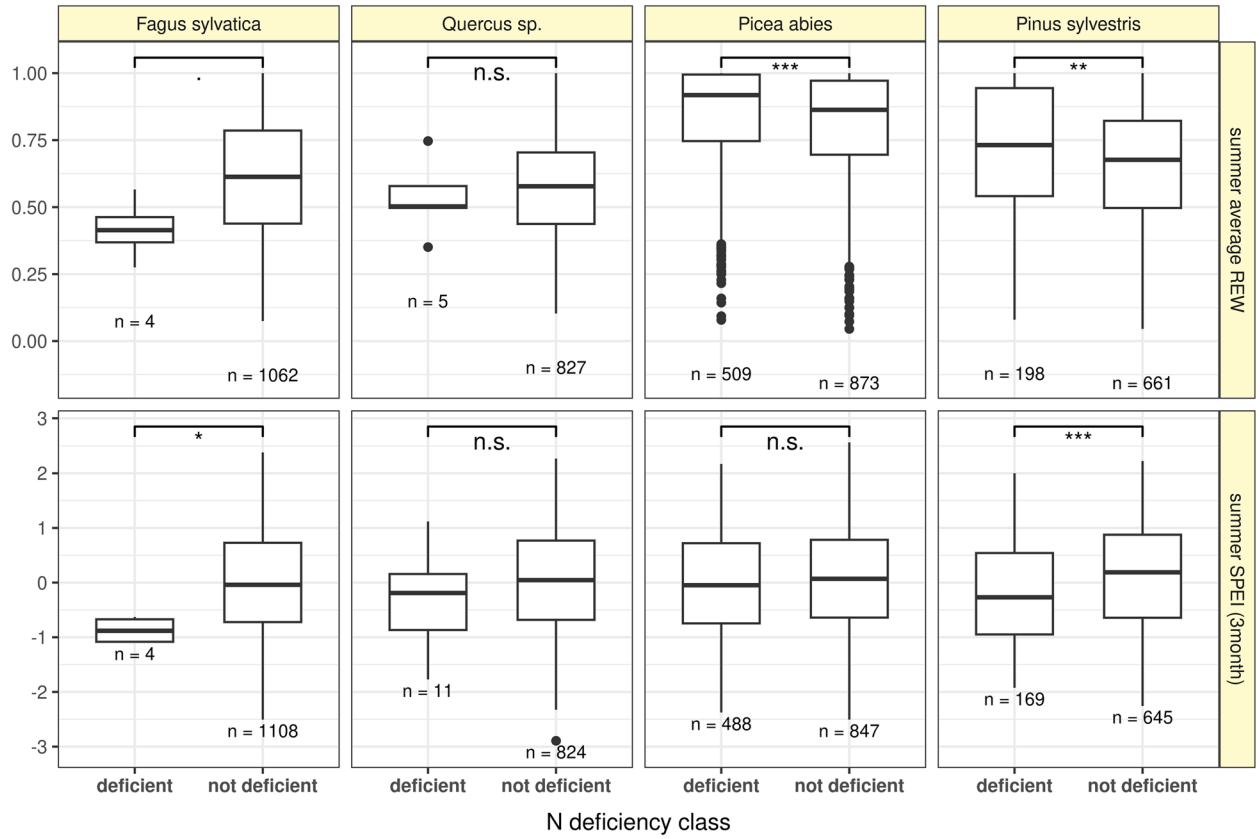

Fig. 23 Values of average relative extractable water (REW, upper pane) in forest soils and 3-month standardized precipitation evapotranspiration index (SPEI, lower pane) during summer (July–Sept.) grouped by N deficiency class (deficient/not deficient) of foliar N concentration per tree species from respective forest monitoring site and foliage survey year. Asterisks denote significance level for differences between foliar N deficiency classes determined by Wilcoxon test (***: 0.001; **: 0.01; *: 0.05;.: 0.1; n.s.: not significant). Please note that values of summer SPEI and REW were not always coincidently available for each monitoring site and foliage sampling year, hence the differences in given *n* values beneath the boxes of upper and lower pane respectively

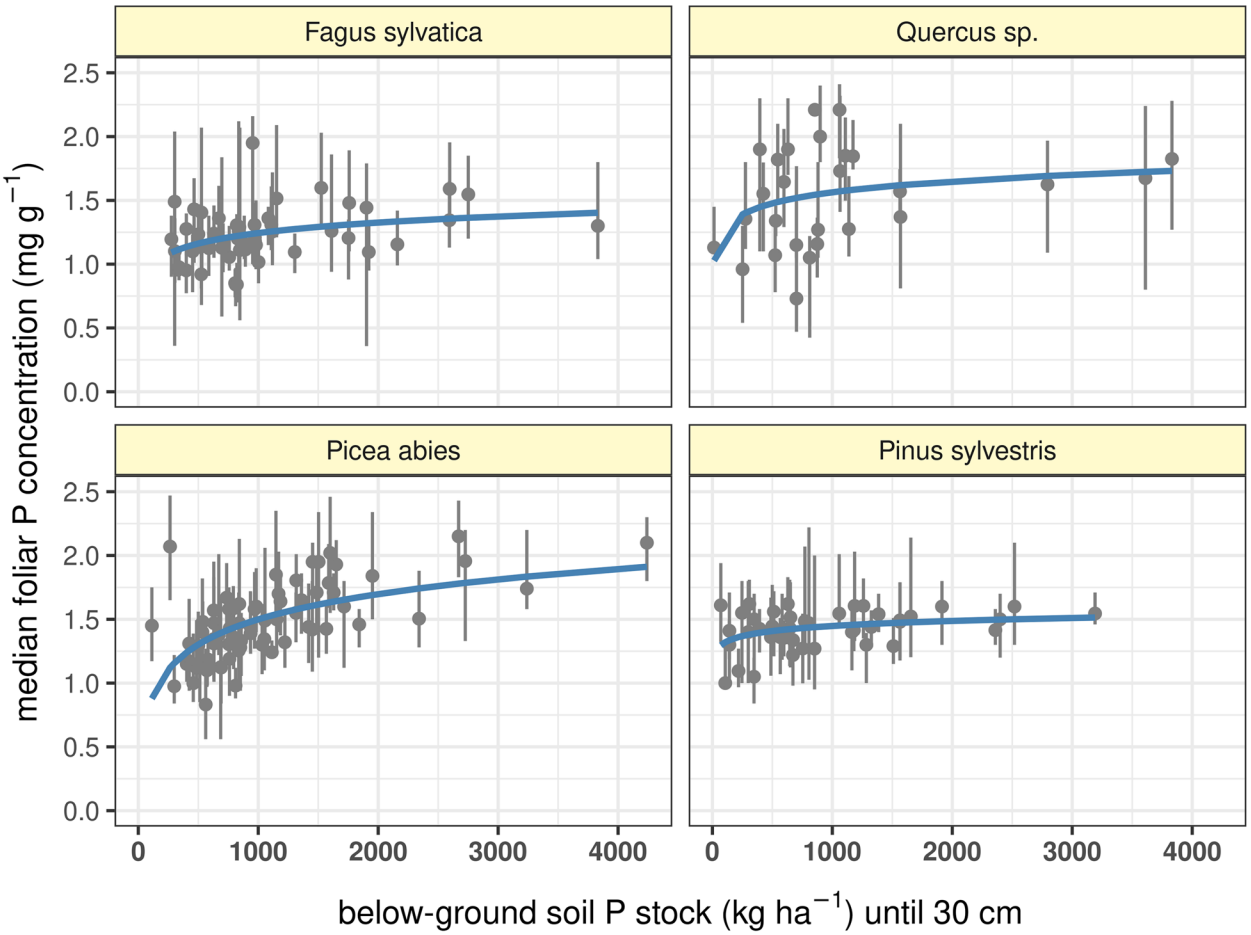

Fig. 24 Median foliar P concentration per monitoring site over the respective monitoring period versus total P stocks of the site topsoil until 30 cm without forest floor. Blue line indicates regression between foliar P concentration and $\log_{10}$ soil P stocks. Error bars indicate minimum to maximum foliar *P* values per site. P stocks are based on ICP Forests soil concentration measurements applying aqua regia extraction

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Authors' contributions
Conceptualization: Lena Wohlgemuth, Kai Schwärzel; Methodology: Lena Wohlgemuth, Kai Schwärzel, Mathieu Jonard, Andreas Schmitz, Paul Schmidt-Walter, Pasi Rautio; Formal analysis and investigation: Lena Wohlgemuth; Writing—original draft preparation: Lena Wohlgemuth; Writing – Lena Wohlgemuth, Mathieu Jonard, Andreas Schmitz, Paul Schmidt-Walter, Heleen Deroo, Peter Waldner, Nathalie Cools, Bruno De Vos, Arne Verstraeten, Inken Krüger, Anne Thimonier, Volkmar Timmermann, Pasi Rautio, Kai Schwärzel; Funding acquisition: Kai Schwärzel; Resources: Mathieu Jonard, Andreas Schmitz, Paul Schmidt-Walter, Heleen Deroo, Peter Waldner, Nathalie Cools, Bruno De Vos, Arne Verstraeten, Inken Krüger, Anne Thimonier, Volkmar Timmermann, Mathias Neumann, Pasi Rautio; Supervision: Kai Schwärzel.

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Data availability
ICP Forests data can be accessed via data request from the ICP Forests database: https://www.icp-forests.net/data-maps/data-requests.

Declarations

Competing interests
The authors declare no competing interests.

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