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Title:

Local site conditions reduce interspecific differences in climate sensitivity between native and non-native pines.

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Conceptualization: MKl and RP; methodology: MKl and JJ; dendrochronological investigation: MKl, MKo, MJ and RP; *P. sylvestris*, *P. nigra*, *P. rigida* occurrence data collection: RP; occurrence data processing and analysis: RP; remote sensing analyses: JJ; dendroclimatic analysis: MKl and JJ; between-class analyses: MN; original draft writing: MKl, JJ and RP; editing: MKl, JJ, RP and MN. All the authors contributed to the final version of the article.

Abstract

Two European pine species, *Pinus sylvestris* and *Pinus nigra*, are experiencing dieback as a result of the increasing frequency and intensity of extreme climatic events. Recent species distribution models predicted shrinkage of ecological niches in the near future and shifted their habitat range towards the northeast. Consequently, *P. sylvestris* may contract its range and *P. nigra* may expand in Central Europe. To test whether native pine species have an advantage over introduced pine species in acclimation to a novel climate in Central Europe, we investigated the climate sensitivity and vitality of *P. sylvestris*, *P. nigra* and *Pinus rigida*. We sampled mature stands of each pine species at three sites in Central Europe, for which we determined climate–growth relationships: temporal stability of temperature and precipitation correlations with tree-ring width and resilience indices. Based on remote sensing data, we assessed differences in surface reflectance and photosynthetic activity obtained from the normalised difference vegetation index (NDVI). Our analyses revealed that the climate sensitivity and surface reflectance of pines are not due to their nativeness in Central Europe but better explained by local site conditions. The specificity and variability of drought events may determine both the homogeneous and diverse susceptibility of species to a negative water balance. Therefore, the character of future climatic extremes seems to be the key to understanding the acclimation of native and non-native pine species in Central Europe. Because our studies do not provide evidence of the superiority of non-native pine species over *P. sylvestris*, and the potential impacts of introduced species on local habitats seem poorly understood in the face of climate change, we urge particular caution in introducing species with unrecognised invasive potential.

KEYWORDS

P. sylvestris, *P. nigra*, *P. rigida*, acclimation, climate sensitivity, drought resilience

1. Introduction

The history of the introduction of non-native tree species in Europe spans only 300 years (Nyssen et al., 2016), although broader attempts to use them in commercial forestry date back to the mid-19th century (Alizoti et al., 2022). These attempts were related to the rapidly shrinking, easily accessible forest resources in Europe and the increasing demand for energy and construction wood during the industrialisation period (Hölzl, 2010). As a result, of the more than 150 tree species introduced into Europe (Brus et al., 2019), interest has focused on those characterised by both fast growth and the expected quality of the wood raw material (Dimitrova et al., 2022). The idea of planting the introduced species was therefore driven by economic considerations, while the ecological requirements of the species were initially not of primary importance (Peterken, 2001; White, 1997). Phylogenetic relationships among plants are often reflected in the phylogeny of their symbionts, parasites and pests (Segraves, 2010). Hence, the introduction of species, especially those with native congeners, involves the risk of unintentional introduction of trophically related species, which may negatively affect native species and ecosystem functioning (Banasiak et al., 2019; Pötzelsberger et al., 2021). On the other hand, species that are phylogenetically distant from native species introduce new functional traits into ecosystems. This can cause alternations in ecosystems and changes in natural biodiversity due to competition with native species, allelopathy, changes in elemental cycling, physical properties of litter, etc. (Piwczyński et al., 2016; Wohlgemuth et al., 2022).

In Central Europe, with commercial forestry dominated by native Scots pine (*Pinus sylvestris* L.) with high tolerance to harsh climate and poor soils (Houston Durrant et al., 2016), attempts were mostly made to plant species adapted to different growing conditions, e.g. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Grand fir (*Abies grandis* Douglas (ex D.Don) Lindl)., or eastern white pine (*Pinus strobus* L.) (Radu, 2008; Thomas et al., 2022). These species appear to be promising as having a lower invasive potential than deciduous species (Carrillo-gavila and Vila, 2010). According to Adamowski (2004), the low invasiveness of conifers in Central Europe is not only due to the small scale of introductions but also to their ability to compete habitats with various degrees of disturbances. In the case of pioneer species, which most cultivated alien pine species are, the spread has rarely been observed, mainly on abandoned agricultural land. On the other hand, the spread of the only invasive Central European pine species, *P. strobus* (Hadincová et al., 2007), is limited by fungal pathogens (Radu, 2008).

Scots pine, the dominant tree species in Central and Northern Europe, is characterised by its wide ecological amplitudes (Carlisle and Brown, 1968). However, the future of Scots pine does not seem optimistic given the observed and predicted changes in climatic conditions (Marqués et al., 2022). In the lowlands of Central Europe, the expected climatic conditions will lead to a northward retreat of this species, leading to a range contraction in relation to its current extent (Bombi et al., 2017; Buras and Menzel, 2019; Dyderski et al., 2018). The results of some studies using recent climate change scenarios for other species have even shown that the effects of climate change expected in 2061–2080 can be expected in 2041–2060 (Puchałka et al., 2023a, 2021). This suggests that the problem of range shifts of native species may also be more urgent than previously thought. These predictions are complemented by evidence from studies that focus on climate–growth relationships and suggest that Scots pine will not be able to cope with climate change in the western part of its range, while it will benefit from projected higher temperatures in Northern Europe (Camarero et al., 2015; Harvey et al., 2020; Metslaid et al., 2018). Moreover, a decline in the vitality of pine stands has been reported in many regions of Europe (Meshkova, 2021; Rebetez and Dobbertin, 2004; Sidor et al., 2019). Although precipitation deficits appear to be the main driver of Scots pine decline (Hunziker et al., 2022), when combined with biotic agents, they can accelerate this process (Lemaire et al., 2022). Even though resilience enhanced by tree growth release may compensate for the dieback effect, projected warming may weaken this process (Margalef-Marrase et al., 2023). These considerations raise the question of whether it is advisable to identify a tree species that is more suitable for future conditions in Central Europe and whether we should choose among the introduced tree species? The introduction of non-native broadleaved species could alter ecosystem functioning and lead to the loss of species associated with natural coniferous forests without satisfactory timber production, as most deciduous trees have higher foil fertility requirements (Leuschner and Ellenberg, 2017). Moreover, deciduous species create more shade, which may further accelerate the expected climate driver declining of boreal species such as *Vaccinium myrtillus* L. and *V. vitis-idaea* L. (Puchałka et al., 2023b; Woziwoda et al., 2019, 2021). Therefore, it seems reasonable to consider species closely related to *P. sylvestris* with similar functional traits and ecological requirements that could serve as alternatives to native species, with minimal impact on ecosystem functioning while being better adapted to the future climate. Alternative species include the North American *Pinus rigida* Mill. (section *Trifoliae*), which is quite commonly cultivated in Central Europe but has hardly been studied dendrochronologically (Klisz et al., 2022; Wilczyński, 2020), and the southern European *Pinus nigra* Arn. ssp. *nigra* (section *Pinus*), which is more closely related to *P. sylvestris* (Gernandt et al., 2005). The general ecological similarities in functional characteristics, ecology, morphology and chemistry between native pine and the introduced species make it possible for these species to provide comparable timber with minor impact on the forest ecosystem (Bellon et al., 1977; Pazdrowski and Szaban, 2002).

Black pine, a species common in Southern Europe from Spain to the Black Sea basin, is found in upland and mountainous regions (Farjon and Filer, 2013a). Its spatial distribution is linked to its variability, which has led to the recognition of five subspecies (López et al., 2004). Most likely used for introduction in Central Europe (Jagielska et al., 2007), *P. nigra* ssp. *nigra* is found mainly in the Balkans, southern Italy (Alpine foothills), eastern Austria and Romania (Enescu et al., 2016). The original aim of the introduction of black pine to Central Europe (Baltic coast, second half of the 19th century) was to stabilise coastal dunes by afforestation (Król and Ostrowicz, 1976). Then, with the emerging problems of Scots pine dieback in heavily polluted areas, black pine was planted as a species with a higher resistance to pollution (Latocha, 1975). Previously considered to be invulnerable to water availability (Leal et al., 2008), *P. nigra* ssp. *nigra* appears to have become increasingly drought sensitive in recent years with increasing aridity (Móricz et al., 2018). However, the precipitation deficit does not yet appear to limit non-native tree stands in Central Europe (Klisz et al., 2022; Thurm et al., 2018). We therefore recognised black pine (*P. nigra* ssp. *nigra*) as a European pine species that may provide an alternative to Scots pine in Central Europe.

Pitch pine is a North American species that limits its occurrence to sites with less fertile, shallow and sandy soils, whose natural range extends from coastal Maine through the Appalachians to northeastern Georgia (Farjon and Filer, 2013b; Little, 1959). In Europe, low ecological requirements have resulted in poor habitats, often lacking woody vegetation (e.g. sand dunes), among the most common areas of Pitch pine introduction (Bellon et al., 1977). Although climate suitability was most likely not considered when pitch pine was introduced, a convergent pattern of climatic sensitivity was now observed in native and secondary distributions (Cedro et al., 2013; Klisz et al., 2022; Pederson et al., 2004). Given the comparable ecological requirements, convergent growth performance in native and secondary distributions and a climatic niche in North America similar to the future climate in Europe, we considered pitch pine (an introduced species) suitable for comparing native and non-native pine species.

To understand the advantages and weaknesses of non-native pine species compared to native pine species in terms of secondary growth, we selected Scots pine, black pine and pitch pine as the model species. Therefore, we selected three parallel study sites in Central Europe, each containing a native pine species (Scots pine), a pine species introduced from Southern Europe (black pine) and a pine species introduced from North America (pitch pine) to test their performance under Central European conditions. We focused on climate–growth relationships and the effect of extreme climate events in conjunction with analyses of satellite-based vegetation indices as indicators of tree vitality. Our aim was to determine whether site characteristics or species origins explain the life traits of the studied species. We hypothesised that: (i) despite the diverse origins of pine species (native to Central Europe, non-native to Central Europe and non-native to Europe), growth performance depends on site conditions rather than species, and (ii) satellite-based vegetation indices, similar to climate sensitivity indices, reflect differences among species and site conditions.

2. Materials and methods

2.1 Species selection and study sites

Three phylogenetically related pine species were selected for the study: *P. sylvestris* (PISY), native to Central Europe; *P. nigra* (PINI), non-native to Central Europe and *P. rigida* (PIRI), non-native to the European continent (Fig. 1). In selecting the three study sites, we were guided by the following rationale: each site had to be characterised by the presence of mature stands of each of the three pine species as dominant in their species composition. Thus, each study site consisted of three isolated but closely spaced neighbouring sites. The study sites were geographically within the natural range of PISY and within the climatic envelope of each of the three pine species (Figs. 1 and 2). All study sites were located in a lowland region in central and western Poland: Chojnów, Mazovia (CHO, N52.0979, E20.8751), Piaski, Greater Poland (PIA, N51.6086, E17.1022) and Toruń, Pomerania (TOR, N53.0481, E18.5644). The study sites are characterised by favourable climatic conditions (temperate climate) for tree growth with moderate annual precipitation sums (from 483 to 526 mm, CHO and PIA, respectively) and a mild annual temperature average (from 8.3 to 8.8 °C, TOR and PIA, respectively) (Fig. A.1; Haylock et al., 2008, E-OBS version 22.0e). Soils at the CHO site are homogeneous for all pine species—rusty soils developed on loose sand. The forest soils in the TOR site are podzolic soil formed on dune sand (PIRI and PISY) and podzolic, post-agricultural soils (PINI). The forest soils at the PIA site are homogeneous for all pine species—dystric arenosols formed on loose sand in a humid continental climate.

2.2 Growth data

For each pine species, 20 sample trees were selected at each study site based on their biosocial (dominant or co-dominant trees), health status (vital individuals without any visible damage) and location in a closed stand (avoiding trees at the edge of gaps and stand margins). Two increment cores were collected from each sample tree at a height of 1.3 m. The increment cores were taken from two perpendicular directions using 5-mm diameter Pressler drills. To make the annual ring boundaries clearly visible, the dry cores were treated with a series of progressively finer sandpapers (grit sizes up to 1,000). Finally, wood samples with distinct growth ring patterns were digitised at 2,400 dpi (Epson Expression XL12000). We assisted the cross-dating by identifying the boundaries between annual rings using a binocular (80x magnification LEICA S8APO) to verify the possible occurrence of false rings as a result of intra-annual density fluctuations in earlywood.

2.3 Dendrochronological analysis

We averaged two growth series per tree into one series and then detrended using a cubic smoothing spline with a cut-off of 50% of the frequency at a wavelength of 30 years (Cook and Peters, 1981; Speer, 2010). To remove the remaining temporal autocorrelation and emphasise the high-frequency signal (year-to-year variability) of growth, pre-weighting was performed using the first-order autoregressive model (Cook and Kairiukstis, 2013). Next, we used a bi-weighted robust mean to develop residual chronologies independently for the combination of species and site (Table A.1, Fig. A.3). To assess the quality of developed chronologies (Table A.1), we calculated the Gleichläufigkeit (glk, i.e. the coherence coefficient; Buras and Wilmking, 2015; Eckstein and Bauch, 1969) and mean inter-series correlation (mean rbt, an indicator of the strength of the common signal; Cook and Kairiukstis, 2013; Wigley et al., 1984). We then applied the sub-sample signal strength (SSS) and the first-order autocorrelation (AR1, an indicator of the effects of previous year conditions on current year growth) to test the representativeness of the species chronologies. These parameters were calculated from the index series (RWI, raw ring widths of each tree divided by the average ring width of the tree) for the robust common period from 1943 to 2020 determined according to sub-sample signal strength (SSS > 0.95; Fig. A.2).

2.4 Climate sensitivity

In the climate sensitivity analyses, we employed the *daily_response_seascorr()* function of the dendroTools R package (Jevšenak, 2020; Jevšenak and Levanič, 2018), which applies a moving window of variable widths and calculates partial correlation coefficients between an aggregated climate variable and a selected tree-ring proxy while simultaneously controlling for the second climate variable (Jevsenak et al., 2021). The function was applied to both climate variables: mean temperature while considering precipitation as a control and vice versa. We considered all seasons with lengths from 21 to 270 days, starting in April of the previous year and ending in October of the current year. The final output matrices with correlation coefficients were also transformed with the principal component analysys (PCA) and the resulting biplots were used to infer similarities in climate response among the studied sites and species.

To assess the temporal stability of temperature and precipitation correlations, we repeated the analyses with dendroTools with a fixed season length of 150 days and systematically subsetted the analysed years using a 30-year moving window with a 1-year offset. These analyses were performed for the robust common period from 1943 to 2020.

2.5 Resilience indices

The negative effects of extreme dry years and years with extreme growth reductions were studied based on resilience indices (Lloret et al., 2011, e.g. 1–3) and superposed epoch analysis (SEA) (Chree, 1913). First, we identified negative pointer years (van der Maaten-Theunissen et al., 2021) based on the “Cropper” method, using a window size of 5 years and a series threshold of 60% as criteria for defining negative and positive events (Cropper, 1979). Next, we identified severe dry years based on values of the standardised precipitation-evapotranspiration index (SPEI) (Beguería et al., 2014), using values below −2 as a cutoff criterion (McKee et al., 1993; Paulo et al., 2012) separately at 3- and 6-month accumulation scales. The identified negative pointer years and years with SPEI < −2 were combined and used in the SEA and calculation of resistance, recovery and resilience. The combination of both indicators was necessary, since we were interested in the general response to growth reductions caused by drought or other biotic and abiotic agents.

To calculate the SEA, we applied 1,000-fold bootstrap resamples and 3-year lags before and after a drought event that coincided with negative pointer years (SPEI < −2). These calculations included detrended and prewhitened RWI chronologies (see 2.3 Dendrochronological analysis) with a statistical significance of response ($p < 0.05$). Finally, we determined the significance of departure from RWI before and after extreme drought events.

To determine how pine species cope with extreme drought events, we applied three commonly used indices: resistance, recovery and resilience (Lloret et al., 2011).

$$\text{Resistance (Rt)} = RW_t / RW_{pre} \qquad \text{(Eq. 1)}$$

Recovery (Rc) = RW_{post} / RW_t (Eq. 2)

Resilience (Rs) = RW_{post} / RW_{pre} (Eq. 3)

where RW_t is the radial width of the annual ring during the corresponding year *t*, RW_{pre} is the mean ring width for the 4 years before year *t* and RW_{post} is the mean ring width for the 4 years following year *t*. Each index was calculated at the level of a single tree for 7 negative pointer years coinciding with drought events identified on at least one of the three study sites.

2.6 Vegetation indices and between-class analyses

To highlight the differences in surface reflectance and photosynthetic activity among studied species and sites, we extracted the Landsat 8 remote sensing data and calculated the time series of the normalised difference vegetation index (NDVI), which reflects information on vegetation greenness, photosynthesis and metabolism intensity of vegetation (Buras et al., 2020; Hlásny et al., 2015; Meyer et al., 2020; Zhang et al., 2006). To do so, we first created polygons for each study site and then extracted NDVI time series from the Google Earth Engine (Gorelick et al., 2017) using atmospherically corrected and cloud-free images for the period May 2013–December 2020. The NDVI was calculated based on Eq. 4, where NIR and R are atmospherically corrected surface reflectance in the near-infrared and red bands, respectively (Jiang et al., 2008). We calculated the NDVI on a monthly basis, using only months within a usual growing season (March–September), in which all study sites had NDVI values. Finally, we used PCA and created biplots to show similarities among species and sites in their surface reflectance.

NDVI = (NIR – R) / (NIR + R) (Eq. 4)

To assess similarities and hierarchical clustering patterns between the studied species and sites, the NDVI time series and climate correlation coefficients were analysed using the k-means algorithm. To determine the optimal number of clusters, we used the within-sum-of-squares method (WSS), which minimises the distance between points in a cluster. Finally, we defined three clusters as optimal for grouping species and sites. The optimal number of clusters and k-means were computed with cluster and factoextra packages in R (Husson et al., 2015; Kaufman and Rousseeuw, 2008).

Since PCA mixes the effect of sites and species, we applied between-class analyses (BCA) (Culhane et al., 2002; Dolédec and Chessel, 1987) to assess the difference in growth–climate relationships and NDVI between both sites and species using the results of the PCA. The significance of the difference was checked by employing a permutation test based on the ratio of between-sites or between-species inertia divided by the total inertia. The 999 permutations were performed to calculate the simulated *p*-value. The BCA was implemented with the ade4 package for R (Thioulouse et al., 2018).

2.7 Testing the hypotheses of equal means

To test the hypotheses of equal means of climate–growth response, resilience and vegetation indices among different sites and species, we first tested the assumption of homogeneous variances based on Levene's test and the assumption of normally distributed data based on the Shapiro-Wilk test for normality (Verma and Abdel-Salam, 2019). Because the assumptions were not met (see Tables A.2 and A.3), we used the nonparametric Friedman test to test the hypothesis of equal NDVI values (paired observations) and the Kruskal-Wallis test to test the hypothesis of equal resilience indices and climate growth correlations (independent observations) (Cleophas and Zwinderman, 2016) (Table A.4). For resilience indices, we compared means across all negative pointer years. Due to a large number of correlation coefficients (i.e., 108,125), to avoid comparing less significant climate-growth correlations, and to avoid the problem of small standard errors in such cases (Lieber, 1990), we compared only 1% of the most significant positive and negative correlations, separately for temperature and precipitation correlations. We have also tested different approaches (results not shown here), and the conclusions were robust. All pairwise post-hoc comparisons were based on the

Wilcoxon signed-rank test (paired NDVI observations) and the Wilcoxon rank sum test (independent observations for resilience indices and climate–growth correlations) (Harris and Hardin, 2013), and *p*-values were adjusted using the Bonferroni correction for multiple comparisons (Sedgwick, 2012).

3. Results

3.1 Climate–growth relationships

Analyses of the climate of the three pine species under different climatic conditions (Fig. A.1) showed that local conditions predominated over species-specific growth response (Fig. 3 and A.6). This pattern was particularly pronounced in the response of growth to temperature, in which all pine species growing under the CHO site conditions (the easternmost site) showed a strong climatic signal related to spring and summer moisture conditions, whereas this trend was not so pronounced in pines growing at the PIA and TOR sites (Fig. A.6). An exception to this pattern was the growth response observed in PINI at the PIA site, although here, the climate signal was limited to the pluvial conditions of the spring season. Although general positive effect of precipitation was observed for all pine species at each of the three sites, it was species rather than site specific. The strongest effect was observed for PINI and PIRI under the CHO environmental conditions, where the positive effect covered the summer of the previous year through the autumn of the current year, while PIRI and PISY were weakest under the TOR environmental conditions, covering only the current summer and fall.

Analysis of the temporal variation of climate signals revealed differences in climate sensitivity of pine species (Fig. A.4). Summer precipitation and early-season temperature appeared to be key drivers of radial growth at all sites. Under the CHO conditions, temperature correlations remained temporarily stable, while the same climate effects at PIA and TOR have weakened over the past three decades. In the case of PINI under the CHO site conditions (see CHPN in Fig. A.4), the positive effect of spring temperatures was noticeable throughout the entire period (1943–2020); nevertheless, it gradually weakened, in line with the general trend for the PIA and TOR sites. In contrast, the effect of precipitation was more species-related; namely, PIRI confirmed a time-stable positive relationship with spring precipitation, regardless of site conditions. In contrast, for PINI, the same trend could be observed only under the CHO and TOR site conditions (Fig. A.4).

3.2 Sensitivity to drought events

We identified 7 negative pointer years noted at least one of the three study sites (1953, 1963, 1976, 1989, 2003, 2006 and 2015) and tested site- and species-specific sensitivity to drought events. The overall trend in drought resistance depended on drought duration (SPEI3 or SPEI6), site conditions and species sensitivity. Long-term drought (SPEI6) significantly reduced the growth of PIRI and PISY at the PIA site and PIRI and PINI at the TOR site (Fig. 4). The negative effect of short-term drought was confirmed only for PISY and PINI at the PIA site but 1 year after the drought event. For 2 years of severe drought, a reduction in growth was observed at two study sites (2006: CHO and TOR, 2015: CHO and PIA). Resistance was higher at the CHO site than at the TOR site in 2006 but similar to the PIA site in 2015 (Fig. 5). In general, pines at the CHO site were characterised by consistent resistance to drought events (Fig. A.5). Species-specific resistance was different at each site; at the PIA site, PINI resistance was significantly higher than PIRI (years 1953, 2003 and 2015). In contrast, PINI had the lowest resistance at the TOR site (years 1963, 1989 and 2006; Fig. A.5). No clear site- or species-specific trends were observed with respect to resistance and recovery, although PIRI survived the severe European-wide drought in 2003 the best and achieved the highest recovery index at the PIA site (Fig. A.5).

3.3 Identification of clusters related to surface reflectance and climate correlations

Based on the WSS method applied to NDVI and climate (temperature and precipitation) correlation matrices, we defined three clusters as optimal for grouping species and sites. Clustering of chronologies based on NDVI clearly distinguished the CHO site from PIA and TOR (Fig. 6A), while clustering based on temperature correlation distinguished the PIA site from CHO and TOR (Fig. 6B). In the case of the NDVI PCA biplot, the cluster for the PIA site also included PINI at the TOR site, while the third cluster included only PISY and PIRI for the TOR site. In turn, for the temperature PCA biplot, the cluster for the TOR site also included PISY at the CHO site, while the third cluster included only PINI and PIRI for the CHO site. The first two principal components explained a total of 68.17% of the variability in the case of the NDVI biplot (PC1 48.01% and PC2 20.16%, respectively) and 72.48% of the variability in the case of the temperature correlation biplot (PC1 51.80% and PC2 20.68%, respectively). In contrast, k-means clustering for precipitation correlation did not confirm either site- or species-specific clustering patterns (Fig. A.7).

The statistical significance of the differences between sites in the NDVI and growth–temperature correlations was proved by the results of the BCA. The simulated *p*-value of 0.004 obtained in the BCA indicated significant differences between sites in NDVI values (Table 1). The BCA criterion was 0.56, indicating that 56% of the total variability of the NDVI was explained by site conditions, while species effect was equal to 13% and non-significant. Site conditions' influence on the difference in growth–temperature relationships was less prominent: the BCA criterion reached 0.52, i.e. explaining 52% of total variation, with a *p*-value of 0.008. The species-specific effect on the growth response to temperature was non-significant and equal to those for the NDVI, reaching only 13%. Neither species nor sites had a significant influence on the growth–precipitation correlations structure revealed by a PCA.

3.4 Differences among species and site conditions

The pairwise comparisons between the sites and species of the NDVI and resilience indices revealed that most of the significant differences were among the sites and not within them (among species; Table A.5, Fig. 5). Differences in resistance and recovery among the TOR and CHA sites were pronounced with no differences between species; however, there were exceptions, e.g. PIPN and PIPR have different recovery rates (Fig. 5). Pairwise comparisons between all possible pairs (sites and species) confirmed the significance of differences between most of the pairs (Fig. A6). Only in four cases there were no significant differences. The general trend shows a tendency toward clustering within sites and increasing differences between sites (Table A6, Fig. A6).

Table 1. Results of the BCA of the NDVI and growth–climate correlations.

Variable	Grouping factor	Ratio of the between-class inertia to the total inertia	Simulated *p*-value
NDVI	Site	0.557	0.004
NDVI	Species	0.132	0.942
Growth–temperature correlation	Site	0.522	0.008
Growth–temperature correlation	Species	0.131	0.919
Growth–precipitation correlation	Site	0.397	0.062
Growth–precipitation correlation	Species	0.204	0.704

4. Discussion

4.1 Site-specific response to climate

Under Central European climatic conditions, three pine species responded positively to growing season precipitation, with highly consistent responses to end-of-season pluvial conditions (Fig. 3 and A.6). However, the site-specific and time-stable growth response was pronounced for the end-of-winter and spring temperatures (Fig. A.4). Although our studies have not confirmed the species-specific climate sensitivity of pines, the positive effect of end-of-summer precipitation on introduced pine species is reflected in their growth response in their natural range (Lévesque et al., 2014; Patterson et al., 2016). Studies of the natural range of *P. nigra* confirm the decrease in sensitivity of tree-ring growth to summer precipitation observed in the late 20th century (Leal et al., 2008); yet, our results suggest that this trend may depend on local conditions (observed at the PIA and TOR sites but not at the CHO site, Fig. A.4). Site-specific climate–growth relationships reported for pine species in Europe were related either to marginal populations under mountain climate conditions (Herrero et al., 2013) or to lowland populations in the species' core range (Cedro et al., 2022). Therefore, our results may reflect a more general pattern for the effects of local conditions on the radial growth of pine species. The positive effect of winter–spring temperature on the growth of Scots pine, reported for the specific conditions of coastal dunes in Central Europe (Janecka et al., 2020), was confirmed by our results for inland sandy soils (Fig. 3). Furthermore, our results suggest that this relationship also exists between native and introduced pine species. Thus, pine species with distinct natural ranges, but whose climatic niches partially overlap, performed similarly under certain local conditions (Figs. 1, 2). Local site conditions seem to uniformly drive not only the growth pattern (Fig. 6B, Table 1) but also the surface reflectance and photosynthetic activity reflected in the NDVI of pine species (Fig. 6A, Table 1). A similar trend for *P. sylvestris* was confirmed by recent studies in the Czech Republic on the effect of local topographic conditions on leaf and stem biomass (NDVI and RWI, respectively) (Mašek et al., 2023). The site-specific vitality of pines (expressed by vegetation indices, Fig. 6A) may be related to the low water storage capacity of the soil specific to each study site (Móricz et al., 2018).

4.2 Diverse drought effects on sensitivity indices

Despite relatively similar local climatic conditions at the study sites (Fig. A.1), different growing conditions appeared to exist at the CHO site than at the PIA and TOR sites. This may be due to a specific combination of climatic and local site conditions, which have been shown to influence the growth of Scots pine in different parts of its range (Bauwe et al., 2013; Henttonen et al., 2014; Lange et al., 2018). Our previous study on the acclimation of non-native conifer species (including four pine species) under conditions similar to those at the CHO site confirmed that *P. nigra*, *P. rigida* and *Pinus banksiana* are similarly sensitive to climate. However, they differ from *P. strobus* (Klisz et al., 2022). Thus, while selected non-native pine species in Central Europe appear to respond similarly to *P. sylvestris* in terms of growth, the evidence to date does not allow generalisation to all introduced pine species. Prolonged drought at the PIA and TOR sites resulted in a significant growth decline for each pine species, while the same pattern was not confirmed for the CHO site (Fig. 3). Under certain site conditions, the occurrence of soil drought can override favourable climatic conditions (Bauwe et al., 2012). Yet perhaps favourable soil conditions can reduce the effect of climatic drought. This could explain why the pine species at the CHO site cope better with drought conditions than at the PIA and TOR sites. Of the drought sensitivity indices tested, the resilience and recovery indices were found to be the most consistent among species, yet site specific (Fig. A.5). In Scots pine, reduced water supply due to drought results in reduced tree ring width; however, at the cell structure level, the conductive function is optimised relative to investment in the cell wall structure, resulting in conduits with larger lumens but a smaller number of cells (Eilmann et al., 2009). Therefore, resilience and recovery as indices related to tree-ring width may indirectly indicate improved availability of carbon resources that allow unrestricted investment in cell walls while maintaining conductivity. We therefore hypothesised that the studied pine species adapt their strategies to cope with drought similarly, probably depending on the retention capacity of the soil (Lévesque et al., 2014). Seven episodes of severe drought were not observed at all the study sites over all the years ($SPEI < -2$; Fig. A5). Therefore, we assumed that each drought event may have had a different character (intensity, duration) and spatial extent within Central Europe. This explains why drought sensitivity indices varied between years and not just between study sites (Spinoni et al., 2015). Looking at the detailed results of the sensitivity indices, it is clear that some drought years elicited a uniform response from the pine species, while in other years, the pines responded differently (Fig. A.5). Therefore, we hypothesised that the drought sensitivity of the studied pines is related not only to site conditions but also to the specificity of the drought event. This, in turn, raises the question of whether the increasing frequency of drought episodes observed in recent years (Ionita and Nagavciuc, 2021; Spinoni et al., 2018, 2017) is related to a homogeneous or rather to the varying vulnerability of native and non-native pine species? The severe droughts observed in recent years suggest that they have a different character (Buras et al., 2020). Therefore, at least a few years of severe drought will likely result in a species-specific drought response.

4.3 Complex implications for the pines' acclimation

According to recent projections, the ranges of *P. sylvestris* and *P. nigra* will contract in Western and Southern Europe in the coming years and most likely expand in northeastern Europe (Buras and Menzel, 2019; Dyderski et al., 2018; Thurm et al., 2018). These predictions are in line with growth models for *P. sylvestris*, which show the largest increase due to climate change in mid-latitudes (Matías et al., 2017). In Southern Europe, *P. nigra* copes better with drought than *P. sylvestris* (Marqués et al., 2016). However, obstacles in the adaptation of newly emerging plants to new environmental conditions could prevent the spread of *P. nigra* (Tíscar et al., 2018), confirming the importance of considering both mature and juvenile stages in predictive models (Andivia et al., 2020). Such evidence for the adaptation of non-native pine species to extreme climatic conditions in Central Europe is scarce and mainly limited to local conditions (Klisz et al., 2022; Kreyling et al., 2012). The results presented here, although representing relatively similar climatic conditions of the study sites (Fig. A.1), add to the knowledge on the acclimation of native and non-native pine species to Central European conditions and provide evidence of the key role of drought events (Figs. 4, 5, A.5). However, they suggest that future growing conditions will have complex implications for the acclimation of pine species, depending on the intensity and type of climatic anomalies (Bussotti et al., 2015). Thus, different pine species may cope uniformly with certain Central European drought conditions. In contrast, other drought events may differentiate pines in terms of drought sensitivity, i.e. they may or may not be limiting for native or non-native species (Fig. A.5). Unfortunately, the complexity of climate–growth relationships in pine species complicates the use of species distribution model projections in planning strategies for future European forestry (Lindner et al., 2014). Our studies do not provide evidence for the superiority of introduced pine species over native *P. sylvestris* with respect to changing climatic conditions in Central Europe (Fig. 5). However, given the uncertainty about the direction of climate change in this part of the continent (Lhotka et al., 2018), we cannot rule out the possibility that *P. nigra* or *P. rigida* will exhibit a better strategy for coping with climatic anomalies. Furthermore, the decision to introduce alien organisms into the local environment should always be preceded by a thorough assessment of the potential threat to local biodiversity posed by the spread of alien species may pose (Pötzelsberger et al., 2020). Despite the various approaches that have been developed (Whitney and Gabler, 2008), risk analysis always includes an element of uncertainty due to the unpredictability of climate change, which may create favourable conditions for introduced species relative to native ones (Kleinbauer et al., 2010).

5. Conclusions

Despite the recent decline of Scots pine observed in several areas of Europe, consideration of alien species as an alternative for European forestry appears questionable given the limited evidence of acclimation of North American conifer species. The few studies comparing the growth performance of different alien species appear to be either outdated in light of recent climate anomalies, limited to local conditions of the study area or lack reference to closely related native species. Therefore, our study at least partially fills these gaps because it is up to date, considers three lowland sites in Central Europe and compares native and non-native pine species growing under the same climate and environmental conditions. Although the assumptions important for comparing the acclimation of alien species with the adaptation of native species are met, the relatively similar climatic sensitivity of the species with the apparent site-specific growth response does not justify recommending alien species for Central

European forestry. The low invasiveness of the introduced conifer species in Europe allows them to be planted in managed forests without a high risk of expansion into naturally valuable habitats. However, given their similar growth responses to climate as native species that cannot cope with climate change, it seems insufficient to consider alien species when planning the species composition of future forests.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Data statement

The research was performed based on a dataset obtained from the Global Biodiversity Information Facility (GBIF) database:
GBIF.org (12 December 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.97g9j6
GBIF.org (25 December 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.hnusyy
GBIF.org (25 December 2022) GBIF Occurrence Download https://doi.org/10.15468/dl.3qp7ng
The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supplementary materials

Appendix A. Supplementary tables and figures.

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Figures captions:

Fig. 1. Natural distribution of *Pinus rigida* (green; Panel A), *Pinus nigra* and *Pinus sylvestris* (blue and red, respectively; Panel B). Study sites: CHO, black square; PIA, black triangle; TOR, black circle.

Fig. 2. Climatic envelope of *Pinus nigra* (red), *Pinus rigida* (blue) and *Pinus sylvestris* (green). Study sites: CHO, black square; PIA, black triangle; TOR, black circle. MAT – mean annual temperature; BIO18 – precipitation of the warmest quarter.

Fig. 3. Species- and site-specific significant ($p < 0.05$) partial Pearson correlation coefficients between aggregated daily temperature and precipitation. For chronology IDs, see Table A.1.

Fig. 4. Superposed epoch analysis showing negative and positive tree growth departures (residual species chronologies) for the severe drought year (SPEI < −2) and 3 years before and after the drought events. Bar graphs for severe drought events characterised by SPEI3 (upper nine panels) and SPEI6 (lower nine panels). The dark grey bars denote significance ($p < 0.05$) of the departures from the RWI. The x-axis shows the period of 3 years preceding and following the event year (0). For chronology IDs, see Table A.1.

Fig. 5. Comparison of resistance, resilience and recovery among different sites and species across all negative pointer and extremely dry years. The pairwise comparisons are based on the Wilcoxon rank sum test, and only significant results with $p < 0.001$ are shown here. For a complete comparison, see Appendix A. Supplementary tables and figures (Tables A.5 and A.6). For site IDs, see Table A.1.

Fig. 6. PCA biplots of species- and site-specific NDVI (A) and temperature correlations (B). Red, blue and green colours assigned to k-means clusters. For chronology IDs, see Table A.1.

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Term: MKl

Conceptualization: MKl

Methodology: MKl, JJ

Software: JJ

Validation: MKl, JJ

Formal analysis: MKl, JJ

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Data Curation: MKl

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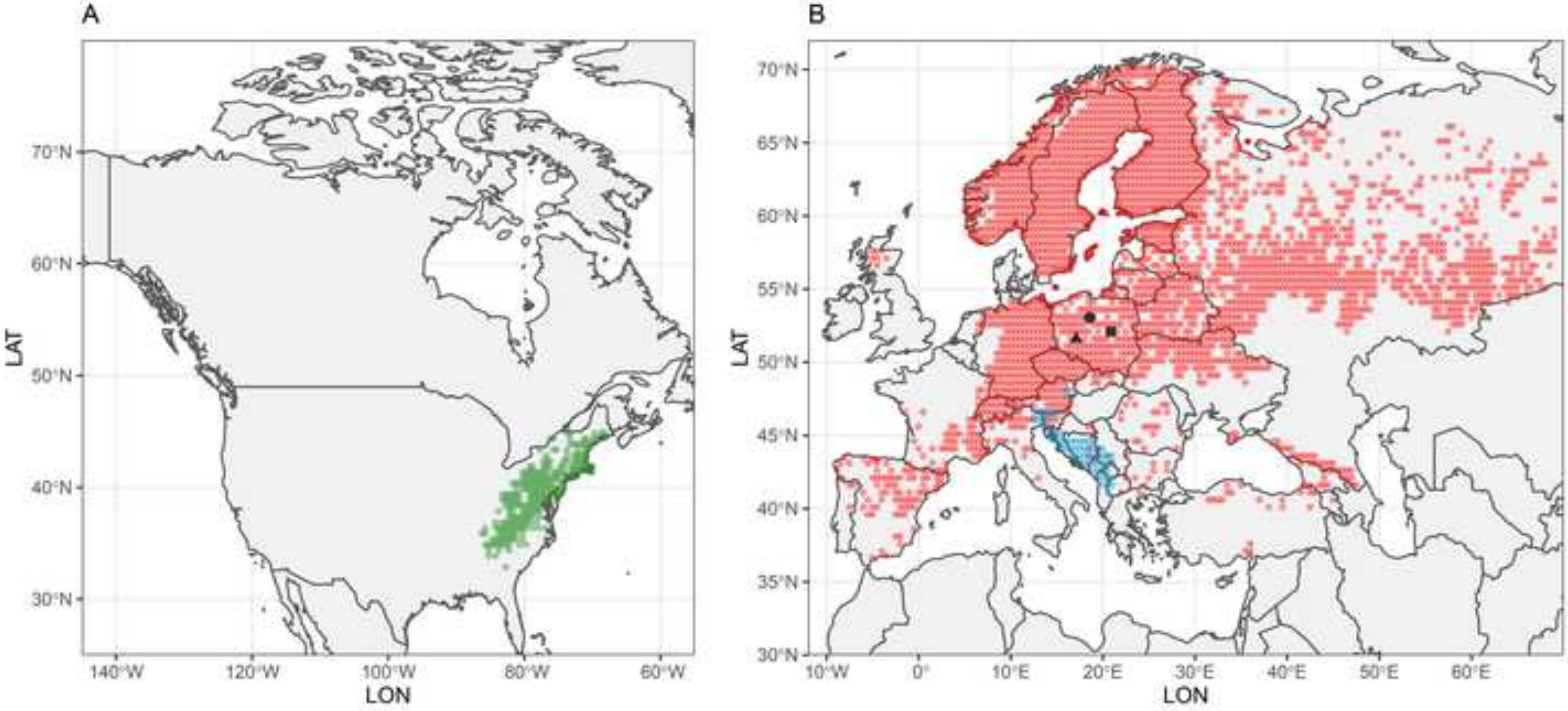
Figure 1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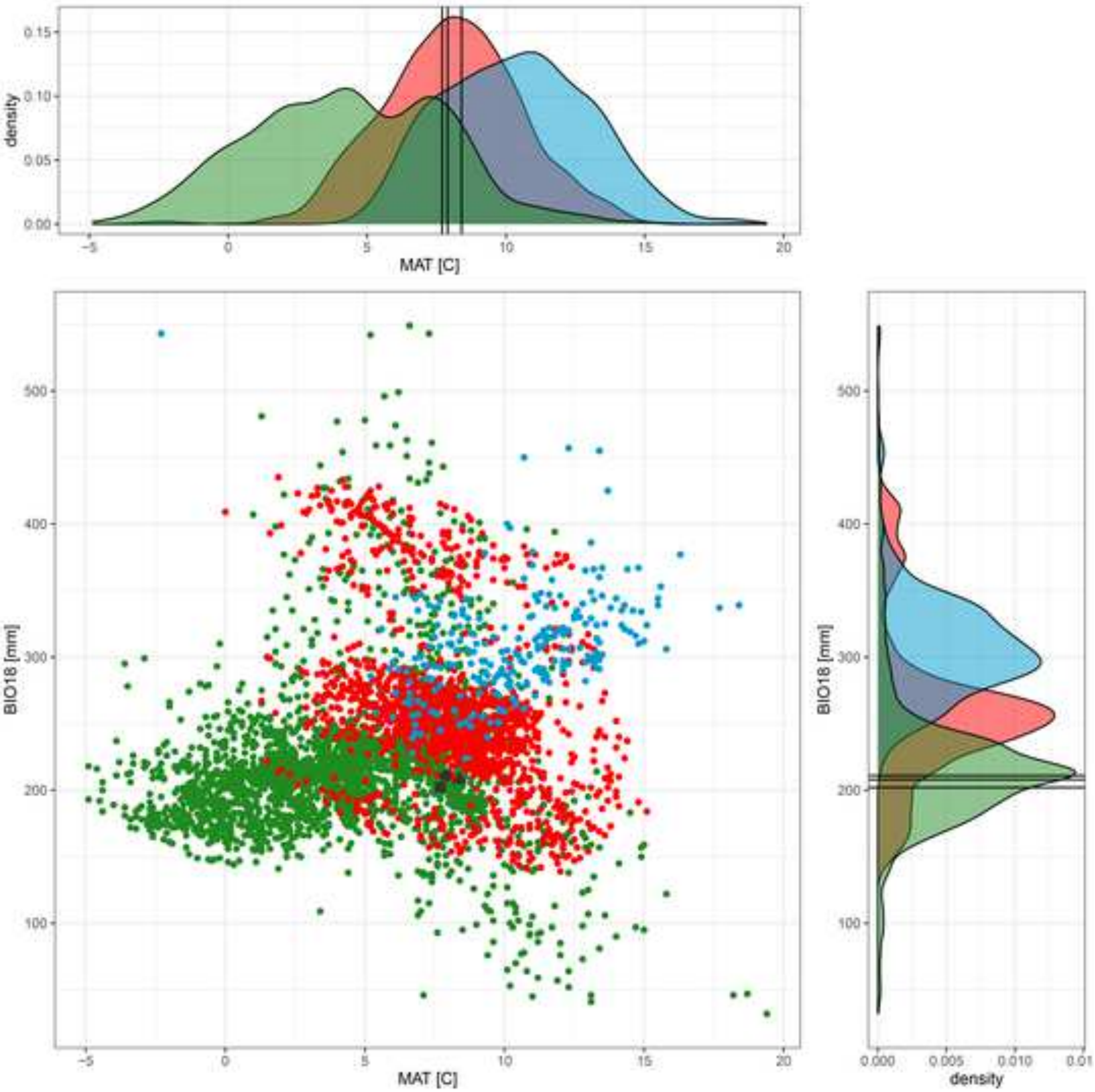
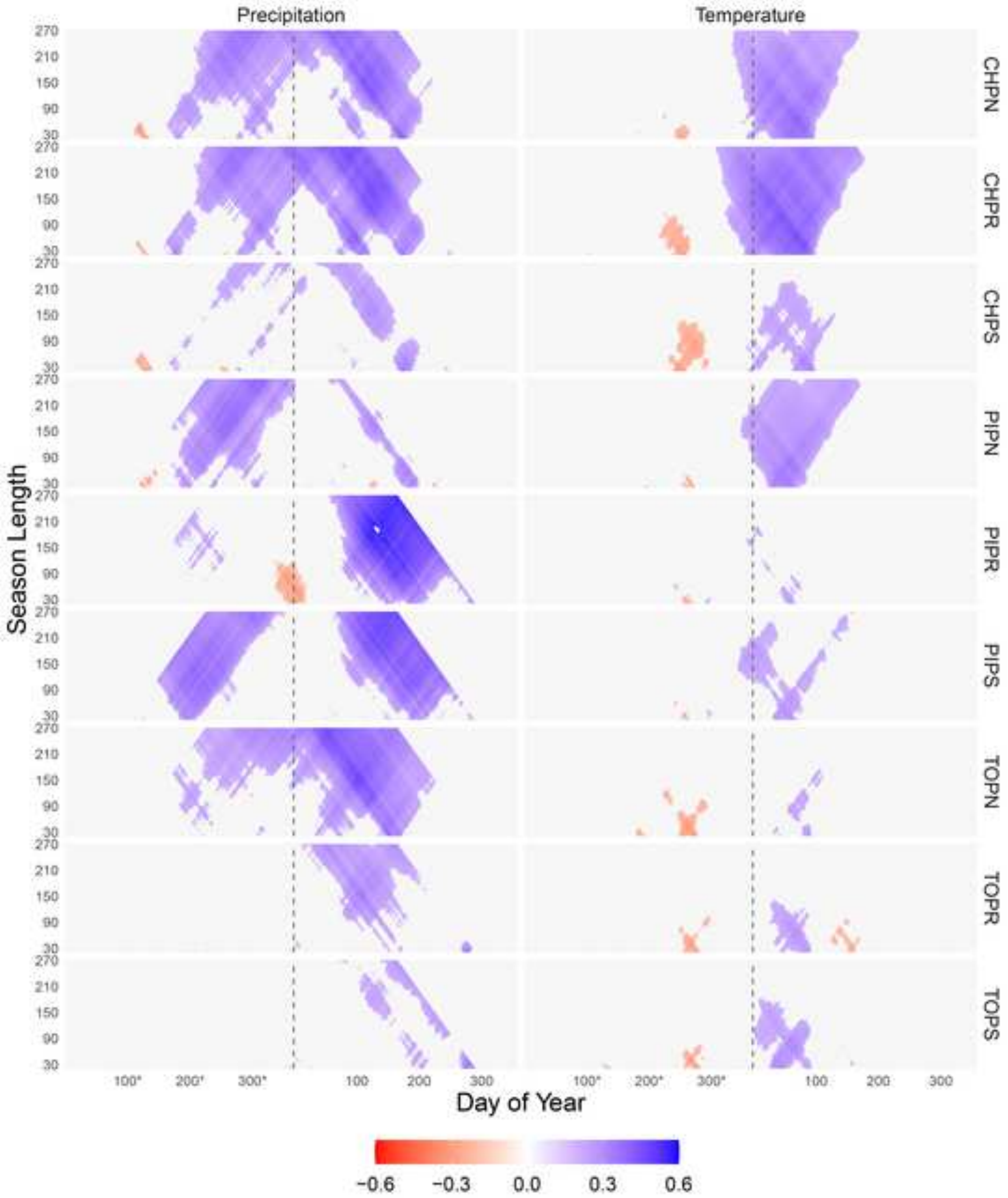


Figure 3



Precipitation
Temperature
Season Length
270
210
150
90
30
CHPN
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PIPR
PIPS
TOPN
TOPR
TOPS
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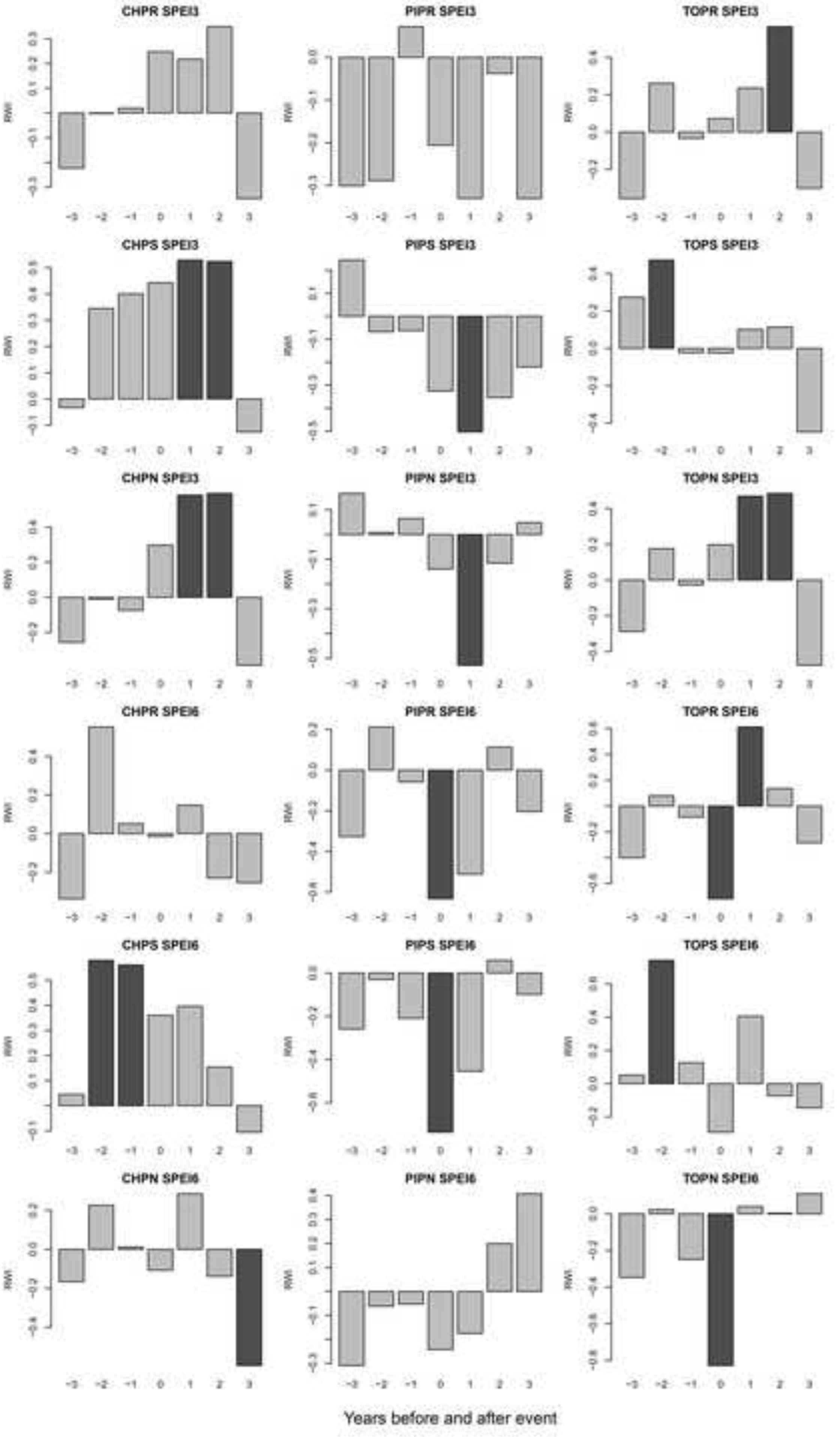
200*
300*
100
200
300
Day of Year
−0.6
−0.3
0.0
0.3
0.6

Figure 4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Years before and after event

Figure 5

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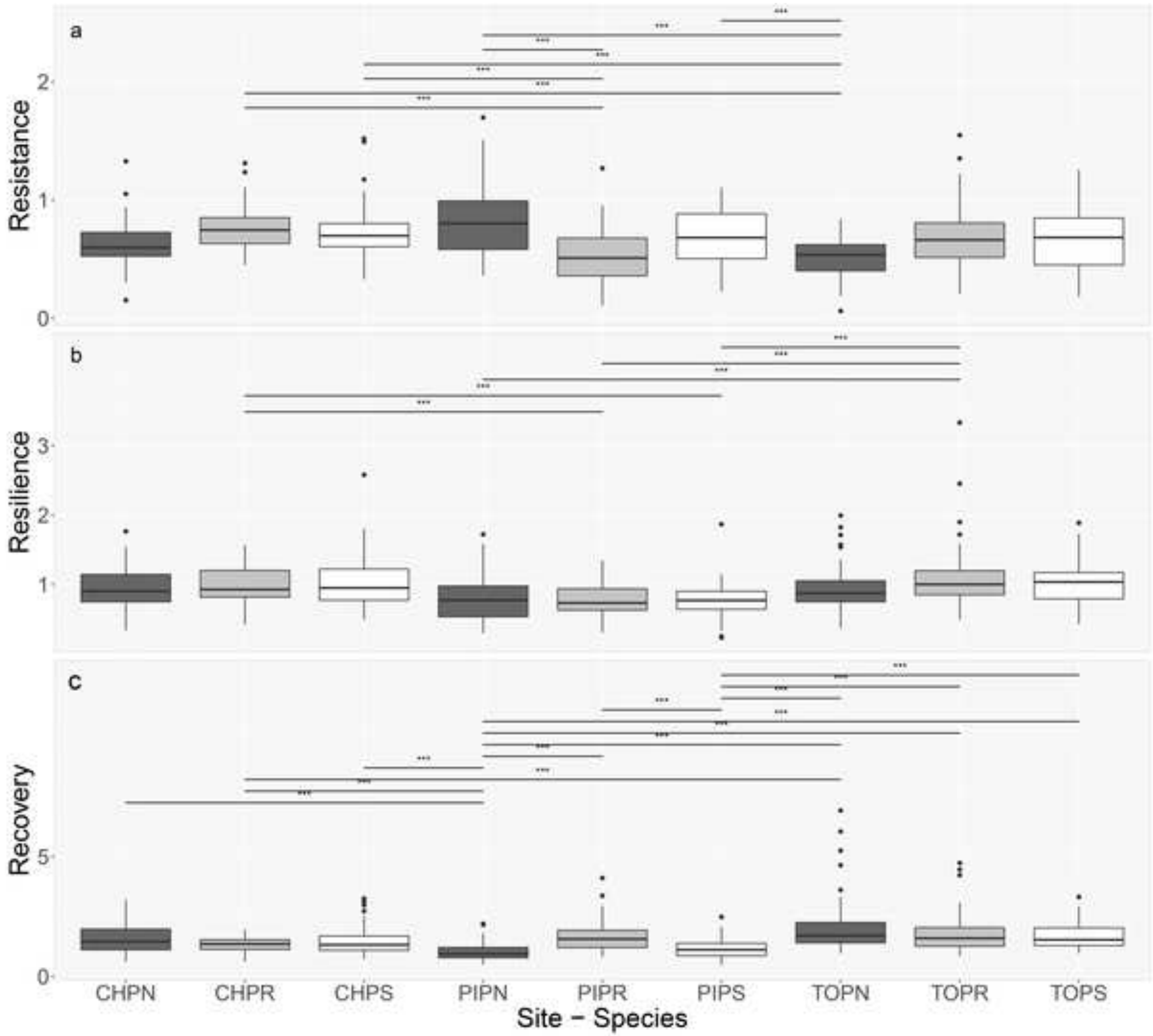
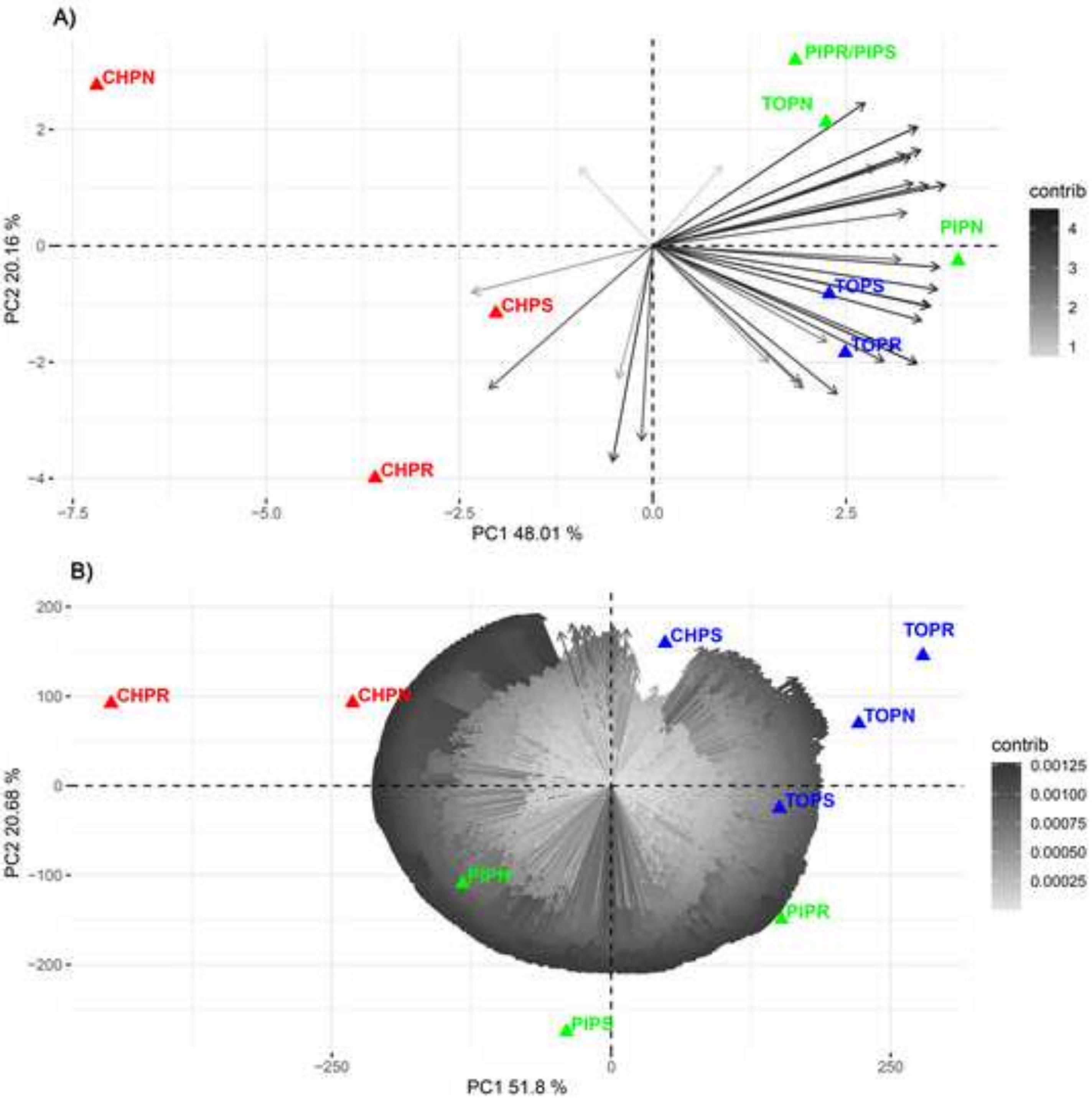


Figure 6


A)
CHPN
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CHPR
PIPR/PIPS
TOPN
PIPN
TOPS
TOPR
contrib
4
3
2
1
2
0
-2
-4
-7.5
-5.0
-2.5
0.0
2.5
PC1 48.01 %
PC2 20.16 %
B)
CHPR
CHPN
CHPS
TOPR
TOPN
TOPS
PIPN
PIPR
PIPS
contrib
0.00125
0.00100
0.00075
0.00050
0.00025
200
100
0
-100
-200
-250
0
250
PC1 51.8 %
PC2 20.68 %

Appendix A

Declaration of Interest Statement

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: