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RESEARCH ARTICLE

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Fewer chromosomes, more co-occurring species within plant lineages: A likely effect of local survival and colonization

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Abstract

Premise: Plant lineages differ markedly in species richness globally, regionally, and locally. Differences in whole-genome characteristics (WGCs) such as monoploid chromosome number, genome size, and ploidy level may explain differences in global species richness through speciation or global extinction. However, it is unknown whether WGCs drive species richness within lineages also in a recent, postglacial regional flora or in local plant communities through local extinction or colonization and regional species turnover.

Methods: We tested for relationships between WGCs and richness of angiosperm families across the Netherlands/Germany/Czechia as a region, and within 193,449 local vegetation plots.

Results: Families that are species-rich across the region have lower ploidy levels and small monoploid chromosomes numbers or both (interaction terms), but the relationships disappear after accounting for continental and local richness of families. Families that are species-rich within occupied localities have small numbers of polyploidy and monoploid chromosome numbers or both, independent of their own regional richness and the local richness of all other locally co-occurring species in the plots. Relationships between WGCs and family species-richness persisted after accounting for niche characteristics and life histories.

Conclusions: Families that have few chromosomes, either monoploid or holoploid, succeed in maintaining many species in local communities and across a continent and, as indirect consequence of both, across a region. We suggest evolutionary mechanisms to explain how small chromosome numbers and ploidy levels might decrease rates of local extinction and increase rates of colonization. The genome of a macroevolutionary lineage may ultimately control whether its species can ecologically coexist.

KEYWORDS

chromosome number, coexistence, ecological genetics and ecogenomics, genome size, life-history traits, locally species-rich families, polyploidy, species communities, species richness of lineages

Plant lineages differ dramatically in species richness and at global geographic scale such differences have often been explained by whole-genome characteristics (WGC). Specifically, some plant lineages are rich in species and others are poor, such as the emblematic contrast between a single extant species of Amborellaceae and more than 250,000 species of its sister clade, the remaining angiosperms (Chase et al., 1993; Christenhusz and Byng, 2016). The richness of a lineage across the globe obviously increases with rates of speciation and decreases with rates of extinction. Lineages differ among others in WGC with respect to ploidy level, monoploid chromosome number, and monoploid genome

size (Soltis et al., 2005, 2014; Bromham et al., 2015), and WGC of lineages have often been used to explain rates of speciation, global extinction, and richness of lineages (Wood et al., 2009; Kraaijveld, 2010; Mayrose et al., 2011; Soltis et al., 2014; Puttick et al., 2015). For genome size and numbers of chromosomes results were partly inconclusive (see Fawcett et al., 2013; Greilhuber and Leitch, 2013; and Husband et al., 2013 for reviews; Tank et al., 2015; and see Kapralov and Filatov, 2011 on archipelagos). In contrast, for ploidy level, results often indicate that high ploidy fosters speciation and diversification (Van de Peer et al., 2009, 2017, 2021; Parisod et al., 2010; Jiao et al., 2011; Soltis et al., 2014; Vannestre et al., 2014; Wendel, 2015; Nieto Feliner et al., 2020; Wu et al., 2020), and possibly reduced extinction rates during deep past mass extinctions (Bottini et al., 2000; Fawcett et al., 2009, 2013; Van de Peer et al., 2017, but see Soltis et al., 2014; Nieto Feliner et al., 2020; Van de Peer et al., 2021).

Plant lineages differ in species richness also regionally and locally, but we do not know whether this depends on WGC. Globally species-rich lineages may be species-poor within several regions (like Moraceae in temperate regions) or globally relatively poor lineages may be regionally rich (like Cycadaceae in Southeast Asia). Finally, within a given region, some lineages may be species-rich but represented at any occupied locality by only a single species, or inversely, regionally species-poor lineages succeed in maintaining multiple coexisting species in any locality occupied, a phenomenon only relatively recently recognized (Prinzing et al., 2016; Večeřa et al., 2021). In young regional floras, such as those resulting from postglacial recolonization, speciation will be of comparatively little importance for explaining why some lineages are more species-rich than others (Kadereit et al., 2004; Willis and Niklas, 2004; Kadereit, 2017; but see Abbott and Brochmann, 2003; Smyčka et al., 2022). Moreover, speciation will be of practically no importance for explaining why in some lineages more species locally co-occur than in others. In contrast, local and regional richness of lineages will be driven by the rate of local extinction, local colonization, and turnover of species compositions between localities. As we will show below, each of these drivers may in theory strongly depend on WGC. But we do not know whether WGC explains richness of lineages within young regions and within the localities occupied.

Local diversity depends on local extinction and local colonization, and WGC might drive both. Specifically, for each site occupied by a given lineage, the richness of species that can co-occur will increase with a decrease in local extinction rate and an increase in local colonization rate. Extinction is low in species that can maintain even small populations and can persist under local stress, disturbance, or enemy pressure. Colonization rates are high in species producing many descendants of high dispersal capacities. Each of these characteristics may be driven by WGC. First, polyploidization might reduce the risk of local extinctions given the high survival of polyploids after environmental disturbance (te Beest et al., 2012; Van de Peer et al., 2017, 2021). However, polyploidization might also increase the risk of local extinction as it accelerates the rate of genetic and genomic mutations due to transposable elements (Hedges and Batzer, 2005; Pennisi, 2007; Šímová and Herben, 2012), and most of these mutations will be deleterious (Krasileva et al., 2017). Moreover, the genomic shock following whole-genome merger and doubling (i.e., allopolyploidization) may temporarily trigger disadvantageous and detrimental effects in the early stages of the polyploids formation (Comai, 2005; Mayrose et al., 2011, Douglas et al., 2015; and refs above). Also, polyploidization increase cell size, potentially slowing down life history (Comai et al., 2003) and increasing the risk of not surviving until maturity. This increase in cell size in polyploids might ultimately reduce the number of diaspores produced per year, and thereby, reduce the rate at which localities are colonized. Second, a large monoploid number of chromosomes might increase the risk of local extinction by increasing the risk of chromosome mutations during mitosis (Mayr, 1963). Finally, a large monoploid genome size (quantified as 1Cx-value) might also increase the risk of local extinctions by reducing photosynthetic rate (Knight et al., 2005; Simonin and Roddy, 2018) and creating a saturation DNA "surplus", potentially constraining the evolution of phenotypes (see Knight et al., 2005; Greilhuber et al., 2005; and Faizullah et al., 2021 for reviews on effects of genome size). Large monoploid genome size combined with high ploidy gives a heavy total holoploid genome, potentially increasing the number of lethal alleles in small populations (LaBar and Adami, 2020), and thereby, the risk of extinction (Vinogradov, 2003, Organ et al., 2007; Kang et al., 2014; Souza et al., 2019; but see Qiu et al., 2019), and consequently, again potentially increasing the rate of local extinctions and thereby possibly the local richness of lineages. Overall, we hypothesize that large monoploid chromosome number or genome size or their combination reduce local species richness of lineages and that polyploidy either increases or decreases local richness.

Regional richness increases with local richness and with the turnover of species among localities, and WGC might also drive this turnover. For a given region, the richness of a lineage will increase with its local richness and with the turnover of species between localities. This species turnover will be large if different species within a lineage are adapted to different environments. Such a capacity to develop adaptations to different environments may depend on WGC. First, polyploids frequently differ markedly from their diploid progenitors and exhibit novel morphological, physiological, and life-history traits, which are often associated with increased vigour and ability to successfully adapt to novel ecological conditions (Schierenbeck and Ainouche, 2005; Fawcett et al., 2013; Mounger et al., 2021 for reviews, and López-Jurado et al., 2022), likely facilitating the differentiation of species among environments within a region. In contrast, polyploidization may render natural selection less efficient because any given allele of a gene

might be masked by multiple other copies (Stebbins, 1971; Mayrose et al., 2011; Soltis et al., 2014), thereby possibly preventing adaptations of different species to different environments within a region. Second, a large monoploid chromosome number might facilitate the adaptation of species to different environments within a region: large monoploid chromosomes number decrease coupling of genes on the same chromosome and increase the genome-wide recombination rate, in particular when combined with a low genome size (Mayr, 1963; Trickett and Butlin, 1994). Finally, a small monoploid genome size combined with low ploidy level might increase the capacity to establish new populations given the comparatively higher invasion success of species with such small holoploid genome size (Grotkopp et al., 2004; Pandit et al., 2014), In addition, small genomes might evolve faster than large ones after a genome duplication (Levin and Wilson, 1976). Again, these processes might facilitate adaptation of different species within lineages to different environments, thereby increasing beta diversity across environments within region and regional species richness of lineages. Overall, we hypothesize that regional species richness of lineages depends on WGCs: it increases with monoploid chromosome number, decreases with monoploid or polyploid genome size and might either increase or decrease with ploidy level.

Testing for statistical effects of WGC on local and regional species richness of plant linages within a region requires exceptionally rich information across many species in many lineages. It requires information on the richness of these lineages across the entire region and for each lineage across many localities occupied by this lineage. Such testing also requires information on covarying richness of the same lineages across the continental species pool. The continental species pool is likely strongly influenced by speciation, possibly resulting in a pseudocorrelation between of WGC with regional richneess via the effect of WGC on continental species richness. Testing such statistical effects of WGC on local and regional species richness further requires information on covarying richness of other lineages in the same localities as some lineages might be locally rich simply because they occupy sites that harbour many species in general of all lineages. Finally, such testing requires information on niche characteristics and life-history characters that might mediate the relationships between WGC and species richness of lineages, as indicated above, involving life span (Grotkopp et al., 2004; Beaulieu et al., 2010), life form, stress and disturbance tolerance (Hedges and Batzer, 2005; Pennisi, 2007; Šímová and Herben, 2012), and extreme ecological distributions (e.g., Grime and Mowforth, 1982; Beaulieu et al., 2007; Organ et al., 2007; and for reviews, see Knight et al., 2005; Fawcett et al., 2013; Greilhuber and Leitch, 2013). For instance, species with a large (holoploid) C-value or chromosome number have been reported to be restricted to temperate and humid regions (Grime and Mowforth, 1982; and Jacob et al., 2004 and references therein), and threatened plant and animal species have been reported to have high C-values (Vinogradov, 2003; Organ et al., 2007; Kang et al., 2014; Souza et al., 2019; but see Qiu et al., 2019). Finally, polyploidization has been reported to facilitate naturalization and invasion of introduced species (Pandit et al., 2011; te Beest et al., 2012; Moura et al., 2020), and niche expansion in space and time (Hegarty and Hiscock, 2008; Veselý et al., 2012, 2013).

Here we used exceptionally rich data from western central Europe to test the above hypotheses on statistical effects of WGC on the numbers of species that lineages can maintain regionally and locally. We profit from extensive databases from Czech Republic, Germany, and The Netherlands, on WGC, life histories, niche positions, as well as the local species composition across hundreds of thousands of local plots (e.g., Ellenberg et al., 1992; Klotz et al., 2002; Jandt and Bruelheide, 2012). The family level is a particularly appropriate level to capture the variation of genome characteristics (Soltis et al., 2005) and largely avoids difficulties due to insufficient resolution or reticulate evolution at finer taxonomic levels (Soltis et al., 2014). We hence used these databases to characterize families by the average ploidy level, monoploid C-value (i.e., 1Cx), and monoploid chromosome number of their species. We accounted for randomly expected relationships between species numbers and genomic characters: largest families may approach overall averages for any traits, including genomic ones. For this, we calculated standardized effect sizes of WGCs. Our main aim was to use these standardized WGCs to test whether the number of species a family maintains within a region and its localities increases or decreases with ploidy level, monoploid C-value, and monoploid chromosome number. We statistically accounted for phylogenetic non-independence among families. We supplemented our main tests by a set of relevant secondary tests. In these tests, we accounted for the possibility that richness patterns at a finer scale might just reflect sampling from broader-scale patterns or that a broad-scale pattern might emerge as the sum of fine-scale patterns, without any relationships genuine to the intermediate scale. We finally explored whether the effect of WGCs on species richness can be explained by the effect of the WGCs on ecological distribution and life history, i.e., WGC becoming insignificant once the ecological distribution and life history are included into the model. We stress that this study is an exploration of macroecological patterns consistent with particular groups of the abovementioned processes that influence performance and survival of species. This study cannot and does not aim at isolating and proving individual aspects of these processes such as local extinction.

MATERIALS AND METHODS

Characterization of species

Genome characters

Monoploid chromosome number (x) and ploidy level of German species were taken from Biolflor (Klotz et al., 2002;

https://wiki.ufz.de/biolflor/index.jsp, database last accessed 14 July 2022), of species from Czech Republic from Šmarda et al. (2019), and of species from Dutch flora from Zonneveld (2019). Together, from these three floras, chromosome numbers were available for 3473 species and ploidy levels for 3542 species of the 72 families for which all variables were available, representing 94% and 96%, respectively, of all species. We calculated the monoploid chromosome number as total chromosome number divided by ploidy levels. Since Zonneveld (2019) did not provide ploidy levels for most of species, we used two other databases to infer ploidy levels for species in this flora, using total chromosome numbers in correspondent species for reference. Monoploid genome size was first defined as 1Cx-value (Greilhuber et al., 2005), which is equivalent to 2C-values divided by the ploidy level. 1Cx-values were available for 2812 (77%) species in the combined data set of the three floras (available from all three mentioned above sources) with added data from The Plant DNA C-values database (release 7.1) (Pellicer and Leitch, 2020) on species listed in the three floras. We used the data on 1Cx in picograms from Šmarda et al. (2019), and as 2 C divided by ploidy levels of specimens with correspondent measurements from Bioflor. For the Dutch data, we again needed a more complicated approach. To get 1Cx values from 2 C values in Zonneveld (2019), we used information on ploidy and chromosome numbers from the other two sources. When multiple data were available for a character of a species, we calculated the arithmetic mean.

We note that 21% of species with ploidy data had variable ploidy levels, and 10% of species with chromosome number data had variable monoploid chromosome numbers. It may be argued that if within a species WGC parameters vary, the species should be split. However, splitting was not appropriate in our case: it would result in circularity between using WGC to define species and using WGC to explain the richness of these species. It would also lead to more splitting in species for which WGC have been more frequently studied increasing the probability of finding different WGC. And it would define species that botanists and ecologists cannot identify in the field when documenting local richness of families. Moreover, we could show that within-species variation of WGC is unlikely to have any impact on results of our analyses: We characterized average WGC per family across species based on either the per-species minimum, mean or maximum. We calculated for each family standardized effect sizes (SES) from these values as explained below. We finally compared for a given WGC the SESs based on per-species minima, means, and maxima and found them to be very highly correlated (Pearson correlation: 0.995–0.999). The only exception was a relatively weak correlation (0.61) between the SES of ploidy calculated from minimal and mean values per species. Overall, whatever extreme one takes from a within-species variation to calculate family averages, the relative values are mostly practically identical, and at least similar, suggesting that the within-species variation did not bias our analyses. Finally, families with many species of unknown genomic variables did not score differently for means of the three genomic variables than more completely known families (correlations of means against completeness = –0.1006 to 0.0483), so that "correcting" for completeness is not needed and would even render the analyses less representative of the more poorly studied, rare families.

Life-history traits

We extracted 10 life-history traits (Table 1, including references) related to dispersal ability, reproductive capacities, and responses to environmental variation. The selected traits are known to be related either to genome characteristics (such as stress tolerance or life span, e.g., Grime and Mowforth, 1982; Grime, 2002; Husband et al., 2013) or to the ecological success of species and hence possibly to the numbers of species maintained per family (Durka, 2002; Klotz et al., 2002). For life form, we followed Veselý et al. (2012, 2013, 2020) who showed that geophytes often have large genome sizes (when including in the definition of "geophytes" the presence of subterranean storage organs). Storage organs were bulb, hypocotyl bulb, shoot tuber, root tuber, runner with tuberous tip, primary storage root, secondary storage root, rhizome, or rhizome-like pleiocorm.

Distributions in ecological space

We characterized distributions along six abiotic environmental gradients, such as temperature, using Ellenberg indicator values (Table 1; Ellenberg et al., 1992). Although they are based on expert knowledge (itself based on hundreds of original publications), these values have proven useful as a descriptor of species abiotic niches (see for instance, Diekmann, 2003, for a review). In addition, the relative position of species along these gradients has proven surprisingly constant across continents (Niinemets and Valladares, 2006). Such indicator values appear to be the only practical solution to account for niche axes related to soil reaction, moisture or light requirements when characterizing thousands of species of an entire flora.

Characterization of families

Traits

The appropriate level of phylogenetic resolution must ensure a sufficient number of species per phylogenetic lineage and a sufficiently large sample of lineages. These precautions help to avoid uncertainties due to incomplete sampling or reticulate evolution (see introduction). We hence selected the family-level to conduct our core analyses. Angiosperm families are mostly monophyletic (APG IV, 2016) but, like any taxonomic

TABLE 1 Species characters considered to explain the link between genome characteristics and species richness of families: life history, and ecological niche positions. Life-history traits are from Klotz et al. (2002), niche characteristics refer to indicator values from Ellenberg et al. (1992).

Trait	Scale	Definition
Life-history trait		
Stress tolerance	Ordinal, 0, 0.5, 1	Sensu Grime (2002) inferred from life histories[a]
Disturbance tolerance	Ordinal, 0, 0.5, 1	Sensu Grime (2002) inferred from life histories[a]
Life span	Ordinal, 1 to 4	Entirely annual to entirely perennial
Type of reproduction	Ordinal, 1 to 5	Entirely sexual to entirely vegetative reproduction
Breeding system	Ordinal, 1 to 5	1 = entirely allogamy, 5 = entirely automixy
Beginning of flowering	Month (or number of months)	Phenology of flowering: referring to the beginning, duration and end of flowering time, given as month (no flowering period transcending December)
Duration of flowering		
Seed mass	g, ln transformed	Average measures of mass
Seed width	mm	Width of seed
Seed length	mm	Length of seed
Geophytes with storage organs	Proportion	Proportion of geophytes with subterranean storage organs
Niche characteristic		
Temperature	Ordinal, 1 to 9	From high-altitude cold to southern-exposed hot
Moisture	Ordinal, 1 to 12	Dry to permanently submerged soils
Soil acidity	Ordinal, 1 to 9	Acid to basic soil reaction
Light intensity	Ordinal, 1 to 9	Shaded to open during the growing period
Nutrient availability	Ordinal, 1 to 9	Nutrient poor to nutrient rich (during growth period)
Continentality	Ordinal, 1 to 9	From oceanic to continental Europe

[a]Note that low disturbance strategy combined with low stress strategy implies high competitiveness, which we hence did not include as a separate variable to avoid artificially inflated multicollinearity.

level, to some degree arbitrary, as some families represent much older units than others and may have accumulated more species than others (Wiens, 2011; but see Tank et al., 2015). However, we note that our analyses control for phylogenetic non-independence among families (see next section), which identifies cases where families have similar species richness only because they are closely related and have similar age. There were 72 families for which information on all traits was available (details in Appendix S1). Using the abovementioned databases, we characterized families by their regional mean values for WGC, life-history traits, and niche positions.

Species richness

We recorded for each family the number of species across the continental pool from which the regional flora is sampled. We defined this pool as Europe+Middle East +Mediterranean following The Euro+Med PlantBase (https://www.emplantbase.org/home.html), one of the main resources on current taxonomy and ranges of species and intraspecific taxa in the biogeographic realm to which the West Eurasian flora belongs. We calculated continental species richness in each angiosperm family listed in the database using species lists available on the website and adjusted taxonomies of continental and regional floras according to The Euro+Med PlantBase. We $\log_2$-transformed species richness to ensure residual normality and homogeneity. We recorded "regional" species richness of families from the German database Biolflor (Biolflor online version at www.ufz.de/biolflor). Some local plots contained species not listed in Bioflor, and many plots were close to Czechia or The Netherlands, two comparatively much smaller countries that are covered exclusively by vegetation formations and subformations also present in Germany (Bohn and Neuhäusl, 2000/2003). We hence decided to include into the regional richness also species from Czechia and The Netherlands (from the respective complete databases of Šmarda et al., 2019 and Zonneveld, 2019), as done for the genomic data. Regional richness was again $\log_2$-transformed. Databases at local to regional to continental (and up to global) scales may treat the same taxon differently: as an accepted species (of hybrid origin) and include it or as a hybrid and possibly exclude it. They may also be more or less open to hybrids species

as such. We nevertheless found that continental richness was by far the strongest predictor of regional richness ($t > 14.0$, $P < 0.0001$; Table 3), and regional richness was by far the strongest predictor of local richness ($t > 7.6$, $P < 0.0001$; Table 3). We finally recorded the mean local richness of species for each family across 193,449 plots, representing 2,195,946 species observations, of the German Vegetation Reference Database (GVRD, Jandt and Bruelheide, 2012). For each family, we included only plot records in which the respective family was present, as absence in the remaining plots reflects limited regional distribution rather than low local richness. Plot sizes follow standards in vegetation science (Mueller-Dombois and Ellenberg, 1974), i.e., increase with the size of the dominant plants (ranging from few centimetres to many meters). A given family might maintain many species locally only because it grows in a location where most families maintain many species due to favorable environment or simply because the sampling plot in that location was excessively large. We hence recorded for each plot and target family also the local species richness of all other locally co-occurring species in the plot. We accounted for this "local richness of nonfamily members" as explanatory variables in the models explaining local species richness as depicted in Tables 3D, E, F. Throughout, we accounted for both, native and exotic species, because many species may be introduced to a given locality but native to the region or introduced to the region but native to the continent. The issue of inclusion of exotics has likely little relevance because regional species richness of families without exotics related strongly to richness with exotics ($r = 0.98$), similar to findings for continental flora.

Phylogeny

A largely resolved, ultrametric, dated phylogeny of angiosperms for the study region based on *rbcL* gene was described by Hermant et al. (2012) and further resolved by Bartish et al. (2016). To account for the families not included into the earlier phylogeny, we inferred a new phylogeny by adding the correspondent sequences of *rbcL* gene. We also extended the data set by adding sequences of *matK* and *ndhF* genes for all the families because increasing the sample of sequences improved the phylogenetic resolution and statistical support for the topology of the tree. We note that some poorly supported nodes in the tree were not congruent with the topology of the recently published tree based on Angiosperms353 genes (Baker et al., 2022). Because the tree we obtained was similar to the APG IV tree (APG, 2016), these incongruencies were similar to those between the Angiosperm353 and APG IV trees (see Supplementary Fig. S6 of Baker et al., 2016). According to Baker et al. (2022), the nodes of incongruence between the trees were at the level of orders in APG IV and were generally weakly supported (mean LPP 0.75) in the Angiosperm353 tree. A list of species representing each family and Gene Bank codes for each of the species and genes that we included in our phylogenetic analyses is provided in Appendix S2. We inferred the dated phylogeny following the same approach used by Bartish et al. (2016), i.e., employing Bayesian method and dating the tree by secondary calibrations available from literature for the main clades. The dated tree of all families included into our analyses is available in Appendix S3.

Statistical analyses

Null models

Inference of any relationship of a trait to richness may suffer from a purely numerical bias: families of larger species richness are likely to converge on the overall mean tendency of a given trait. Despite the often highly asymmetric distributions of raw values, we found strong hump-shaped relationships between means of randomized trait values and the richness of families across which these trait values were randomized. Such a null-expected relationship will bias relationships between any trait and richness, and such a shared bias will introduce major collinearities among explanatory variables, with tolerance values far below 0.1. For instance, using all three WGCs and their interaction terms (Table 3B) result in tolerances between 0.009 and 0.066. Such tolerances quantify the amount of variation in a given independent variable not explained by other independent variables, and values ≥0.1 are considered tolerable (Dormann et al., 2013). In contrast, analyses based on the approach described below of standardizing by the null expectation yielded much lower multicollinearities and hence higher tolerances (0.335–0.921). We hence opted to build our analyses entirely on trait values that were corrected for the hump shaped trait/richness relationship that occurs from random expectation. We did so by randomizing 1000 times trait values across species, calculating means and SDs of these randomized values for each family and then using these statistics to standardize observations by calculating standardized effect sizes (SES) as: $(\text{Observed} - \text{Mean}_{\text{randomized}})/\text{SD}_{\text{randomized}}$). For these randomizations, we used a macro script for Excel (available from the first author). The SES calculations for all families and traits are reported in Appendix S1.

Relating genome characteristics to richness

All our analyses accounted for possible phylogenetic non-independence among families using a phylogenetic generalized least squared (PGLS) approach (Grafen, 1989) as implemented in the R package phytools (Revell, 2011; R Core Team, 2021) and its default settings. The PGLS approach has the advantage of not imposing corrections where phylogenetic non-independence does not bias the observed relationships between dependent and independent variables. In addition, data points represent families and not relative differences among families as in phylogenetically independent contrasts, which especially facilitates interpretation of interaction terms

TABLE 2 Models explaining $\log_2$ of species richness of families across the study region ("Regional") and $\log_2$ of mean richness within local vegetation plot records ("Local") by whole-genome characteristics (WGCs). Only the direction of significant trends is shown; parameter estimates and *P*-values are provided in Table 3A–F, as specified in the last line. Explanatory variables are genomic characters without and with pairwise statistical interactions between these variables. The model involving interaction terms is then expanded by including other variables that might mediate or hide the statistical effect of WGCs on species richness per family: species richness of the same families in the respective species pool; mean local species richness of the same families or of co-occurring families; and life-histories and niche characteristics of the same families. 1Cx = monoploid genome size; NbC = number of monoploid chromosomes; Pl = ploidy level; "–" = negative at $P < 0.05$ (all significant results are negative), () = marginally significant $0.05 \le P < 0.1$, "0" = $P \ge 0.1$. Where needed, results without | with residual outliers are given. SES = standardized effect sizes. NA = not applicable. All analyses were carried out with phylogenetic generalized linear models to account for phylogenetic non-independence among families.

		Models explaining the dependent variable by genomic variables alone		The model with interaction terms including…					
				… species richness of families across species pool		… mean local species richness…		…both species pool and m. local richness	… species pool and m. local richness, life histories and niches of species
Dependent variable	**Genomic independent variables (SESs)**	**Without interaction terms**	**With interaction terms**	**Continental**	**Regional**	**… of family**	**…of all other species**		
Regional: species richness within families	1Cx	0 | 0	0 | 0	0 | 0	NA	0	NA	0	0
	NbC	– | 0	– | –	0 | 0	NA	0	NA	0	0
	Pl	0 | 0	– | –	(–) | –	NA	(–)	NA	0	0
	1Cx:Pl	NA	0 | (–)	0 | 0	NA	–	NA	0	0
	NbC:Pl	NA	– | –	– | –	NA	0	NA	0	0
	1Cx:NbC	NA	0 | 0	0 | 0	NA	0	NA	0	0
Local: Mean species richness within families in localities where the family is present	1Cx	0 | 0	0 | 0	NA	(–) | 0	NA	– | 0	0 | 0	0 | [a]
	NbC	0 | 0	0 | –	NA	0 | –	NA	(–) | –	0 | –	0 | [a]
	Pl	– | 0	– | –	NA	– | 0	NA	– | –	– | 0	– | [a]
	1Cx:Pl	NA	0 | 0	NA	– | 0	NA	– | 0	– | 0	– | [a]
	NbC:Pl	NA	0 | –	NA	0 | –	NA	0 | –	0 | –	0 | [a]
	1Cx:NbC	NA	0 | 0	NA	– | 0	NA	– | 0	– | 0	– | [a]
Full analysis in:		Table 3A	Table 3B, Figure 1	Table 3C		Table 3D		Table 3E	Table 3F

[a]Analysis including outliers does not retain niche characteristics and traits.

(interaction terms turned out to be essential). We tested multiple relationships of increasing complexity (as summarized in the top line of Table 2). For consistency, we present all analyses only using the 72 families for which we have information on all variables used in the most complete analyses. We note, first, that "1Cx × ploidy level" and "basic chromosome number × ploidy level" correspond to holoploid C-value and holoploid chromosome number, respectively, while "1Cx × basic chromosome number" has no such equivalent. For all analyses, we graphically inspected the residual distribution (notably quantile-quantile, and predicted vs. observed) plots and excluded outliers where needed. We report results with and without residual outliers and the identity of these outliers.

RESULTS

Local species richness of families, i.e., means across localities where the respective family was present, ranged from 1 (multiple families) to 4.53 (Poaceae), i.e., $\log_2 = 0$ to 2.18, (coefficient of variation of 131; coefficients of variation permit comparisons between variation around means that are bound to be very different). Regional species richness of the same families ranged from 1 (Portulacaceae) to 516 (Rosaceae), i.e., $\log_2 = 0$ to 9.01 (coefficient of variation of 50). Within-family means of ploidy level ranged from 2 to 6 (multiple families each), within-family means of monoploid genome size ranged from 0.2 pg (Lentibulariaceae) to 22.07 pg (Liliaceae), and within-family means of monoploid chromosome number from 4.75 (Callitrichaceae) to 21.50 (Oleaceae).

A qualitative summary of the observed relationships between WGCs of families and their regional or mean local richness is given in Table 2, which gives an overview for the full analyses that are provided in Table 3.

Regional richness

We first aimed at explaining regional species richness by WGCs. We found that without accounting for interactions

TABLE 3 Models explaining species richness of families across the study region or within localities occupied by families within that region by monoploid size of genome (1Cx), monoploid number of chromosomes (NbC), and ploidy level (Pl). A–F show different models as outlined in Table 2. Some analyses suffer from residual outliers; often these residuals are major families. To provide comprehensive information, we present analyses with and without outliers. The independent variable "pool richness" refers to the species richness of the respective families across the continental pool in the analyses explaining regional species richness of families and refers to the regional richness in the analyses explaining mean local richness of families. The independent variable "mean local richness" refers to the mean local richness of the respective family in analyses explaining regional species richness of families and refers to the mean local richness of co-occurring families in the analyses explaining mean local richness of families. Richness variables are $\log_2$-transformed. Trait and genomic variables are standardized effect sizes (SES, hence avoiding spurious random relationships resulting from randomly sampling a given number of species from a given trait distribution, see Materials and Methods). All analyses apply phylogenetic generalized linear models to account for phylogenetic non-independence among families. For WGC, bold indicates $P < 0.05$, underlined $-0.05 \leq P < 0.1$. Note that in the analyses in F, the following traits were never retained and are hence not presented: light preferences, continentality preferences, moisture preferences, pH preferences, life span, type of reproduction, breeding system, start of flowering, duration of flowering, geophytes with storage organ, disturbance strategy, stress strategy, ln seed-mass, seed width, seed length. Results for WGC are qualitatively summarized in Table 2.

	Regional species richness of families				**Mean local species richness of families**			
	Without outliers		**With outliers**		**Without outliers**		**With outliers**	
Independent variables (SESs)	***t***	***P***	***t***	***P***	***t***	***P***	***t***	***P***
A.								
1Cx	−1.294	0.2002	−0.490	0.6255	−0.034	0.9729	−0.186	0.8528
NbC	**−2.774**	**0.0072**	−0.333	0.7400	−1.477	0.1445	−1.019	0.3118
Pl	−0.963	0.3390	−0.295	0.7690	**−3.236**	**0.0019**	1.117	0.2680
AIC	302.123		326.511		45.180		109.853	
Residual df	65		68		65		68	
Outliers	Liliaceae, Orchidaceae, Cyperaceae				Rosaceae, Poaceae, Cyperaceae			
B.								
1Cx	−0.358	0.7214	−0.626	0.5336	−1.347	0.1832	−0.131	0.8963
NbC	**−2.430**	**0.0179**	**−2.789**	**0.0069**	−0.853	0.3972	**−5.041**	**<0.0001**
Pl	**−3.041**	**0.0034**	**−3.837**	**0.0003**	**−3.389**	**0.0012**	**−3.364**	**0.0013**
1Cx:Pl	−0.630	0.5311	−1.703	0.0933	−1.628	0.1089	0.065	0.9481
NbC:Pl	**−2.961**	**0.0043**	**−5.093**	**<0.0001**	−0.407	0.6857	**−8.224**	**<0.0001**
1Cx:NbC	−0.009	0.9926	−0.724	0.4719	−0.515	0.6088	−0.958	0.3414
AIC	298.890		304.519		6.517		58.249	
Residual df	63		65		60		65	
Outliers	Cyperaceae, Rosaceae				Poaceae, Asteraceae, Fabaceae, Rosaceae, Cyperaceae			
C.								
Pool richness	16.132	<0.0001	14.021	<0.0001	8.025	<0.0001	7.625	<0.0001
1Cx	−0.415	0.6798	−0.439	0.6623	−1.807	0.0756	0.411	0.6822
NbC	−0.741	0.4617	−0.841	0.4035	−0.382	0.7035	**−4.037**	**0.0001**
Pl	−1.715	0.0913	**−2.005**	**0.0492**	**−2.477**	**0.0160**	−0.887	0.3786
1Cx:Pl	−0.423	0.6739	−0.622	0.5364	**−2.571**	**0.0126**	1.664	0.1011
NbC:Pl	**−3.254**	**0.0018**	**−3.450**	**0.0010**	0.468	0.6411	**−5.459**	**<0.0001**
1Cx:NbC	−0.138	0.8903	−0.076	0.9395	**−2.326**	**0.0233**	−0.627	0.5329
AIC	187.218		205.429		−24.131		13.713	
Residual df	63		64		62		64	
Outliers	Plumbaginaceae				Poaceae, Asteraceae			
D.								
Mean local richness	**no outliers**		7.625	<0.0001	0.303	0.7630	−0.740	0.4620
1Cx			−0.734	0.4656	**−5.819**	<0.0001	−0.106	0.9161

TABLE 3 (Continued)

Independent variables (SESs)	Regional species richness of families				Mean local species richness of families			
	Without outliers		With outliers		Without outliers		With outliers	
	t	*P*	*t*	*P*	*t*	*P*	*t*	*P*
NbC			0.800	0.4266	−1.948	0.0562	**−4.981**	**<0.0001**
Pl			−1.918	0.0596	**−7.174**	**<0.0001**	**−3.420**	**0.0011**
1Cx:Pl			**−2.396**	**0.0195**	**−6.162**	**<0.0001**	0.002	0.9980
NbC:Pl			0.558	0.5791	0.206	0.8378	**−8.150**	**<0.0001**
1Cx:NbC			−0.085	0.9327	**−5.567**	**<0.0001**	−0.905	0.3689
AIC			259.983		0.552		59.636	
Residual df			64		60		64	
Outliers					Poaceae, Asteraceae, Rosaceae, Liliaceae			
E.								
Pool richness	**no outliers**		10.542	<0.0001	8.076	<0.0001	7.909	<0.0001
Mean local richness			4.315	0.0001	−0.959	0.3411	−1.830	0.0720
1Cx			−0.584	0.5613	−1.626	0.1091	0.494	0.6233
NbC			1.084	0.2824	−0.494	0.6234	**−3.952**	**0.0002**
Pl			−1.294	0.2004	**−2.557**	**0.0131**	−1.039	0.3028
1Cx:Pl			−1.312	0.1942	**−2.492**	**0.0154**	1.577	0.1198
NbC:Pl			−0.204	0.8391	0.346	0.7303	**−5.359**	**<0.0001**
1Cx:NbC			0.243	0.8089	**−2.279**	**0.0262**	−0.501	0.6181
AIC			188.785		−23.180		11.984	
Residual df			63		61		63	
Outliers					Poaceae, Asteraceae			
F.								
Pool richness	**no outliers**		10.4088	<0.0001	7.814	<0.0001	no niche characteristics or traits retained	
Mean local richness			3.908	0.0002	−1.484	0.1430		
1Cx			−0.363	0.7182	−1.471	0.1465		
NbC			0.772	0.4429	−0.681	0.4983		
Pl			−1.538	0.1291	**−3.128**	**0.0027**		
Termperature			−2.033	0.0463				
Fertility					−2.397	0.0196		
1Cx:Pl			−1.208	0.2315	**−2.676**	**0.0096**		
NbC:Pl			−0.624	0.5350	0.186	0.8529		
1Cx:NbC			0.299	0.7661	**−2.432**	**0.0180**		
AIC			186.138		−27.582			
Residual df			62		60			
Outliers					Asteraceae, Poaceae			

between WGCs (Table 3A), regional species richness declined with the monoploid number of chromosomes but only when the residual outliers Liliaceae, Orchidaceae, and Cyperaceae were excluded.

After including interaction terms (Table 3B; Figure 1A), regional richness declined with monoploid number of chromosomes, ploidy level, and their combination (short expression for a negative interaction term, i.e., one variable

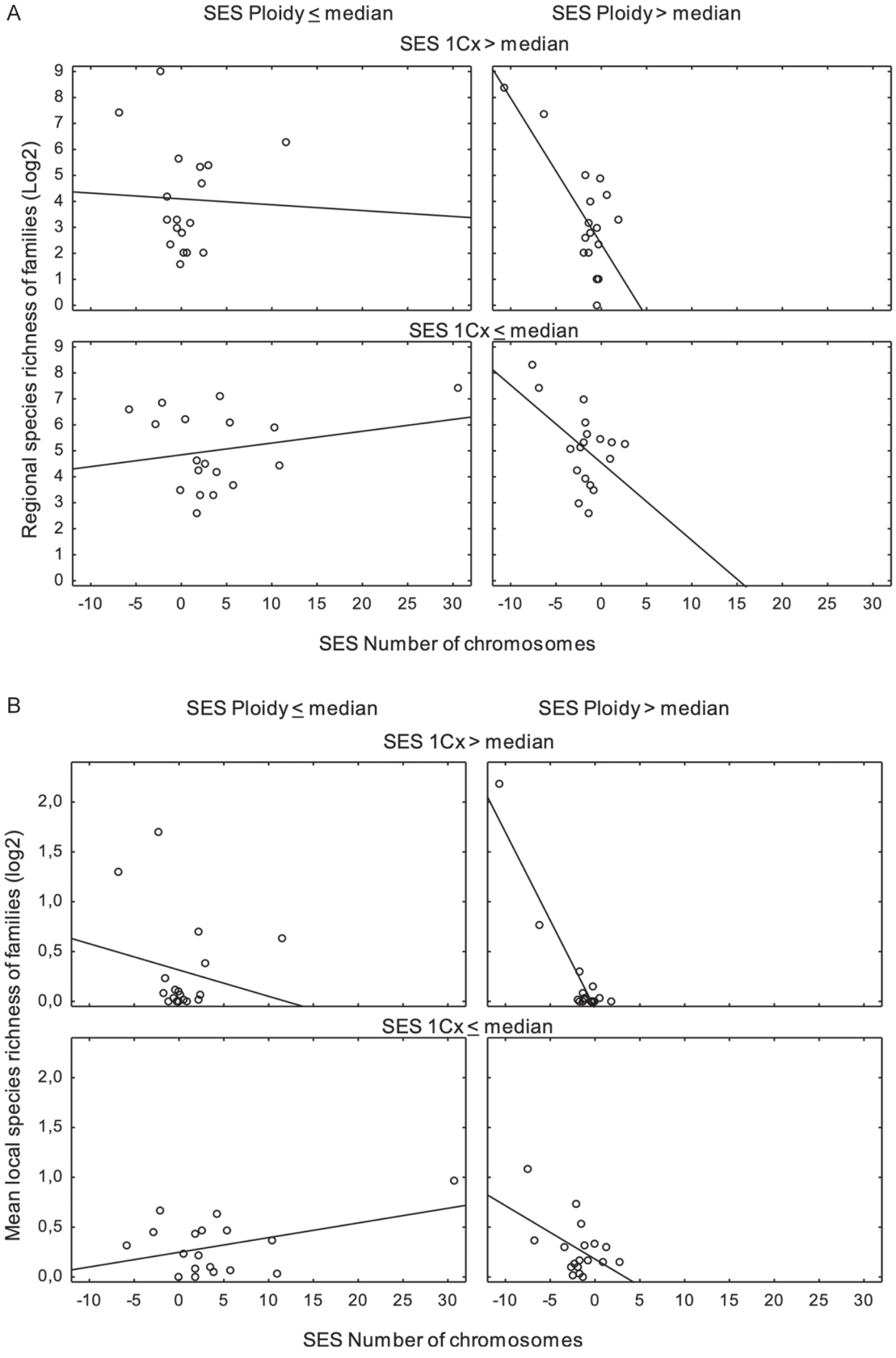

FIGURE 1 Relationship between $\log_2$ richness of species within families of angiosperms and standardized effect sizes (SESs) of monoploid chromosome numbers, ploidy, and monoploid genome size (1Cx). Species richness of the families is (A) within the study region and (B) within local plots occupied by the respective family within the region. Statistical analyses are shown in Table 3. Ploidy and 1Cx are presented in a binary way (and lines fitted separately for each plot) but were treated as continuous in statistical analyses. Figures show all data points, statistical analyses were conducted with and without outliers.

intensifying the negative effect of another). Regional richness also marginally significantly declined with high Cx combined with high ploidy (but only when the residual outliers Cyperaceae and Rosaceae were included).

Including richness of the continental pool (Table 3C) into the model maintained the decline of richness with ploidy level and with ploidy level combined with monoploid chromosome number. Including mean local richness (rather than richness of the continental pool, Table 3D) maintained the decline of richness with ploidy, alone and in combination with high Cx. After including both continental and mean local richness (Table 3E), none of the relationships of regional richness to WGCs were maintained, while both continental and mean local richness were highly significant. This result suggests that the above relationships of WGCs to regional richness is to a large degree reflecting relationships at larger (continental) and smaller (local) scales.

Accounting in addition for niche characteristics and life histories of species (Table 3F) again showed no relationship between regional richness and WGCs.

Mean local species richness

We then aimed at explaining mean local richness by WGCs. We found that without accounting for interactions between WGCs (Table 3A), mean local richness declined with ploidy level, but only when the residual outliers Rosaceae, Poaceae, and Cyperaceae were excluded.

After including interaction terms (Table 3B, Figure 1B), mean local richness declined with ploidy level (independent of outlier exclusion) and with monoploid number of chromosomes and its combination with monoploid genome size (after exclusion of residual outliers Poaceae, Asteraceae, Fabaceae, Rosaceae and Cyperaceae).

Including richness of the regional pool (Table 3C) maintained the negative relationships of mean local richness to WGCs, most consistently with ploidy level and monoploid number of chromosomes: Across all data points, mean local richness declined with a large monoploid number of chromosomes and with a large monoploid chromosome number combined with a high ploidy level. After excluding the residual outliers Poaceae and Asteraceae, mean local richness declined with high ploidy and with high ploidy combined with high 1Cx as well as with high 1Cx combined with high monoploid chromosome number.

Including mean local richness of nonfamily members (rather than richness of the regional pool, Table 3D) maintained the negative relationships of mean local richness to WGCs, most consistently with ploidy level and monoploid numbers of chromosomes: Across all data points, mean local richness declined with monoploid chromosome number, ploidy level, and their combination. After excluding Poaceae, Asteraceae, Rosaceae, and Liliaceae as residual outliers, mean local richness again declined with ploidy level and with the combination of high ploidy level and high 1Cx value. Mean local richness also declined with monoploid numbers of chromosomes when combined with high 1Cx value and declined with high 1Cx as such.

Including both, richness of the regional pool and mean local richness of non-family members (Table 3E), maintained the negative relationships of mean local richness to WGCs, most consistently with ploidy and monoploid numbers of chromosomes: Across all data points, mean local richness declined with monoploid numbers of chromosomes, alone and in combination with ploidy. After excluding Poaceae and Asteraceae as residual outliers, mean local richness declined with monoploid numbers of chromosomes combined with 1Cx. Mean local richness then also declined with ploidy level, alone or in combination with 1Cx.

Accounting in addition for species niche characteristics and life histories (Table 3F) did not change the conclusions; ploidy level was significantly negatively related to mean local richness both alone and in combination with 1Cx, and monoploid chromosome number was negatively related to species richness in combination with 1Cx in analyses excluding Poaceae and Asteraceae as residual outliers (without exclusion, no niche characteristics or life-history traits had been selected).

DISCUSSION

To our knowledge, our study is the first to characterize the relationship between whole-genome characters (WGC) of lineages and the species richness of the same lineages at scales at which speciation is of little importance: within a young regional flora and within the local species communities in which the respective families are present. While the fact that lineages differ in richness across an entire region is obvious and has been documented for centuries, the variation among lineages in the numbers of species that can co-occur in local ecological communities had received little attention (see also Prinzing et al., 2016; Večeřa et al., 2021). We here showed that the coefficient of variation of mean local richness of families is even much higher than of regional richness. Families that are species-rich within occupied localities have low levels of ploidy, small numbers of monoploid chromosomes, intensified by the interaction of both. This relationship was independent of regional richness of these families and total richness of all locally co-occurring families. Across the entire region, we found that angiosperm families that are regionally species-rich have a low level of ploidy and small monoploid chromosome numbers or both, but relationships disappeared after accounting for both the continental and mean local richness of families. Relationships between WGCs and species richness of families were maintained or even reinforced by accounting for niche characteristics or life histories.

There is the risk that the relationships we tested are biased by random effects of sampling small or large numbers of species from a trait distribution or by

phylogenetic non-independence of families. We avoided both types of biases by standardizing trait means by a null model and applying phylogenetical generalized least squared models. In addition, variation of WGC within some of the species might suggest that, strictly, each of them consists of multiple biological species differing in WGC. However, such a definition of species based on WGC is inapplicable for vegetation scientists in the field (Benton, 2000; Hillis, 2007; Majesky and Krahulec, 2017), rendering any analysis of local richness impossible, and such a definition risks introducing other biases as explained in the Materials and Methods. To explore the impact of within-species variation of WGC on our analyses, we recalculated family values by averaging the within-species minima or maxima and found that these per-family averages were almost always perfectly correlated to those obtained by averaging within-species means (Materials and Methods). Moreover, mean local richness was quantified based on vegetation plot records. Vegetation plot records are snapshots that do not necessarily represent all species present across the year, in particular among short-lived species and life forms with dormant buds below the soil surface (Mueller-Dombois and Ellenberg, 1974). However, we found that including these (and other) species traits did not change the conclusions. Moreover, we here only considered families for which information on all traits and niche preferences was available, i.e., families well established in the region since at least many decades and observed in many plots, providing a robust data basis for quantifying mean local richness.

Finally, we note that our analyses are only valid for a given region and a given level of taxonomic resolution, the family. Our analyses should be repeated in other regions, notably for floras that are older and may have been shaped more strongly by speciation (e.g., Rull, 2008). Analyses may also be repeated at coarser or finer levels of classification. Finer levels of classification such as that of genera likely show less variation in species richness than that of families, and recognition of apomictic species sometimes causes relatively small or even non-existent genera to become comparatively more species-rich genera (e.g., *Hieracium pilosella* became a species-rich genus of its own; Jäger et al., 2017). Coarser levels of classification might show a stronger signal of the continental species pool as an ultimate limit to maximum species richness. The family level might be the one at which units are particularly well established as monophyletic with strong statistical support (Durka and Michalski, 2012; Hermant et al., 2012; for our flora), reflecting recent re-definitions based on molecular phylogenies (APG, 2016).

Accounting for species richness of families from continental pools to local communities permitted interesting insights into the scale at which genomic characteristics might affect species richness. When analyzing regional species richness of families, we found that accounting for either the continental pool or the mean local richness decreased the signal of monoploid number of chromosomes and accounting for both made disappear also the number vs ploidy interaction. Therefore, the high regional species richness of families with few monoploid chromosomes and high ploidy might be explained by the high richness of the same families across the continental pool and locally. At the continental level, speciation probably contributes strongly to species richness (e.g., Rull, 2008), at the local level richness is likely controlled by mechanisms of coexistence (Prinzing et al., 2016; Večeřa et al., 2021), which we will discuss below. When analyzing mean local species richness of families, we found that accounting for the regional pool or for the richness of other co-occurring species did only result in minor changes, suggesting that processes operate indeed at the local level. We will hence focus our below discussion on the mean local richness of families and on processes that may drive such local richness: the rate of local extinction and of local colonization. We will not further consider regional richness and the process that explains richness only at regional level: an increase in species turnover between localities. We will also do not further consider effects of genome size as the statistical signal of genome size was dependent on exclusion of residual outliers, i.e., outliers being particularly species rich.

We found that mean local species richness of families decreases with an increase in ploidy level, alone or in interaction with an increased monoploid number of chromosomes. This result appears broadly consistent with the fact that in the study region and other temperate regions of the world polyploids are proportionally more frequent than in warmer regions (Rice et al., 2019), whereas species richness is lower than in warmer regions (Mittelbach et al., 2007; Qian and Ricklefs, 2007). In contrast, this result seems inconsistent with the widely shared view that across the globe polyploidy fosters diversification and in particular extinction (Wood et al., 2009; Kraaijveld, 2010; Mayrose et al., 2011; Soltis et al., 2014; Puttick et al., 2015). There is indeed growing evidence that, following severe biotic and abiotic environmental changes, polyploidization may provide selective advantages to descendants in the long run, such as higher survival than their preadapted diploid progenitors in the new environmental range (te Beest et al., 2012; Van de Peer et al., 2017, 2021). However, consistently with our results, it is known that the genomic shock following whole-genome merger and doubling (i.e., allopolyploidization) may temporarily trigger disadvantageous and detrimental effects in the early stages of polyploid formation (Comai, 2005; Mayrose et al., 2011; Van de Peer et al., 2021), and not all polyploids will be able to succeed and diversify in the long term (Van de Peer et al., 2017, 2021, and references therein). Others argued that polyploidization might temporarily favor extinctions due to decreased individual fitness resulting from increasing cell size and hence slow life cycles of cells and the entire organism (Šimova and Herben, 2012; De La Torre et al., 2017), or from increased mutation rates (Hedges and Batzer, 2005; Pennisi, 2007). Polyploid species also might suffer from

inefficient natural selection due to the masking of each allele by multiple other copies (Stebbins, 1971; Whitney et al., 2010; Mayrose et al., 2011). In consequence, polyploidy might at least temporarily have lower diversification rates through increasing extinction rates in the recent Quaternary past (Mayrose et al., 2011), albeit rates of global extinctions in polyploid species still remain under debate (see Soltis et al., 2014; Nieto Feliner et al., 2020; Wu et al., 2020; Van de Peer et al., 2021). Such extinctions might still be ongoing locally today. Among the above mechanisms affecting local extinction, those operating via ecological performance such as increased stress or disturbance tolerance or slow life cycles may not be pertinent; accounting for stress or disturbance tolerance and life span did not change the negative relationships of polyploidy to mean local species richness (Table 3F). After exclusion of these ecological mechanisms, we are left with more evolutionary mechanisms involving mutation rates and efficiency of selection as possible mechanisms.

We found that mean local species richness of families decreases with an increase in chromosome number, alone or in combination with an increased ploidy level. We might imagine that a large number of chromosomes is disadvantageous by increasing the risk of chromosome mutations during mitosis (Mayr, 1963), but the opposite would also be plausible: having many chromosomes is advantageous for the adaptive capacity of species because it decreases coupling of genes on the same chromosome (Trickett and Butlin, 1994). However, little is known so far on how monoploid chromosome number affects the diversity that a lineage can maintain across the globe or within a region or locally. Across the globe, a large chromosome number has been shown to be related to increased invasiveness of species (Pandit et al., 2014). In contrast, a large chromosome number is not related to speciation (Levin and Wilson, 1976). The negative interaction term between monoploid chromosome number and ploidy level might reflect a disproportionally increased risk of mutations in chromosome number (aneuploidy, being highly deleterious) when chromosome number explodes due to polyploidization of a large monoploid chromosome number. In addition, in such a situation, cell cycles may be slowed down disproportionally (Torres et al., 2008). The negative effects of interaction terms between genomic variables might also potentially reflect reduced evolvability of each of the variables involved: chromosome number might more easily evolve if not replicated multiple times in a polyploid genomes or if chromosomes are small. Ploidy might more easily evolve if the monoploid genome consists of only few chromosomes (Zenil-Ferguson et al., 2016). Such evolutionary changes, in turn, may contribute to local survival of populations (or at larger scales to speciation, Puttick et al., 2015). Other than invasiveness, the above mechanisms do not invoke ecological but evolutionary performance and hence cannot be controlled for including niche or life-history characteristics (Table 3F). Consistently, the statistical effects of monoploid number of chromosomes on mean local richness were maintained after including niche characteristics and life histories. We stress however, that these interpretations of our results remain speculative, and each needs to be tested explicitly in the future.

Small monoploid chromosome numbers and low ploidy levels ultimately corresponded to increased local co-occurrence of species within families, and such co-occurrence of related species may have consequences (Webb et al., 2002; Prinzing et al., 2016, 2017). Co-occurrence among related species may require niche differentiation in space and time (MacArthur and Levins 1967), it may increase the load of natural enemies (Yguel et al., 2011) or permit sharing of defences against natural enemies (Gerhold et al., 2018), it may permit sharing of specialist mutualists or trigger competition for specialist mutualists (Gerhold et al., 2015), or of decomposers recycling nutrients (Pan et al., 2015, but see Barbe et al., 2018), Such co-occurrence may also increase the probability of hybridization (Prinzing et al., 2016). All these interactions are usually explained by particular functional relationships among the related species such as character displacement (Dayan and Simberloff, 2005; Prinzing et al., 2008; Hermant et al., 2012). The present study suggests that such local co-occurrence of numerous species within specific families may in part result from these families having few chromosomes—through a low number of monoploid chromosomes or low ploidy numbers or both. Overall, the genomics of macroevolutionary lineages of plants might ultimately explain why species can ecologically coexist and interact in some lineages but not in others.

CONCLUSIONS

The major variation of species richness among angiosperm families within a region is a macroecological phenomenon (Martin and Husband, 2009), and so is the major variation in local species richness among families (Večeřa et al., 2021). Obviously, much of this variation will reflect factors other than WGCs, such as environmental tolerances. Nevertheless, our study suggests that genome characteristics do play an important role, in particular the monoploid chromosome number and ploidy level, often independently of life histories or niche characteristics. Our results are consistent with existing theories on negative effects of high ploidy level or large numbers of chromosomes, mediated via evolutionary processes such as inefficient selection, increased number of lethal alleles, or selfish DNA. Our results suggest new hypotheses on the detrimental effects of having many chromosomes and contribute to understanding non-ecological drivers of ecological coexistence of species. Our study remains correlative and future case studies on individual lineages may help to identify true causation by inferring, for a lineage in a given region, the evolutionary sequence and hence possible causality among changes in WGCs, in niche occupation and in cladogenesis. Obviously, these studies should also involve other regions.

AUTHOR CONTRIBUTIONS

I.V.B., S.B., A.A., and A.P. conceptualized and supervised the study; I.V.B. and A.P. developed methodology; I.V.B.,

S.B., H.B., and A.P. collected data and evidence; H.G. provided data; I.V.B., S.B., and H.G. curated data; M.B. developed software, I.V.B., S.B., and A.P. analyzed the data; I.V.B. and A.P. wrote the first draft of the manuscript, to which all authors contributed.

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DATA AVAILABILITY STATEMENT

Data used are from publicly available databases and are given in the supplemental appendices. In addition, a database is available at https://doi.org/10.25829/idiv.3532-fh8eya (Bartish et al., 2023) with all traits at species level, including information on whole-genome characters of 3906 species from Germany, The Netherlands, and the Czech Republic.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Continental, regional, and mean local richness of families and of locally co-occurring families (first to fourth variables); standardized effect sizes (SES) of WGCs (fifth to seventh variable) and of other traits considered (eighth to 24th variables).

Appendix S2. List of species representing families in the inference of family phylogeny.

Appendix S3. Dated tree of all families included in our analyses.

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