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RESEARCH ARTICLE

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Genomic life-history traits mediate the impacts of habitat loss and nutrient availability on fragmented grassland communities

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Abstract

1. Habitat loss and nutrient enrichment are major drivers of plant species declines. However, local extinction risks vary widely and are shaped by life-history trait syndromes. Genomic life-history traits, which are simple, stable and widely available, offer a promising yet underexplored approach to improving extinction risk assessments and informing conservation efforts.
2. Using a spatial comparison approach, we analysed 256 semi-natural grassland plant communities in four Swedish agricultural landscapes to examine whether genomic life-history traits such as ploidy, genome size and chromosome number mediate differences in plant community diversity and composition along independent gradients of grassland fragment size and phosphorus availability.
3. Our findings show that plant diversity and community composition are increasingly dominated by larger genome species both as grassland fragments become smaller and as more phosphorus becomes available. While all genomic life-history traits proved important, ploidy plays a particularly significant role in explaining differences between observed plant communities.
4. Ploidy mediated deterministic plant community changes along both environmental gradients. Diploid species are especially vulnerable to local extinction, whereas polyploids demonstrate resilience to habitat loss and benefit from increased phosphorus availability, likely leading to the competitive exclusion of diploids.
5. *Synthesis*. By revealing how genomic traits shape plant community responses to land-use change and nutrient pollution—two key drivers of extinction—our study introduces a predictive, genomic trait-based framework for assessing local extinction risks in fragmented landscapes.

KEYWORDS
chromosome number, genome size, grasslands, landscape ecology, plant-available phosphorus, ploidy, semi-natural grasslands, species richness

1 | INTRODUCTION

Vascular plants are disproportionally threatened by extinction compared to many other taxonomic groups (24,000 or ca. 40% of assessed species, Nic Lughadha et al., 2020; IUCN, 2022). This may relate to the limited dispersal capabilities of many plant species, which makes their local and regional long-term survival susceptible to local environmental constraints such as habitat quality (Moreira et al., 2023; Snyder, 2011). The population consequences of dispersal limitation are greatly exacerbated by habitat loss, heightening plant species' extinction risks and eroding plant community diversity at local, landscape, regional and global scales (Auffret et al., 2018; Cousins et al., 2015; Nic Lughadha et al., 2020; Vellend et al., 2013). Furthermore, the widespread decline in habitat quality is a major driver of plant species extinctions, with rising nutrient availability—particularly elevated phosphorus levels—posing significant threats across spatial scales (local, Ceulemans et al., 2014; landscape, Plue & Baeten, 2021; global, Wassen et al., 2021).

There is considerable interspecific variation in extinction risk, and in agriculture-dominated landscapes some plant species seem to cope better with habitat loss and degradation than other plant species (Chichorro et al., 2022). Each species' unique combination of life-history traits dictates its response to environmental change, and thus, its extinction risk (Marini et al., 2012). Both aggregate life-history syndromes (e.g. habitat specialization, range size; Plue & Cousins, 2018; Staude et al., 2020) and specific life-history traits related to spatial and temporal dispersal (e.g. dispersal mode, seed mass, seed longevity, Auffret et al., 2017) or persistence (e.g. clonality, life-form, mating system; Aguilar et al., 2008; Lindborg et al., 2012) affect meta-population dynamics, constraining long-term survival in landscapes subjected to habitat loss. Similarly, life-history traits associated with high competitive ability (plant height, specific leaf area; Ceulemans et al., 2011; Yang et al., 2015; Kaarlejärvi et al., 2017), resource-conservatism (Kaarlejärvi et al., 2017) and mycorrhizal symbiosis (Ceulemans et al., 2011) have been shown to be key in mediating how increased nutrient availability drives plant community turnover (Ceulemans et al., 2014; Duprè et al., 2010), due to competitive exclusion of mostly habitat specialists (Eskelinen et al., 2022; Ewers et al., 2007). Understanding how life-history traits mediate extinction risk is crucial for guiding conservation efforts (Butt & Gallagher, 2018; Zirbel & Brudvig, 2020), particularly in addressing the key drivers of plant extinctions, such as habitat loss and increasing nutrient availability.

From a conservation perspective, the ideal goal is to find simple, reliable and universal traits which could improve predictions of local extinction risk in response to multiple environmental threats simultaneously. Life-history traits linked to the plant genome are strong candidate traits, offering not only simplicity but also stability in trait expression (Swift, 1950; compared to classical plant traits) and this information is also available for a large number of species (Leitch et al., 2019). Given the well-established literature on the biological and evolutionary implications of genomic traits such as genome size (Pellicer et al., 2018), ploidy (Ramsey & Ramsey, 2014) or guanine-cytosine content (Chuckran et al., 2021), genomic traits may be expected to play a significant functional role in plant ecological responses (Pellicer et al., 2018; Segraves, 2017) and for extinction risks (Pandit et al., 2011; Plue et al., 2018). For example, traits such as genome size and ploidy are associated with a suite of life-history traits including clonality, apomixis and self-compatibility (Pyšek et al., 2023; Suda et al., 2015; te Beest et al., 2012), all traits which can potentially help species postpone and/or escape extinction in fragmented landscapes (Lindborg et al., 2012; Saar et al., 2012). Moreover, genomic traits per se may alleviate the negative genetic and demographic consequences of habitat loss. Polyploidy, for example, has been associated with slower erosion of genetic diversity, higher offspring vigour, masking of deleterious recessive alleles and enhanced phenotypic plasticity (Birchler et al., 2010; Soltis & Soltis, 2000; Vamosi et al., 2007). In contrast, small-genome species exhibit greater phenotypic plasticity (Meyerson et al., 2020) and can support additional one-on-one trait relationships, such as smaller seed mass (Beaulieu et al., 2007), providing alternative advantages for long-term persistence in fragmented landscapes. At the same time, genomic traits may also capture and functionally represent how species respond to increasing nutrient availability. Because N and P are key DNA building blocks, large genomes and high polyploidy levels are resource-costly, particularly in nutrient-limited habitats (Du et al., 2020). With increasing N and P-availability, polyploids and large-genome species appear to be at a selective advantage (Šmarda et al., 2013). They can exploit elevated N and P-availability to build their resource-demanding genome (Guignard et al., 2016; Šmarda et al., 2013), turning them into strong competitors (de Vaz Sousa et al., 2025; Guignard et al., 2016). Though so far only observed in controlled experiments (Guignard et al., 2016; Šmarda et al., 2013), genomic traits may thus underpin the mechanism of competitive exclusion eroding plant species diversity in response to increasing nutrient availability. The immediate link between genomic traits and impacts of habitat loss on one hand and nutrient availability on the other suggest they may be candidates for the simple, reliable, universal traits that conservation science needs, yet their role in local species extinctions and plant community composition in real-world, fragmented landscapes remains untested.

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To address this knowledge gap, we combined genomic trait data with empirical data on 256 plant communities, their soil nutrient status, management and landscape characteristics collected across 16 semi-natural grasslands in four 5 km × 5 km landscapes across southern Sweden. By comparing and analysing semi-natural grassland communities in relation to spatial gradients in grassland fragment size and P-availability, we aimed to infer whether genomic plant traits, that is, chromosome number, ploidy and genome size, may mediate temporal plant community responses to habitat loss and nutrient availability (cf. Blois et al., 2013; Haddad et al., 2015). Given the ecological advantages of large-genome species, we specifically expect that plant communities, in terms of both their diversity and composition, are increasingly dominated by larger genome species (via either higher ploidy, larger genome size or more chromosomes) both as grassland fragments become smaller and as P becomes more available. Finally, we hypothesize that this link between genomic traits and extinction risk in relation to habitat loss and eutrophication may be deterministic in nature (cf. Sasaki et al., 2012; Ulrich et al., 2009). If this were the case, communities which exist as nested subsets along spatial gradients in fragment size and P-availability would be expected to differ in genomic traits, for example from poly- to diploid dominated communities along a small to large grassland fragment size gradient. Such patterns would imply that genomic traits may significantly improve extinction risk predictions, ultimately guiding more effective conservation efforts.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was performed in four 5 km × 5 km Swedish landscapes. We selected two landscapes on calcareous bedrock (low plant-available P; Jordtorp, Öland and Kinnekulle, Västergötland) vs. two landscapes on acid bedrock (high plant-available P; Östra Vätternbranterna, Småland and Aspa, Södermanland). As such, the four landscapes represent an environmental spatial gradient in plant-available P which can be used to infer temporal responses of plant community changes with increasing P-availability (see e.g. Ceulemans et al., 2014). Each landscape contained fragments of semi-natural grasslands embedded in a silvi- and agricultural matrix. Within each of the four landscapes, we selected 16 semi-natural grassland fragments along a gradient in fragment size (total of 64 grasslands; Figure 1), which via spatial comparisons may help infer temporal plant community changes in response to habitat loss (see e.g. Haddad et al., 2015). Grassland fragments had a median size of 1.4 ha, ranging between 0.05 and 157 ha. Using historically available maps, all grassland fragments were confirmed to have been a part of historically large, managed grassland system for several hundred years (e.g. Johansson et al. (2008) and Cousins et al. (2015)).

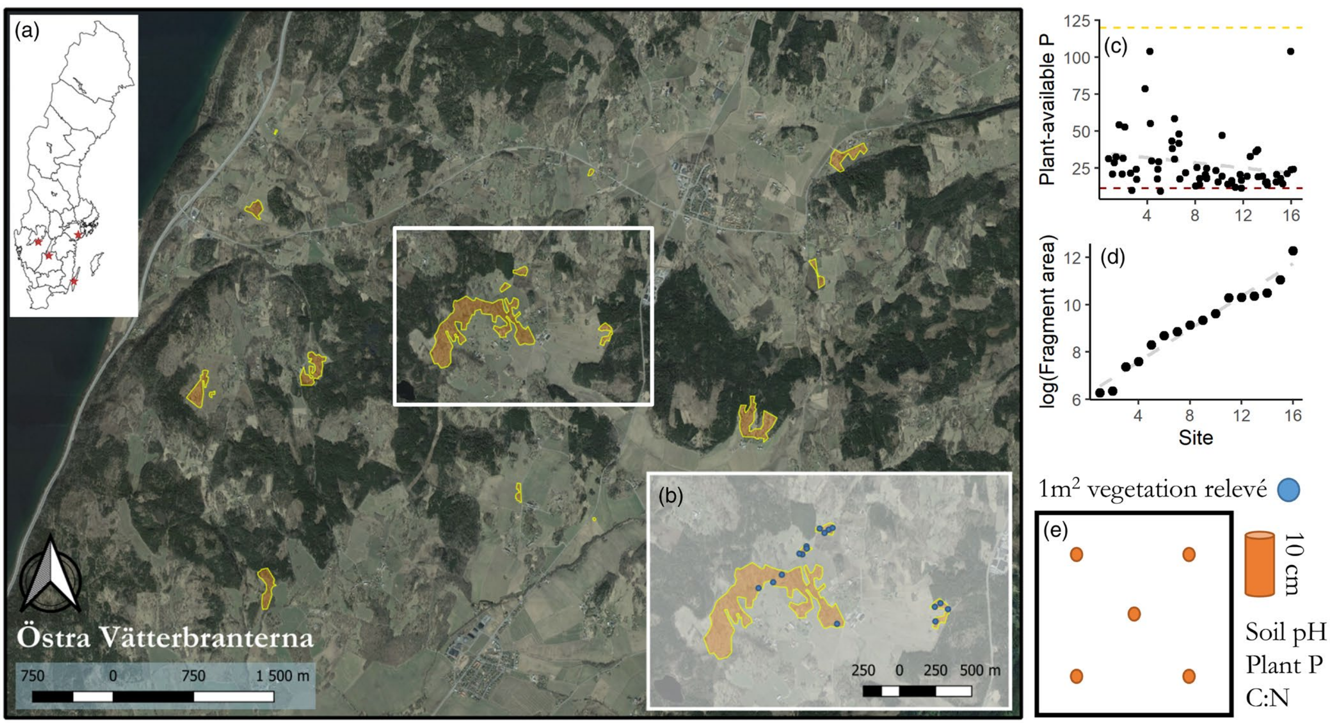

FIGURE 1 The study sample design with four 5 km × 5 km landscapes sampled across southern Sweden ((a), red stars), exemplified by the 16 sampled grassland sites (orange polygons) in the *Östra Vätternbranterna* landscape (Google Earth imagery), along a fragment size gradient (d). Per grassland fragment, the vegetation was inventoried in four 1 m × 1 m plots ((b), blue dots), in which a pooled soil sample ((e), orange dots) was collected to quantify the soil chemical environment. A pronounced relationship between fragment size and P-availability was absent in this landscape, yet the recorded P-levels are within the range of plant-available P inducing species losses (11.5 mg/kg soil; red line) to the point where plant richness stabilizes in spite of increasing P-levels (120 mg/kg soil; yellow line; (c)). For sampling details on the remaining landscapes, see Figure S6.

2.2 | Data collection

2.2.1 | Plant inventories

To assess the plant community in each of the 64 grasslands, we recorded all plant vascular species present in each of four 1 × 1 m vegetation plots, randomly established within each grassland (Figure 1). In total, 256 vegetation plots were inventoried between June and July in 2020 and 2021, recording a total of 257 plant species. All plant community data are available in Plue (2026). Given the Swedish Right of Public Access (Sw. *Allemansrätten*), no fieldwork permits were required.

2.2.2 | Environment

Five mineral topsoil (0–10 cm) samples were taken with a gouge auger and pooled into a single composite sample per plot, using it to quantify each plot's soil abiotic environment. We focus on P-availability, as this is the major driver of plant species occurrences and extinctions in nutrient-poor semi-natural grasslands (Ceulemans et al., 2014), yet we also controlled for other environmental covariates in our analysis (see below). We therefore performed wet-lab measurements of soil pH (soil acidity), C/N ratio (proxy of soil fertility and soil biological activity) and plant-available phosphorus (P). Prior to processing, all soil samples were dried at 105°C for 24 h, ground and sieved (2 mm mesh) to remove coarse plant and organic material. Analyses for soil acidity (pH-KCl) were done by shaking a 1:5 ratio soil/1 M KCl mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP (Thermo Scientific Orion, USA). The C/N ratio was quantified by combusting each individual soil sample at 1150–1200°C and the gases were measured by a thermal conductivity detector in a CNS elemental analyzer (vario Macro Cube, Elementar, Germany). Finally, plant-available P (i.e. available for plant growth during the growing season; Gilbert et al., 2009) was extracted by $NaHCO_3$ (P_{Olsen}; according to ISO 11263:1994(E)) and measured colorimetrically according to the malachite green procedure (Lajtha et al., 1999). Phosphorus concentrations were expressed as mg $P.kg^{-1}$ dry soil.

To control for management intensity (i.e. grazing), the height of the plant community was measured per plot by quantifying height in four cardinal directions outward from the centre of the sampled plot. A white board with height markings was positioned at the edge of the plot and the height recorded equalled the height at which >50% of the white board was visually obstructed by the vegetation. The height of the plant community was the average of these four measurements. All environmental data are available in Plue (2026).

2.2.3 | Genomic plant traits

For each species, we extracted genomic trait data on chromosome number, ploidy and genome size (2C, [Mbp]) from three online databases: Index to Plant Chromosome Numbers (http://www.tropicos.org/Project/IPCN), Royal Botanic Gardens Kew Database (http://cvalues.science.kew.org) and the Database of the Czech Flora and Vegetation (Pladias; http://www.pladias.cz, Šmarda et al., 2019). Ploidy number was cross-referenced and corrected when local Swedish cytotypes deviated from values reported in the aforementioned databases (Lövkvist & Hultgård, 1999). Throughout our analyses, we include two complementary measures of ploidy (An = B): ploidy category (A = 2, diploid; 4, tetraploid; ≥6, polyploid; categorical) and total chromosome number (B; continuous). Tetraploids were treated separately from higher polyploids, allowing the construction of a ploidy gradient. All genomic life-history trait data are available in Plue (2026).

2.3 | Data analysis

2.3.1 | Data preparation

We first calculated a suite of dependent variables quantifying plant community diversity in relation to genomic life-history traits. At the plot level, we calculated total species richness and species richness per ploidy category (di-, tetra- and polyploid) as well as their relative proportions of total plot species richness. We also calculated beta-diversity as the mean Chao similarity (presence/absence based, *vegdist* function in *vegan* package; Oksanen et al., 2023) of a plot's species composition compared to the species composition of all other plots per landscape. Based on each plot's species composition, we calculated community weighted means for ploidy, genome size and chromosome number using their absolute continuous values.

2.3.2 | Data exploration

First, to gain insight into environmental dependencies and address multicollinearity among environmental predictor variables, we used Pearson correlations and *t*-tests to assess the way in which soil abiotic environment, fragment size and vegetation height co-varied with each other. Soil pH, plant-available P, vegetation height and fragment size were log-transformed for normality. Environmental predictor variables did show multicollinearity (Figures S1 and S2). However, most of the correlations among environmental variables were relatively modest ($r_{Pearson} < |0.41|$, $0.96 < p \leq 0.001$), allowing the simultaneous inclusion of all environmental variables in the statistical models. Importantly for our study, there was no correlation between fragment size and plant-available P ($r_{Pearson} = 0.01$, $p = 0.86$), both presenting long, continuous gradients to explore their orthogonal impact on plant communities (Figure S1).

Second, interspecific relations between log-transformed genomic traits were explored using Pearson correlation coefficients to test if the genomic trait data aligned with known positive associations between, for example, genome size and ploidy level (Šmarda et al., 2013). Genomic life-history traits were all positively correlated with one another (Figure S3). Species with higher ploidy both hold a higher number of chromosomes ($r_{Pearson} = 0.65$, $p < 0.001$) and have larger genome sizes ($r_{Pearson} = 0.19$, $p = 0.003$). Similarly, an increasing number of chromosomes was associated with an increase in genome size, albeit a weak relation ($r_{Pearson} = 0.17$, $p = 0.009$).

We chose not to investigate phylogenetic signals and to focus exclusively on observed ecological patterns, assuming each species to be a unique unit of replication. As such, we assumed that phylogeny is of limited importance for understanding the ecological implications of a trait per se (see detailed arguments by de Bello et al., 2015; Westoby et al., 2023), notably on the short time scale under consideration in our study (Westoby et al., 1995). Our interest focuses on how genomic traits directly affect local species' extinction risk, irrespective of the species' phylogenetic history. Therefore, while we assess the local risk of extinction mediated via genomic traits, we do not explore why species may have similar genomic trait values.

2.3.3 | Do genomic life-history traits mediate plant community changes

First, we aimed to establish how plant community diversity is associated with fragment size and phosphorus availability, with genomic trait variation as a key underlying mechanism. How well these environmental variables predict the species richness, the relative proportion in the community, beta-diversity (of different ploidy levels) and community weighted means of genomic traits was analysed using general linear mixed models in case of a response variable with a Gaussian error distribution (*glmer* function from *lme4* package, Bates et al., 2015) or generalized linear mixed models in case of a response variable with a Poisson error distribution (*lme* function from *nlme* package (Pinheiro et al., 2025), see Table S1). We constructed a parsimonious model based on the focal research questions focusing on the combined impact of fragment size and P-availability, while controlling for co-varying environmental variation:

$$\text{Response variable} \sim \text{fragment size} + \text{P} - \text{availability} + \text{fragment size: P} - \text{availability} + \text{pH} + \text{C/N ratio} + \text{vegetation height} + \sim 1 \,|\, \text{landscape/site}$$

This model contained all environmental variables as fixed effects, with site nested in landscape as the random effect to accommodate spatial autocorrelation and other unmeasured co-variation associated with sites and landscapes. Model selection was restricted to removing the interaction term when non-significant and then re-running the model. All models were scaled for standardized effect sizes (SES; Grueber et al., 2011), enabling comparison of each predictor both within and across models. Finally, we calculated variation inflation factors per model to ensure that recorded effects of environmental variables were not inflated by collinearities.

Second, we asked how changes in plant community composition vary with fragment size, P-availability and genomic traits. Therefore, we ran perMANOVA analyses (*adonis2* function in *vegan* package; 999 permutations stratified within landscape, Chao dissimilarity) on the full plot-by-species matrix, followed by subset matrices containing only di-, tetra- and polyploid species, respectively. The model structure and selection were identical as for the linear mixed models described for the univariate response variables.

Third, we assessed whether differences in plant community composition related to fragment size and phosphorus availability followed a deterministic pattern and whether genomic traits played a fundamental role in driving these differences. We therefore first tested for the presence of nestedness among the communities, sensu Ulrich and Almeida-Neto (2012). We calculated the no overlap-decreasing fill metric (NODF; Almeida-Neto et al., 2008) to quantify nestedness, while the observed NODF metric's significance was tested against a NODF distribution built via 999 randomizations of the observed presence–absence plot-by-species matrix under a restricted null model. For this null model, randomized presence–absence matrices were created for which the probability of each cell being occupied is the average probability of occupancy of its row and column. Subsequently, by analysing the characteristics of the nested, maximally-packed plot-by-species matrix, we could then assess (1) if plant communities exist as compositional subsets of other plant communities in function of fragment size and/or P-availability (analysis of plot rank-order); and (2) if genomic life-history traits play a role in which species are deterministically being lost along these environmental gradients (analysis of species rank-order; Ulrich et al., 2009; Sasaki et al., 2012). Using the generalized linear mixed modelling procedure described above, we first modelled the plot rank-order in the nested matrix (i.e. plot rank-order; the plot with the highest rank has the most species and the lowest ranked plot has the least species) in function of the environmental variables. This analysis formally tests whether plant communities on small grassland fragments and/or with high P-availability are nested subset of plant communities on large grassland fragments and/or with low P-availability, controlling for remaining environmental effects. Pearson correlations tested whether di-, tetra- and polyploidy species richness and beta-diversity changed, that is, respectively declined and increased, differentially along these nested plant communities. Finally, we modelled the species rank-order in the nested matrix (hereafter species rank–order; the most common species have the highest rank, the rarest species have the lowest rank) as a function of genomic life-history traits, to understand how these traits mediate the loss of species (Sasaki et al., 2012). However, given large Variation Inflation Factors (*vif* from *car* R package) when combining genomic traits in the model, we investigated their impact on species rank-order on a one-by-one basis, using a general linear model per genomic trait. All data analyses were done in R 4.2.2 (R Core Team, 2023).

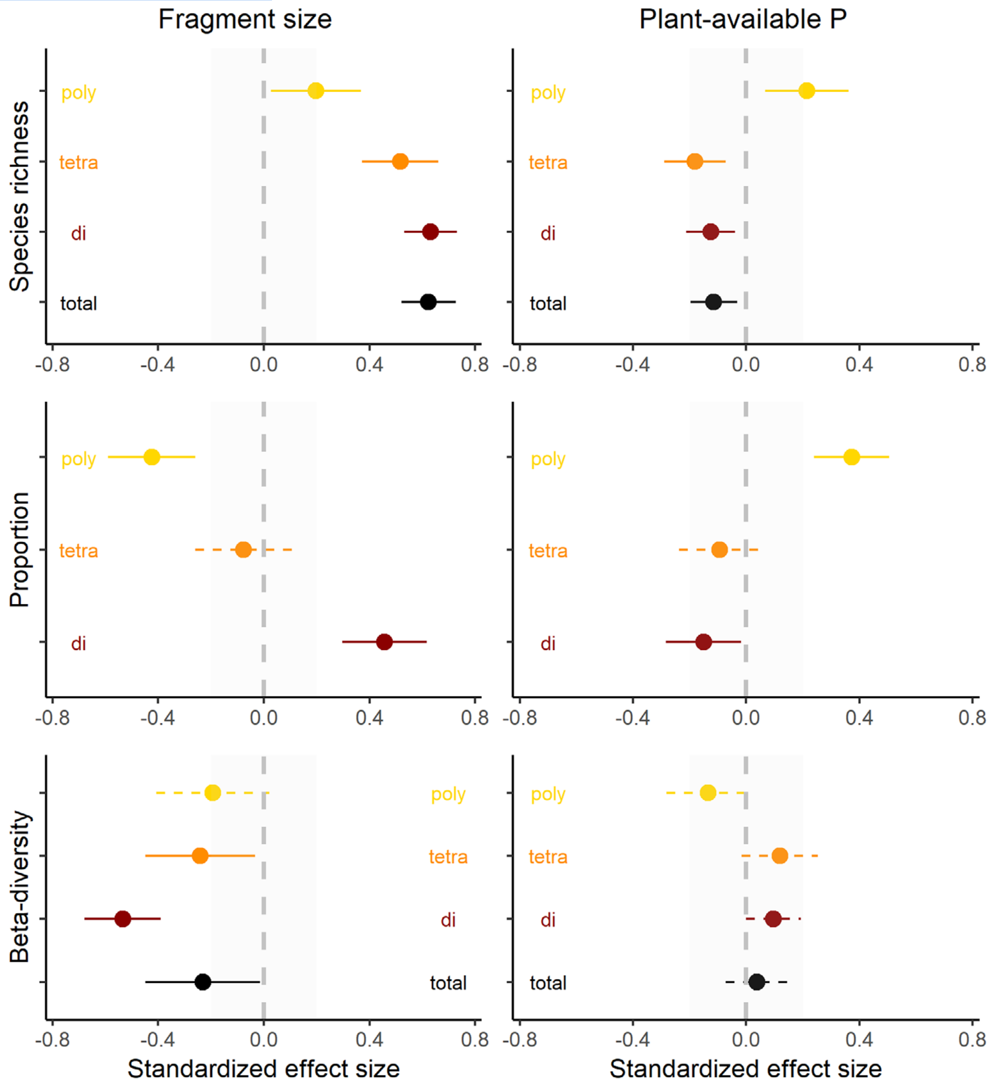

FIGURE 2 Main effects of fragment size and P-availability on plant species richness, relative proportion in the plant community and beta-diversity of di- (dark red), tetra- (orange) and polyploid (yellow) plant species. Plant species richness and beta-diversity of the total plant community were included for reference (black). Standardized effect sizes are calculated via linear mixed effects models using scaled response and predictor variables to enable comparison of effect strength within and across models. Positive/negative standardized effect sizes indicate a positive/negative relationship between diversity variables on the one hand and fragment size or P-availability on the other hand. Dashed confidence intervals indicate a non-significant impact of fragment size or P-availability, that is, 0 falls within the 95% confidence intervals around the effect size. The model results representing the standardized effect sizes of co-varying environmental predictors can be found in Figure S4.

3 | RESULTS

3.1 | Shifts in community diversity

Total species richness per plot decreased with decreasing fragment size (SES = 0.62, $p < 0.001$) and increasing P-availability (SES = −0.12, $p = 0.005$). Species richness of di-, tetra- and polyploid species responded similarly, that is, decreasing as fragment size decreased (Figure 2a). Di- and tetraploid species richness declined with increasing P-availability, whereas polyploid species richness increased (Figure 2b). The interaction between fragment size and P-availability did not affect any of the species richness variables (Table S1).

As fragment size declined, the proportion of polyploids increased whereas the proportion of diploids decreased (Figure 2c). Similarly, along an increasing P-availability gradient, the share of polyploids increased whereas the share of diploids decreased (Figure 2d). For the share of polyploids only, fragment size and P-availability significantly interacted (Table S1), with the share of polyploids increasing rapidly, moderately and not at all, as a function of increasing P-availability in small (mean of 0.16 ha), medium-sized (mean of 13 ha) and large grassland fragments (mean of 65 ha), respectively. The share of tetraploids was unaffected by fragment size and P-availability (Figure 2c,d).

Beta-diversity increased as grassland fragments became smaller (SES = −0.23, $p = 0.04$), though the strength and shape of this relation

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were modified by P-availability (P: SES=0.15, p=0.007; Fragment size×P: SES=−0.15, p=0.007; Table S1). Under high P-availability (P~51 mg/kg soil), beta-diversity increased rapidly as grassland fragments became smaller. Under moderate P-availability (P~21 mg/kg soil), beta-diversity still increased as grassland fragments decreased in area, but less rapidly. Under limited P-availability (P~9 mg/kg soil), beta-diversity was unaffected by fragment size. Diploid and

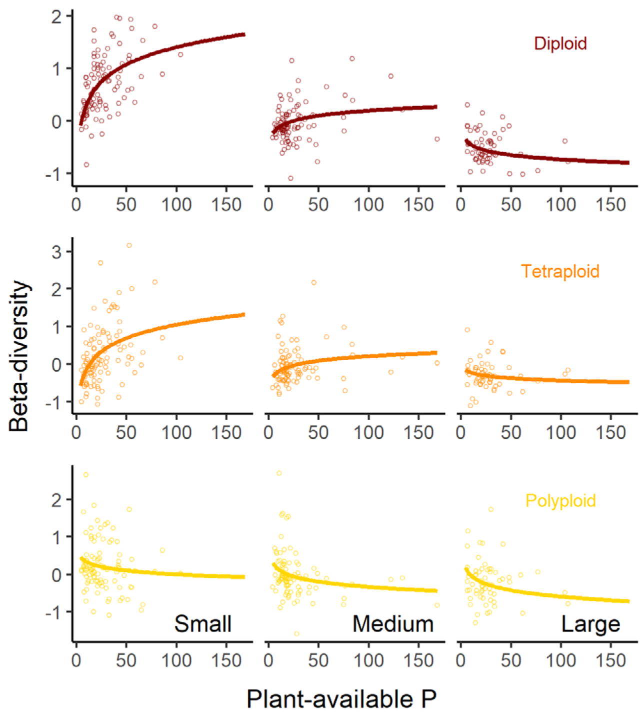

FIGURE 3 Visualization of the interaction between fragment size and P-availability in the significant response of beta-diversity (standardized using the R *scale* function) in diploids (p < 0.001), tetraploids (p = <0.01) but not in polyploids. For visualization of the interaction, the *visreg* R package generates breaks based on the observed fragment size gradient which are held constant (small: Mean 0.16 ha, medium: Mean 13 ha and large: Mean 65 ha) to construct curves showing beta-diversity per ploidy category in function of increasing (non-transformed) plant-available P. The logarithmic curves are a reminder of the logarithmic response of all univariate predictor variables to P-availability.

tetraploid beta-diversity decreased with increasing fragment size, with the effect of fragment size weakening with increasing ploidy (SES_{2n} −0.52 > SES_{4n} −0.24). Polyploid beta-diversity showed no relationship with fragment size (Figure 2e). Beta-diversity of either di-, tetra- or polyploid communities was not affected directly by P-availability (Figure 2f). However, there was an interaction between fragment size and P-availability in the beta-diversity of diploid and tetraploid communities that was not found among the polyploid communities (Table S1, Figure 3). For detailed model output and the relationships of the remaining co-varying environmental variables with various response variables, see Table S1 and Appendix S1, respectively.

3.2 | Shifts in CWMs

Community weighted means of ploidy decreased with increasing fragment size. Mean chromosome number decreased with increasing P-availability (Figure S5). The interaction between fragment size and P-availability affected mean chromosome number (Table S1), but not ploidy community average. Mean chromosome number thus increased with increasing P-availability, but this increase became less pronounced in larger grassland fragments. Mean genome size of the community decreased with increasing fragment size, but displayed no response to P-availability (Figure S5).

3.3 | Deterministic shifts in community composition

The perMANOVAs indicated that the total, tetra- and polyploid plant community composition was affected by fragment size and P-availability, but not their interaction. The diploid plant community varied similarly (Table 1), but included a minor, yet significant interaction term between fragment size and P-availability.

Plant communities were significantly nested (observed vs. mean simulated NODF: 32.21 vs. 13.00, z=211.5, p=0.01). While plant communities are by definition ordered in function of species richness along the nested plant community gradient, we noted a distinct decline in the strength of this relationship with increasing

TABLE 1 Results of the perMANOVA analysis investigating whether plant communities in the full grassland plant community and subsets of the plant community grouped per ploidy level (di-, tetra- and polyploids; n = number of species) differ in function of fragment size and P-availability.

			Fragment size		Plant-available P		Fragment size: Plant-available P	
Plant community	n	Expl. Var. [%]	R^2	p	R^2	p	R^2	p
Full	248	90.3	0.29	***	0.26	***	–	–
Diploids (2n)	136	52.5	0.17	***	0.12	***	0.01	*
Tetraploids (4n)	75	55.3	0.11	***	0.17	***	–	–
Polyploids (≥6n)	32	52.6	0.23	***	0.09	*	–	–

Note: Expl. Var., explained variation (1 − residual sum of squares/total sum of squares); p-value indicates level of significance at $p \leq 0.001$ (***) and $0.01 < p < 0.05$ (*). The impacts of co-varying environmental predictors on differences in plant communities can be found in Table S1.

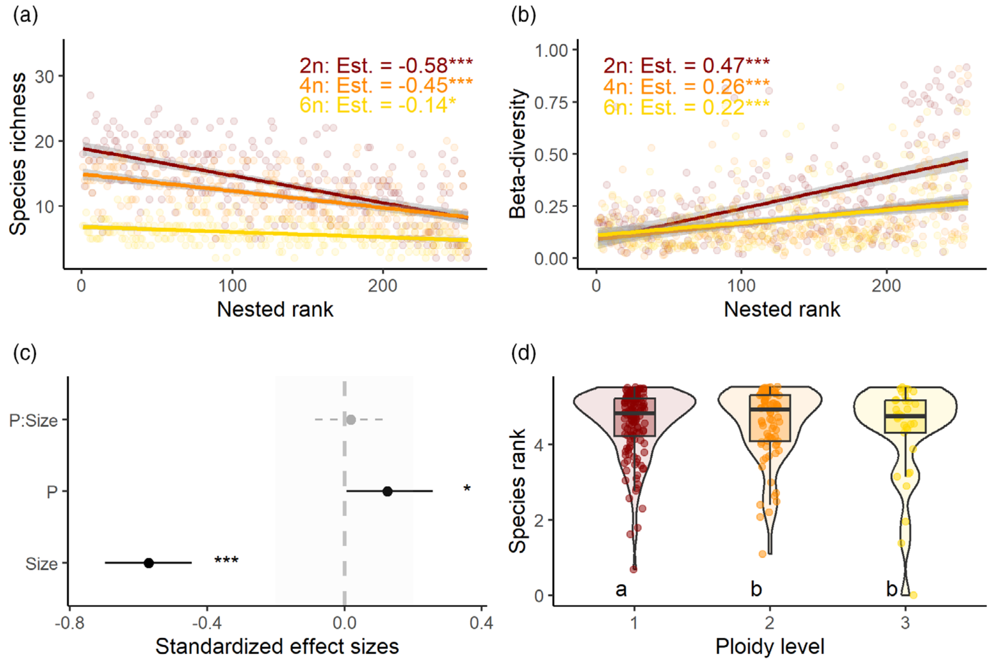

FIGURE 4 Significant relationships between the main characteristics of the maximally-packed nested plant community matrix, that is, plot rank-order (a–c) and species rank-order (d), with species richness (a), beta-diversity (b), fragment size and P-availability (c) and ploidy (d), grouped by ploidy level (di- (dark red), tetra- (orange) and polyploid (yellow)).

ploidy (Figure 4a). The richness of diploids decreased most rapidly (2n SES = −0.58, $p < 0.001$) compared with a rapid, yet 28% slower decline in tetraploid species richness with increasing plot rank-order (4n SES −0.45, $p < 0.001$). Polyploid species richness declined more slowly along the nested community gradient (6n SES −0.14, $p = 0.03$). As communities disassembled along the nested community gradient, beta-diversity increased, with the strength of this relationship depending on ploidy (Figure 4b). Beta-diversity among diploids increased most rapidly with plot rank-order (2n SES 0.48, $p < 0.001$), compared with the ca. 50% slower increase in beta-diversity among tetra- and polyploids (4n SES = 0.26, $p < 0.001$; 6n SES = 0.22, $p < 0.001$).

The nested structure of the plant communities, as expressed by the rank-order, decreased along gradients in increasing fragment size (SES −0.57, $p < 0.001$) and decreasing P-availability (SES 0.12, $p = 0.049$; Figure 4c). Plot rank-order remained unaffected by the interaction of fragment size and P-availability (Figure S6). Species rank-order was neither affected by genome size (SES −0.07, $p = 0.21$) nor by chromosome number (SES −0.06, $p = 0.60$). Ploidy level did affect species rank-order, both in its continuous form (SES −0.35, $p = 0.005$) as well as in its categorical form (Figure 4d). Increasing ploidy led to a lower species rank-order, that is, a lesser likelihood of extinction, with diploids being particularly vulnerable (Figure 4d).

4 | DISCUSSION

Identifying simple, reliable and universal traits that enhance predictions of local extinction risk in response to multiple environmental threats can improve extinction risk assessments and inform conservation efforts. Our study suggests that plant community composition in grassland fragments may be deterministically shaped by genomic traits, which likely influence plant species' responses to habitat loss (i.e. fragment size) and local habitat quality (i.e. phosphorus availability). Plant community changes, both overall and when decomposed according to ploidy level, were often affected independently by fragment size and P-availability—suggesting that differing life-history trait syndromes, related to persistence/dispersal and competition respectively, function independently along these two key environmental gradients. Yet our results imply that these different trait-based mechanisms are underpinned by shared genomic traits. Ploidy emerges as a pivotal trait, given its strong associations with genome size and chromosome number (Figure S3) and its significant statistical relationships with both fragment size and phosphorus availability (Figure S5). For simplicity, we focus our discussion on how the observed deterministic community shifts may be driven by ploidy (Figures 2–4).

4.1 | Genomic traits mediate impact of habitat loss

Extrapolating the observed spatial patterns towards temporal responses to habitat loss and eutrophication (cf. Blois et al., 2013; Haddad et al., 2015), decreasing grassland fragment size may deterministically drive plant community changes, with ploidy determining the order of species extinctions. Overall species losses, and associated plant community changes, may follow a predictable pattern, with extinction rates accelerating from polyploids to tetraploids and diploids. This process may lead to plant communities increasingly dominated by relatively homogeneous, nested subsets of tetra- and polyploids. In parallel, prevalent life-history trait syndromes among fragmented plant communities are dominated by life-history traits which facilitate long-term persistence, enabling them to escape extinction (Auffret et al., 2017). These include traits such as self-compatible mating systems (Aguilar et al., 2008), clonality (Lindborg et al., 2012) and perenniality (Marini et al., 2012) that are widespread in polyploid plant invaders (Pyšek et al., 2023) and habitat loss survivors (Plue et al., 2018). This co-occurrence of persistence-related life-history traits in polyploids may well be a direct result of active selection of adaptive trait states during neo-polyploidization events. As neo-polyploids can be considered novel species arriving in a new habitat (Levin, 1983), any life-history trait adaptations assisting neo-polyploid establishment, such as uniparental and clonal reproduction (Barringer, 2007; Van Drunen & Husband, 2019), perenniality (Rice et al., 2019) or competitive resource acquisition strategies (Anneberg & Segraves, 2023; Castro et al., 2023) are likely to be favoured to overcome high initial extinction risks (Levin, 2019). These life-history adaptations may persist in established polyploids, potentially enhancing their ability to endure, adapt to and survive harsh environmental conditions (Chao et al., 2013; Leitch & Leitch, 2008; Rice et al., 2019), as reflected in the observed community responses to habitat loss. Polyploidy is likely to be more than a compound life-history trait, likely harbouring direct biological adaptations that confer an ability to resist habitat loss. Neo-polyploid establishment has indeed been shown to be favoured by for example, heightened phenotypic plasticity (Ramsey & Schemske, 2002), elevated stress-tolerance that improves plant fitness (Turcotte et al., 2024) and increased pathogen resistance (Oswald & Nuismer, 2007). These characteristics may well enable established polyploids to occupy a wider range of the potentially stressful, sub-optimal environments (Hao et al., 2013; Vamosi et al., 2007) that are typical of increasingly smaller grassland fragments (Hofmeister et al., 2013; Ries et al., 2004).

4.2 | Genomic traits mediate impact of P-availability

Grassland fragments in the study presented a largely natural gradient in P-availability (median 20.92, range 4.18–168.60 mg P.(kg.soil)$^{-1}$). Still, 18.75% of plots are upwards of 40 mg P.(kg.soil)$^{-1}$, a level after which even small increases in plant-available P drive rapid plant diversity loss (50% of species lost towards 80 mg P.(kg.soil)$^{-1}$), in NW-Europe (Ceulemans et al., 2014) and Sweden (Plue & Baeten, 2021). We propose that the plant community patterns observed along the phosphorus availability gradient can be cautiously extrapolated to anticipate the impacts of further phosphorus eutrophication and the role of genomic traits in shaping these responses. In a similar way to the effect of habitat loss (i.e. declining fragment size), the consequent differences in community composition attributable to increased P-availability were structured by aligned species responses aggregated by interspecific variation in ploidy. Plant communities in high-phosphorus environments formed predictable, nested subsets of more phosphorus-limited communities, characterized by the loss of most diploid and some tetraploid species, resulting in increasingly homogeneous, polyploid-dominated assemblages. This observation may provide the first in situ evidence that the competitive advantage of polyploids under increased phosphorus availability—previously demonstrated in greenhouse experiments (Anneberg & Segraves, 2023; Guignard et al., 2016; Šmarda et al., 2013)—acts as a genomic-based driver of natural plant community responses to elevated phosphorus levels and, ultimately, phosphorus eutrophication.

Most natural terrestrial ecosystems suffer strong P-limitation (Du et al., 2020), and increased P-availability triggers enhanced production of above-ground plant biomass (Hou et al., 2020). Rapidly capitalizing, competitive generalists then produce large amounts of biomass, driving low-stature, light-dependent grassland specialists to local extinction (Eskelinen et al., 2022). Our empirical results on ploidy-aligned responses to increased P-availability connect this process to plant species' genomic life-history. Successful polyploids are capable of high biomass production (Pyšek et al., 2023; te Beest et al., 2011). Nevertheless, a compositionally stable polyploid community is present along the entire P-availability gradient (low community turn-over; Figure 3) with their competitive abilities likely kept in check at low levels of P-availability (Guignard et al., 2016; Šmarda et al., 2013). Indeed, once a release from P-limitation occurs, polyploids can rapidly acquire P (Anneberg & Segraves, 2023; Castro et al., 2023) to support increased biomass production and a parallel large-genome assembly. We argue, however, that P-limitation primarily acts via the genome rather than other cellular P-requirements during growth, as up to 60% of cellular phosphorus is contained within nucleic acids alone (Veneklaas et al., 2012). Furthermore, the relative increase in the competitive release among polyploids (from tetra- to higher polyploids) provides additional support for a potential causal link between increasing cellular phosphorus requirements with rising ploidy levels and the resulting, predictable ploidy-aligned differences in community composition under increasing phosphorus availability.

4.3 | Diploids are disproportionally at risk

Based on the nestedness analysis, habitat loss and increased P-availability did generally not seem to interact to amplify species diversity losses and community shifts (as in e.g. Chase et al., 2020; Plue & Baeten, 2021; Hooftman et al., 2021), apart for the subset of diploid plant species. Only diploids were predictably lost from plant communities, and that at significantly faster rates than tetra- and polyploids. Moreover, the observed interaction between habitat loss (i.e. declining fragment size) and increased P-availability on diploid beta-diversity suggests a high degree of randomness in diploid extinctions under increased environmental stress, underlining that other advantageous persistence and dispersal life-history traits do not appear to lower diploid extinction risk (Plue et al., 2018). Elevated diploid extinction risk may thus almost only link back to their genomic life-history, and its consequences for population genetic dynamics. Genetic erosion is a well-established mechanistic driver of extinction in response to habitat loss, to which diploids appear particularly vulnerable. In addition to the fact that a lower number of chromosome copies reduces the total gene pool of a diploid individual (and thus the population) (e.g. Zozomová-Lihová et al., 2015), diploid populations may suffer more rapid declines in heterozygosity (Moody et al., 1993; Soltis & Soltis, 2000) and faster expression of recessive deleterious alleles (Soltis & Soltis, 2000; Rosche et al., 2017) than those shown in polyploids. The detrimental population genetic effects of habitat loss may then more rapidly manifest themselves on population demography and fitness (Aguilar et al., 2008; Jacquemyn et al., 2012). Moreover, reduced diploid population fitness may explain why increased P-availability may exacerbate diploid extinctions in smaller habitat fragments. Diploids inherently benefit from the release of phosphorus limitation just as polyploids do, showing a similar increase in biomass (Guignard et al., 2016). However, if small, fragmented diploid populations experience disproportionately declining demographic dynamics due to reduced population fitness, they are more likely to succumb to increased light competition. This competition, driven by the selective advantages of tetra- and polyploids (cf. de Vaz Sousa et al., 2025), further heightens the risk of local diploid extinctions (Eskelinen et al., 2022; Ewers et al., 2007). In sum, because of their genomic life-history, and no obvious buffering effect from other life-history traits, diploids appear particularly vulnerable to extinction under both habitat loss and habitat quality degradation—reinforcing the fact that diploids are overrepresented among the world's red-listed species. (Pandit et al., 2011).

4.4 | Genomic traits as unifying traits

Genomic life-history traits have been proposed to be unifying species traits, linking a species biology with its ecology (Bennett & Leitch, 2005; Pandit et al., 2014; Plue et al., 2018). Yet, they remain persistently ignored when identifying universal, multi-taxa traits of extinction risk (Chichorro et al., 2019; Chichorro et al., 2022). Such attempts overshoot their goal, often only returning singular 'traits' which are either complex multi-trait life-history syndromes (habitat specialization, range size; Chichorro et al., 2019; Staude et al., 2020) or individual traits (see Chichorro et al., 2022) which are difficult to assess (e.g. dispersal, González-Varo et al., 2024) and/or susceptible to substantial interspecific variation (e.g. body size, Einum et al., 2012). Nevertheless, our study supports the conceptual idea that singular, easily quantifiable and stable traits capable of predicting extinction risk may exist, much like those successfully used to predict invasion success (te Beest et al., 2012; Pandit et al., 2014; Pyšek et al., 2023). Even if different traits within a single species differentially affect its susceptibility to particular global change drivers (Purvis et al., 2000), we identified at least a single genomic trait—i.e. ploidy—that shapes consistent, congruent interspecific extinction risks, as in Plue et al. (2018). Ploidy-associated biological life-history attributes thus capture interspecific variation in the ability to resist different, simultaneously operating ecological mechanisms such as genetic erosion, pollen limitation or elevated competition. Habitat loss (i.e. declining fragment size) and increasing P-availability affect these latter processes differently, whilst requiring very different biological attributes in capabilities to persist/adapt or compete, respectively, yet seemingly coalescing with variation in ploidy. The independent responses to habitat loss and increasing P-availability observed in higher ploidy levels, combined with the near-independence of diploid extinction risk from remaining life-history traits, may thus suggest that orthogonal species life-history facets resisting different global change drivers are potentially encapsulated and well-represented by interspecific variation in ploidy. Genomic traits such as ploidy or genome size thus have the potential to act as unifying proxies for a suite of traits quantifying high adaptability, long-term persistence and strong competitive ability that are desirable biological qualities limiting extinction risk to most global change drivers (cf. Pandit et al., 2011; Vinogradov, 2003).

AUTHOR CONTRIBUTIONS

Jan Plue conceived the ideas and designed methodology, collected and analysed the data; Jan Plue led the writing of the manuscript, with James Bullock, Sara Cousins, Olivier Honnay, Robin Pakeman, Meelis Pärtel, Honor Prentice and Vigdis Vandvik contributing critically to the drafts and giving final approval for publication.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to report. Honor C Prentice is an Associate Editor of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper.

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DATA AVAILABILITY STATEMENT

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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. Results of co-varying environmental variables on plant community diversity and composition.

Figure S1. Box- and violinplots visualizing differences in soil chemical environment and grassland fragment descriptors as a function of bedrock type (acid vs. calcareous). Significance of differences was tested using independent *t*-tests on the log-transformed variables (except C/N ratio). Significance level is indicated by number of stars: ***$p<0.001$, **$p=0.003$.

Figure S2. Correlation matrix of Pearson correlations calculated between the measured soil chemical environment (soil pH, C/N ratio, Plant-available P) as well as grassland fragment descriptors (fragment size and vegetation height, the latter as a proxy of management intensity). All variables except C/N ratio were log-transformed for normality. Red squares indicate positive correlations whereas blue squares indicate negative correlations; the deeper the colour, the more significant the correlation. Blank squares indicate the absence of a significant correlation.

Figure S3. Pearson correlations between the log-transformed genomic life-history traits (Ploidy level, Chromosome number and Genome size [Gbp]) for the species for which trait information was available (Ploidy level and Chromosome number: 243; Genome size: 235). Each trait was log-transformed for normality, and each correlation proved significant.

Figure S4. Main effects of C/N ratio, soil pH and vegetation height on species richness, relative proportion in the plant community and beta-diversity of di- (dark red), tetra- (orange) and polyploid (gold) plant species. Plant species richness and beta-diversity of the total plant community were included for reference (black). Standardized effect sizes (SES) are calculated via linear mixed effects models using scaled response and predictor variables to enable comparison of the strength of the effect within and across models. Positive/negative standardized effect sizes indicate a positive/negative relationship between diversity variables on the one hand and fragment size or P-availability on the other hand. Interrupted lines indicate a non-significant impact of a predictor variable, that is, 0 falls within the 95% confidence intervals around the SES. X-axis is scaled on the same similar to the effects of fragment size and plant-available P in Figure 2 to enable comparison of the size of the SES across both figures. See Table S1 for detailed statistical model output.

Figure S5. Scatterplots showing the relationship between community weighted means (CWM) of genomic life-history traits, that is, ploidy, genome size [Gbp] and chromosome number, in function of fragment area [m^2] and plant-available P [mg P/kg soil]. Standardized effect size estimates and associated *p*-values are calculated based on general linear mixed models (site nested in landscape as a random effect) testing for the direct effects of fragment size and P-availability while correcting for co-varying environmental effects (C/N ratio, soil pH and vegetation height). Regression lines are black when the effect of fragment size or plant-available P on CWM of the genomic trait was significant.

Figure S6. The study sample design in the three remaining 5 km × 5 km landscapes sampled across southern Sweden, showing the 16 grassland sites (orange polygons) sampled per landscape (Google Earth imagery), along a fragment size gradient. Per grassland fragment, the vegetation was inventoried in four 1 m × 1 m plots (blue dots, inset figures only), in which a pooled soil sample was collected to quantify the soil chemical environment.

Table S1. Full results of Generalized Linear Mixed models investigating the impact of fragment size and P-availability (P) on plant community characteristics (total and grouped by ploidy) and community weighted means (CWM) of genomic traits, while controlling for co-varying environmental variation in soil acidity (pH), fertility (C:N) and management intensity (vegetation Height).

Table S2. Complementary results of the perMANOVA analysis investigating the impact of fragment size and P-availability on plant community shifts in the full plant community and subsets of the plant community grouped per ploidy level (di-, tetra- and polyploids), presenting the impacts of the co-varying environmental predictors on plant community shifts.

Figure S6. Main effects of each environmental predictor in the full examining the response of nestedness in the plant community, quantified as the plot rank-order in the nested matrix. Standardized effect sizes (SES) were calculated via general linear mixed effects models using scaled response and predictor variables to enable comparison of the strength of the effect within the model. Interrupted lines indicate a non-significant impact of a predictor variable, that is, 0 falls within the 95% confidence intervals around the SES. Significance level is indicated at levels $p < 0.001$ (***) and $0.01 < p < 0.05$ (*).

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