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RESEARCH ARTICLE

Phenotypic diversity influenced by a transposable element increases productivity and resistance to competitors in plant populations

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Abstract

1. An accumulating body of evidence indicates that natural plant populations harbour a large diversity of transposable elements (TEs). TEs, which are especially mobilized under genomic and/or environmental stress, provide genetic and epigenetic variation that can substantially translate into a diversity of plant phenotypes within populations. However, it remains unclear what the potential ecological effects of diversity in TEs within an otherwise genetically uniform population are in terms of phenotypic diversity's effects on coexistence and ecosystem functioning.
2. Using *Arabidopsis thaliana* as a proof-of-concept model, we assembled populations from individuals differing in the number and positions of *ONSEN* retrotransposon and tested whether the increasing diversity created by the *ONSEN* retrotransposon increased the phenotypic diversity of populations and enhanced their functioning under different environmental conditions.
3. We demonstrate that TE-generated variation creates differentiation in ecologically important traits connected to different axes of the plant 'economics' spectrum. In particular, we show that *Arabidopsis* populations with increasing diversity of individuals differing in the *ONSEN* retrotransposon had higher phenotypic and functional diversity in resource use-related traits. Such increased diversity enhanced population productivity and reduced the performance of interspecific competitors.
4. *Synthesis*. We conclude that TE-generated phenotypic and functional diversity can have similar effects on ecosystems as are usually documented for other

Vít Latzel and Javier Puy are equally contributed to this work.

biological diversity effects. The results of our experiment open up new fields of investigation, highlighting the ecological relevance of unexplored sources of phenotypic variability and hopefully inspiring functional trait ecologists and evolutionary biologists to begin exploring new questions at the intersection of their fields.

KEYWORDS
Arabidopsis thaliana, biological diversity, ecosystem functioning, (epi)genetic functional diversity, functional traits, *ONSEN* retrotransposon, overyielding

1 | INTRODUCTION

It has been continuously demonstrated that biological diversity is one of the key determinants of ecosystem functioning (Huston, 1997; Loreau & Hector, 2001). Diversity effects have been mostly assessed at the level of species diversity (typically number of species; Díaz et al., 2007; Tilman et al., 1997) and interpreted as the effect of phenotypic differences between species, that is, greater functional trait diversity enhancing ecosystem functioning (Díaz et al., 2007; Gross et al., 2017). In species diversity studies, positive diversity effects imply that communities composed of phenotypically diverse organisms are expected to be more productive and resistant to abiotic and biotic stresses, such as competition from potential invaders, compared to less diverse ones (Gross et al., 2017). This positive diversity effect on ecosystem functioning could be because greater species richness increases the likelihood that a species with a large effect on any given ecosystem property would be present (i.e. the so-called selection or sampling effect; Loreau & Hector, 2001) or because greater niche differences between coexisting species result in better utilization of resources by the community (i.e. so-called complementarity; Loreau & Hector, 2001).

Important evidence has been accumulating that, likewise, phenotypic diversity within populations can have strong and positive effects on ecosystem functioning comparable to that of species diversity (Crutsinger et al., 2006; Ehlers et al., 2016). This phenotypic variation within populations has been most often attributed to genetic variation (Hughes et al., 2008; Kotowska et al., 2010; Zhu et al., 2000; Zuppinger-Dingley et al., 2014) originated from spontaneous genetic mutations and recombination or migrations from surrounding populations (Ulukapi & Nasircilar, 2018), as well as epigenetic processes (Latzel et al., 2013; Puy et al., 2021). Additionally, at the crossroads between genetic and epigenetic variation, differences in insertion sites of transposable elements (TEs; i.e. mobile genetic elements that can replicate and/or change position within genomes; Slotkin & Martienssen, 2007) represent one of the main drivers of DNA sequence variation and epigenetic regulation of gene expression, which both can generate phenotypic variation (Kidwell & Lisch, 1997; Mirouze & Vitte, 2016; Niua et al., 2019). However, it remains unclear whether variation in TEs within populations causes sufficient phenotypic variation to substantially affect ecosystem functioning.

TEs are a ubiquitous component of the DNA of most eukaryotes (Feschotte et al., 2002), making up the majority of DNA in some plant species (Bennetzen et al., 2005; Schnable et al., 2009; Vitte et al., 2014). TEs are commonly divided into two major classes: DNA transposons and retrotransposons. While DNA-TEs (Class II-TEs) mostly move by a 'cut-and-paste' mechanism, retrotransposons (Class I-TEs) multiply via an RNA intermediate with a 'copy-and-paste' strategy (Wicker et al., 2007). The mutational power of unrestricted TE-mobility can result in genomic instability and have negative effects on host function. To protect their genome, plants have evolved complex silencing mechanisms such as RNA-directed DNA methylation to restrict their activity (Matzke & Mosher, 2014). Because TEs can act as transcriptional regulators (Butelli et al., 2012) and also attract epigenetic regulation such as DNA-methylation and histone modifications to their insertion site (Sigman & Keith Slotkin, 2016), transposition events can substantially alter host gene expression in plants (Joly-Lopez & Bureau, 2014; Roquis et al., 2021). Thus, TE-induced phenotypic diversity can not only be explained by genetics but also be based on altered epigenetic regulation (Domínguez et al., 2020; Dubin et al., 2018; McClintock, 1984).

Importantly, the phenotypic variation generated by TEs can arise over very short time scales, even within one or a few generations, due to heritable transpositional bursts (Feschotte et al., 2002). Transpositional bursts are large numbers of simultaneous transpositions of TEs that are triggered by challenging situations, including genomic or environmental stress (Ito et al., 2011; Kidwell & Lisch, 1997; Maumus et al., 2009; McClintock, 1984; Rey et al., 2016; Wessler, 1996). Hence, even originally genetically (quasi-) uniform populations (e.g. newly established small populations from a limited diaspora, selfing or clonal individuals) can potentially develop substantial and rapid phenotypic variability due to stress-induced mobilization of TEs (e.g. Belyayev et al., 2010; Domínguez et al., 2020). Overall, TEs can contribute to increasing the phenotypic variation, or, in other words, enhancing the diversity of ecologically important (i.e. functional) traits in the population (i.e. functional diversity).

While the effect of TEs on plant phenotypic variation has been studied almost exclusively at the level of individuals (either from an ecological or evolutionary perspective), there is scarce information on the effect of TEs on the functioning of plant populations or whole ecosystems. Theoretically, such intraspecific functional diversity in a population could have a similar effect to that produced by interspecific

functional diversity, that is, species diversity in a community (Cadotte, 2017; Loreau & Hector, 2001). In a within-population context, mixtures of individuals differing in the number and positions of TEs in the genome, by increasing the functional diversity of the population, could be more productive and resistant than monocultures consisting of individuals with identical numbers and positions of TEs. Functional diversity mechanisms, though common in plant populations, are unexplored from the TE's perspective. It is thus highly desirable to test whether TE-generated diversity affects the population's functioning similarly to species diversity or genetic diversity effects.

In our study, we took advantage of available *Arabidopsis* lines (further referred to as TE lines) created by Thieme et al. (2017). TE lines were obtained by inducing the mobilization of the endogenous *ONSEN* (AtCOPIA78) retrotransposon by applying heat stress and epigenetic drugs to the Col-0 accession (heat-responsive copia-like retrotransposon, Cavrak et al., 2014; Ito et al., 2011; more details on TE line creation are provided in Methods or Thieme et al., 2017). Importantly, the novel *ONSEN* copies are stable in their positions in DNA and heritable over at least three generations (Thieme et al., 2017). From the original pool, we used 20 TE lines, for which we characterized several functional traits important for species coexistence and ecosystem functioning. We constructed populations that differed in the number of TE lines: populations were composed of one TE line ('monocultures') or two, four or 16 different TE lines ('mixtures'). Then, we subjected the designed mixtures and monoculture populations to different abiotic and biotic conditions (control, drought, interspecific competition or a combination of drought and competition). This design allowed us to answer whether there is a substantial effect of TE diversity on the productivity and resistance of plant populations to abiotic and biotic stress. Specifically, we tested (T1) to what extent TE lines differed in terms of key functional traits associated with plant fitness and ecosystem functions; (T2) whether an increasing number of TE lines increased the functional diversity of populations and enhanced their functioning (increased *Arabidopsis* productivity and decreased performance of interspecific competitors); and (T3) whether this effect was consistent across abiotic conditions (changes in water regimes). Such an effect of functional diversity could be attributed to niche complementarity effects (Cadotte, 2017; Díaz et al., 2007). Finally, we also tested (T3) whether the effect of specific TE lines and their characteristics (corresponding to the so-called 'selection effect'; Loreau & Hector, 2001) affected population functioning beside the effect of diversity, estimated by either the number of TE lines or functional diversity (see T2).

2 | MATERIALS AND METHODS

2.1 | Plant material: TE Lines

TE lines were derived from an *A. thaliana* Col-0 accession that was germinated and transiently grown on a medium containing zebularine and α-amanitin. Zebularine is a cytidine analogue known to inhibit DNA-methyltransferases in plants, which leads to a decrease in DNA-methylation resulting in de-repression of TEs (Baubec et al., 2009), while α-amanitin inhibits RNA polymerase II (Pol II), which has been suggested to repress the *ONSEN*-TE (Thieme et al., 2017). The combined transient treatment of seedlings with both drugs together with an exposure to heat stress led to the mobilization of *ONSEN*, which resulted in an increase in genomic *ONSEN* copies in DNA (Thieme et al., 2017). From the list of available TE lines, we selected 20 lines of the 4th self-pollinated generation, with the total number of *ONSEN* copies ranging from 8 (endogenous copies of Col-0 accession) to 60 (Thieme et al., 2017). Five out of the 20 TE lines were considered controls because they originate from plants that were exposed either to heat stress or epigenetic drugs, that is, not to the simultaneous effect of the two factors, which is needed for *ONSEN* mobilization. Although these control lines did not phenotypically deviate from the rest (see later, Figure 1 and Figure S2), we included them in the population mixtures to account for potential unknown effects of heat stress or epigenetic drugs on plant phenotype. Thus, for simplicity, we further consider them as TE lines in our study (TE lines 15–20). At the time, in the data analysis phase, we took into account the potential effects of these lines by different means.

In addition to mobilizing the *ONSEN*, applied chemicals (e.g. Liu et al., 2015) and/or heat stress (e.g. Belfield et al., 2021; Lu et al., 2021) could potentially induce stochastic genetic variation that contributes to the phenotypic variation observed in TE lines. For example, zebularine is known to form irreversible adducts with DNA, leading to random alterations in the DNA sequence (Bhalla & Navada, 2016). Additionally, elevated temperatures are likely to amplify the mutagenic effects of oxidative stress or radiation by increasing the rate of errors in DNA repair (Belfield et al., 2021)To compare the specific role of *ONSEN* mobilization and other potential genetic variation (single nucleotide polymorphisms (SNPs) and insertion–deletion mutations (indels), further referred to as non-*ONSEN* variation) on traits of each TE line, we performed whole genome sequencing for all TE lines. The molecular approach together with the results (Tables S1–S3; Figure S1) are presented in the Supporting Information.

2.2 | Biodiversity-population functioning experiment

The study was carried out in a heated greenhouse of the Institute of Botany in Průhonice, Czechia, from January to April 2019. From the pool of 20 TE lines, we established populations of *A. thaliana* with differing diversity, achieved by manipulating the number of different lines sown in each population. Populations consisted of 48 seeds sown into pots (12 cm in diameter), either of the same TE line (i.e. monocultures) or mixtures of two TE lines (24 seeds per TE line), four TE lines (12 seeds per TE line) and 16 TE lines (three seeds per TE line). For the mixtures, for each diversity level, we selected TE lines randomly (random generation of combinations) with the condition

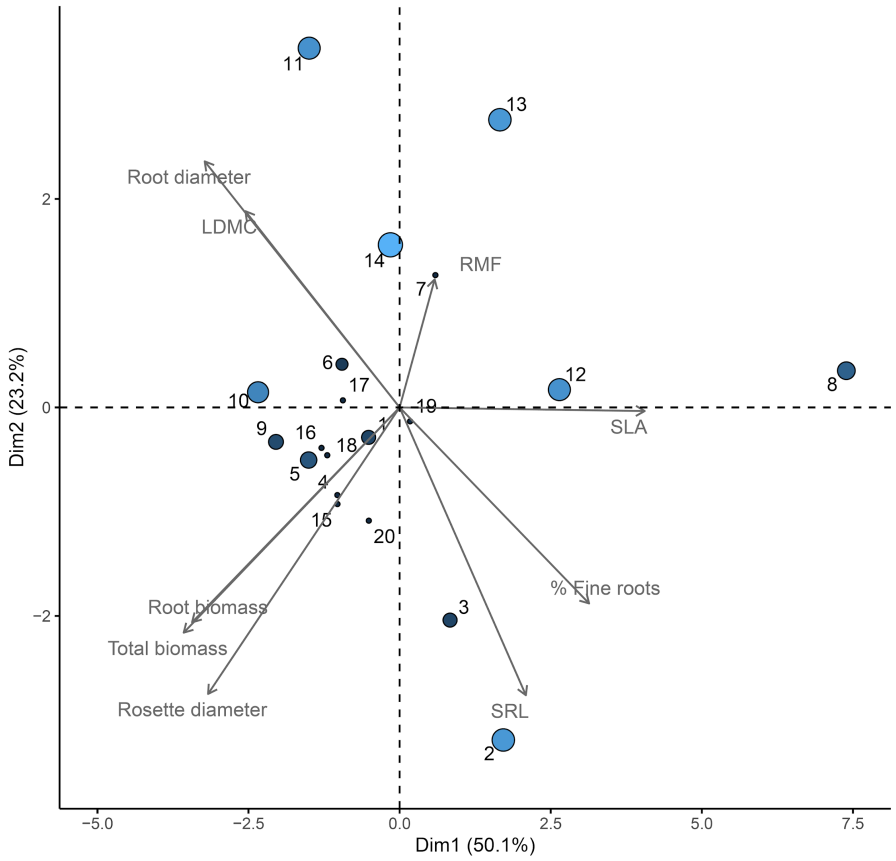

FIGURE 1 Principal component analysis (PCA) showing relationships among functional traits of transposable element (TE) lines. Grey arrows represent the traits used to build the principal component, that is, rosette diameter, root and total individual biomass (together above-ground and root biomass); specific leaf area (SLA), specific root length (SRL) and percentage of fine roots (% Tiny roots), which are typical traits indicative of a resource acquisitive strategy; and root mass fraction (RMF) and leaf dry matter content (LDMC), which are indicative of a resource conservative strategy. The different size and colour of the points, from small dark ones to bigger blue ones, represent the number of unique *ONSEN* insertions of each TE line (see Table S1).

that all 20 TE lines are equally represented (i.e. across populations within each treatment combination, see next). Further, all the populations were randomly assigned to one of the four following treatments that differed in the abiotic and biotic conditions: control—no manipulation; drought—population watered only if showing significant drought stress, that is, leaves were wilting, competition—we planted three seeds of *Plantago lanceolata* and 15 seeds of *Poa annua* into the pot; drought + competition—we combined drought and competition described above.

The monoculture for each TE line was replicated four times per treatment (4 × 20 × 4 = 320), and the mixtures were replicated 20 times per treatment and diversity level (20 × 4 × 3 = 240). Thus, the final set-up comprised a total of 560 experimental populations from 26,880 sown seeds of *A. thaliana* that resulted in 15,390 harvested individuals 12 weeks after the establishment of the experiment. At the end of the experiment, we harvested above-ground biomass in all pots and recorded the number of *A. thaliana* individuals in each population. The biomass of *A. thaliana* and, when present, both competitors (*Plantago lanceolata* and *Poa annua*) were separated, dried at 60°C for 48 h and weighed. *Arabidopsis'* biomass and competitors' biomass (of each pot) were used as estimates of population functioning: (a) *Arabidopsis* total productivity and (b) the performance of the competitors, respectively.

The lowest germination rate was around 65% for some lines (determined in a germination trial prior to the population's construction), suggesting that at least one individual per line germinated in each mixture. The number of harvested individuals of *A. thaliana* in monocultures showed that the lowest establishment rate was 35% of sown individuals of TE line 1 and the highest establishment was 78% of sown individuals of TE line 12, $F = 5.77$, $p < 0.0001$. We used a standardized soil substrate mixed with sand in a 1:1 volume ratio. We distributed seeds randomly and evenly on the soil surface using two layers of tiny mesh. All pots were placed in a cold chamber room (4°C) for 4 days for stratification before being moved to the heated greenhouse. In the greenhouse, we set the day regime to 9–10 h (ambient light conditions) during the first month and to a long day regime of 14 h for the rest of the experiment (artificial light supplemented in the morning and late afternoon). The mean temperature was maintained at 23/18°day/night.

2.3 | Phenotyping of TE lines

To approximate the phenotypic variation of the 20 selected TE lines, we set up a parallel study to the main experiment where we screened the phenotypes of each of the lines and measured a number of plant functional traits known to affect an organism's fitness, species coexistence and ecosystem functions (Adler et al., 2014; de Bello et al., 2010). This separate experiment was set up because the measurements were destructive. In this experiment, we grew 10 replicate plants of each line (10 replicates × 20 lines, 200 plants in total) alone in the controlled environment of a growth chamber (Fitotron® Plant Growth Chamber) set to an 8 h day with a temperature regime of 22°/18°C day/night. We used the same substrate as in the main

study. We changed the positions of all pots on a weekly basis. After 5 weeks from germination, we measured the rosette diameter (cm) and the total dry biomass of each individual (including both above-ground and root biomass), as well as several above- and below-ground vegetative traits connected with the so-called 'plant economic spectrum' (Díaz et al., 2016; Reich, 2014), reflecting resource use strategies in plants. For each plant, one leaf was scanned to estimate the leaf area and weighed for fresh mass and dry mass after drying at 60°C (48 h). We used these measurements to estimate specific leaf area (SLA; leaf area per dry mass, mm^2/mg) and leaf dry matter content (LDMC; leaf dry mass per leaf fresh mass, mg/mg). In addition, roots were carefully extracted, washed and scanned at 1200 dpi with an Epson Perfection 4990 scanner. From the scans, total root length, average root diameter (mm) and the distribution of root length per different diameter classes were determined by using the image analysis software WinRHIZO Pro, 2008 (Regent Instruments Inc.). After scanning, roots were dried for 48 h at 60°C and weighed. We used these measurements to estimate root biomass allocation (i.e. root mass fraction; RMF; root biomass per total biomass, g/g), specific root length (SRL; root length per dry mass, m/g) and percentage of very fine roots (roots with a diameter <0.2 mm from the total).

2.4 | Data analysis

2.4.1 | Phenotypic differences across TE lines (T1)

To assess phenotypic differences across TE lines (T1) we followed two approaches. First, using the 10 replicate plants of each TE line, we tested the variation of every single trait (i.e. non-highly correlated ones, Pearson coefficients <0.7; Figure S2; total biomass, RMF, SLA, LDMC, SRL and % of fine roots) across lines, with line identity as a predictor in a one-way ANOVA. Tukey post-hoc tests were used to verify significant differences between lines (Figure S3). Second, we tested trait differences across all traits together. This was done by computing a multivariate trait dissimilarity between each pair of the 200 individual plants using Euclidean distance based on scaled trait values (i.e. values were centred by the mean and divided by one standard deviation unit for each trait). Then we used the multivariate trait dissimilarity as a response variable and line identity as a predictor in a PERMANOVA (Anderson, 2001), which is the non-parametric corresponding multivariate approach to univariate ANOVA, although in this case the significance value is computed by permutations.

Then, we tested the effect of *ONSEN* insertions versus non-*ONSEN* genetic variation (i.e. SNPs and indels) on trait differences across lines. Specifically, we tested the effect of the number of unique (i.e. not shared insertions by any other TE line) *ONSEN* insertions versus non-*ONSEN* variants on trait dissimilarity between TE lines using a PERMANOVA test based on randomization of dissimilarity (in these cases of trait dissimilarity across lines), particularly adapted to tests on dissimilarity between samples. With this approach, we could test the variance explained by *ONSEN* versus non-*ONSEN* insertions on trait dissimilarity and the *p*-value of their specific effects. The non-*ONSEN* effect was tested both as SNPs and indels and their sum, although only the latter is presented for simplicity and because the results were convergent. We repeated the test using directly the (square-root transformed, to improve the normality of the response) trait dissimilarity obtained from the Euclidean distance approach after extracting the two main axes of variation of the PCA shown in Figure 1.

2.4.2 | Diversity effect on population functioning (T2)

Number of TE lines diversity effect

We applied a number of different approaches to assess the effect of the diversity of TE lines on productivity and competitors' performance. First, we assessed the effect of the number of TE lines in the population (i.e. 1, 2, 4, 16) on productivity (total *Arabidopsis*' population dry biomass) and on the performance of the competitors (dry biomass of *Plantago lanceolata* and *Poa annua*). To compare productivity across treatments and TE diversity (i.e. number of TE lines) we fitted a linear model with treatment (four levels: control, drought, competition and drought + competition) and number of lines (1, 2, 4 and 16) and their interaction as predictors of productivity. The number of lines was log-transformed so that the tested relationship would be linear. A significant interaction term would indicate that diversity effects on population functioning (i.e. productivity and resistance to competitors) are different across treatments. The whole genome sequencing analysis, which was performed after the execution of the main diversity study, revealed that lines 4 and 7 had no additional *ONSEN* copies in their genome (Table S1) and, thus, were ecologically comparable to controls in terms of the number of *ONSEN* copies. Therefore, they are unlikely to have contributed unique *ONSEN* insertions to diversity effects. To validate whether these lines (L4, L7) together with controls did not contribute to diversity effects, we ran an additional analysis but only with the 'true' ONSEN diversity, that is, the number of lines that truly differed in the number of unique *ONSEN* copies as a predictor (i.e. with unique *ONSEN* insertions; further referred to as the Number of lines with *ONSEN* insertions; Model 7 in Table S4, Figure S4). Hence, the number of lines (i.e. diversity level) was reduced in some populations, now ranging up to 13.

Conditional plots (using the visreg function of the {visreg} R package) were chosen to visualize the effect of both experimental factors. Since the interaction term between treatment and diversity was not significant (Table S4), the partial effects of treatments are plotted under the median values of diversity, and the ones of diversity are visualized under competition treatment.

2.4.3 | Functional trait diversity effect

Then, we assessed the effect of the functional trait diversity resulting from mixing TE lines on productivity and competitors' performance. To do so, similar models to the ones described in the previous

section were employed, using treatments and functional diversity instead of the number of TE lines as predictors (i.e. the same test but with functional diversity instead of a number of TE lines in the model) to explain both productivity and competitors' performance. The following steps were taken to compute functional trait differences between TE lines within each pot and compute functional diversity: We first computed for each measured trait its average for the 10 replicates for each of the 20 TE lines. Following this step, we used a Principal Component Analysis or PCA, to inspect the main axes of trait variation across TE lines, which also helped to visualize the main correlations between traits (for all results, see Figure S2). Using trait averages per TE line, we then computed a mean trait dissimilarity between each pair of TE lines (Euclidean distance based on scaled trait values). Based on these values, we could compute an average trait dissimilarity between TE lines for each pot using the commonly used Rao index of functional trait diversity (de Bello et al., 2016). The index provides zero dissimilarity for monocultures (as the dissimilarity within a TE line is considered to be zero). The effect of functional diversity can be interpreted as a biodiversity effect attributed to niche complementarity (Cadotte, 2017; Díaz et al., 2007).

2.4.4 | Effect of specific TE lines and their traits on population functioning (T3)

Parallel to these analyses, we tested whether the presence of specific TE lines in the mixtures influenced *Arabidopsis* productivity and competitors performance. We did this by first running a model selection (based on the most parsimonious stepwise selection process using AIC's model fit) with either *Arabidopsis* productivity or competitor's performance as dependent variables and treatments, plus the presence of the 20 lines as predictors. This led to the identification of a few lines whose presence affected productivity or competitor performance more strongly. Following this step, we combined the models described for T2 (with treatments and diversity of the number of TE lines as predictors) to include those specific TE lines (stepwise selection process using AICs). The effect of specific lines on the functioning of populations can be interpreted in this case as a biodiversity effect due to selection effects (Loreau & Hector, 2001).

Similarly, to test whether specific functional traits of the TE lines, rather than line-specific identity, influenced productivity and competitor performance (i.e. a functional trait-based approach), we ran an identical model selection including the population functional trait means (i.e. average value of each of the six functional traits per population) instead of the 20 lines as predictors. The improved predictions of these new models, that is, comparing T3 against T2 in the ones using TE lines (Models 1, 3 and 5 in Table S4) and in the ones using a functional trait-based approach (Models 2, 4 and 6 in Table S4) separately, were assessed by checking changes in R^2 between models as well as the Akaike information criterion (AIC). For all the models, a drop of >2 AIC points was considered to be an improved model (Burnham & Anderson, 2004). For all models, homoscedasticity and normality of the residuals were checked visually via qq-plots and residuals versus fitted plots to ensure assumptions were followed.

3 | RESULTS

3.1 | Phenotypic differences across TE lines (T1)

The experimentally induced bursts of *ONSEN* TE elements in the *Arabidopsis* Col-0 accession caused phenotypic differences associated with important functional traits (T1). TE lines differed in almost all measured functional traits except LDMC (Figure S3). The highest variation was recorded for total plant biomass (above-ground and root biomass). Overall, TE lines differed in their multi-trait phenotypic variability (TE line identity explained 35% of the trait dissimilarity between individual plants; PERMANOVA $R^2 = 0.35$, $p = 0.001$). The main differences between TE lines were associated with the so-called plant economic spectrum (the first axis of the PCA axis, explaining ~50% of trait variation between lines; Figure 1). The control lines (L 15–20) and L4 and L7 with no *ONSEN* mobilization (Figure 1, Table S1 and Figure S3) did not differ in functional traits, suggesting a limited effect of non-*ONSEN* genetic variation on the phenotypes of the lines.

The number of *ONSEN* transpositions significantly affected the trait variation of TE lines, whereas the non-*ONSEN* related genetic variation had no effect on the trait variation of TE lines (Tables S2 and S3). *ONSEN* insertion explained around 5% of the total variability in traits across samples alone and 8% together with non-*ONSEN* insertions, which alone explained about 1% of the total variability (Figure S1). These results, rather convergent with the ones obtained with PERMANOVA, show the relatively greater effect on *ONSEN* (up to 13%, Tables S2 and S3) with respect to non-*ONSEN* (up to 6%, Tables S2 and S3) and the partial overlap, that is, covariation, between their effects.

3.2 | Diversity effect on population functioning (T2)

Compared to control conditions, all treatments (i.e. drought, competition and drought & competition) had a negative effect on the productivity of *A. thaliana* populations (Figure 2a; Model 1 in Table S4). The strongest reduction in productivity was observed in the treatment that combined biotic and abiotic stress: competition and drought. The performance of competitors (biomass of *Plantago lanceolata* and *Poa annua*) also decreased with drought (Figure 2c) and decreased with increasing biomass of *A. thaliana* (Figure S3). Mixtures of *Arabidopsis* TE lines were more productive than monocultures (Figure 2b), leading to positive overyielding for productivity (Figure S5; i.e. lines in mixtures produced more biomass compared to the averaged expectation from their biomass when grown alone). This effect was irrespective of the treatment (no significant interaction between treatment and number of TE lines; Model 1 in Table S4) although the effects tended to be slightly lower

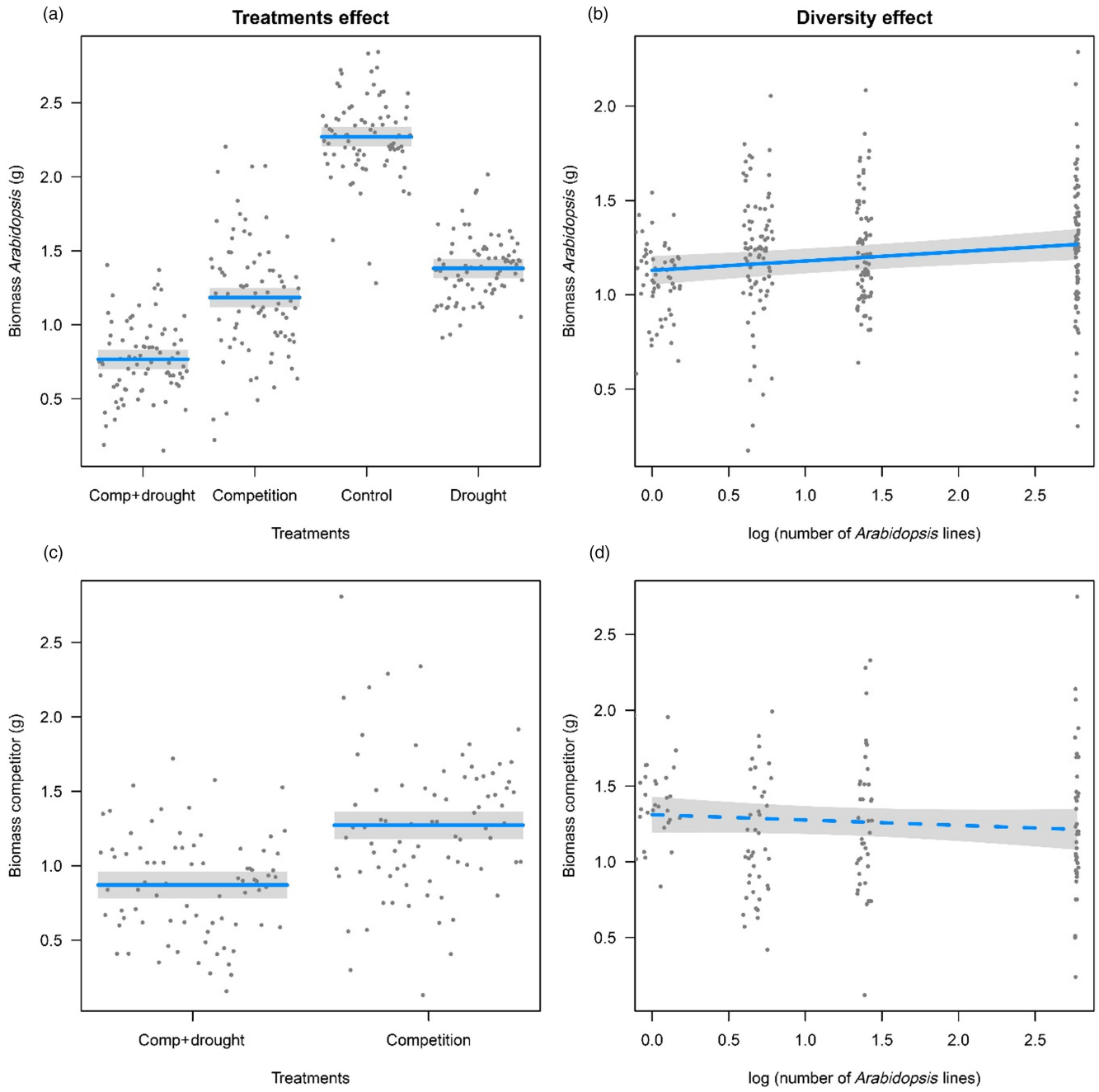

FIGURE 2 Conditional plots of both experimental factors: treatment (a and c) and diversity, measured as the number of transposable element lines in the population (b and d) on the biomass of *Arabidopsis* (a and b) and biomass of the competitors (c and d). Each panel represents the partial effect of a single factor on the response variable when others are held constant, that is, to their mean diversity value for panels (a and c) and competition treatment for panels (b and d). The coloured lines represent the mean values or slope predicted by the selected models, solid or dashed when the predictor was significant in the model or not, and enveloped by the 95% confidence interval shaded in grey.

under drought conditions. Mixtures of *Arabidopsis* TE lines, compared to monocultures, also reduced the competitors' performance, although not linearly (Figure 2d) and also irrespective of drought treatment (no significant interaction between treatment and number of TE lines; Model 1 in Table S4). Although mixtures of *Arabidopsis* TE lines were more productive and induced lower performance in competitors than monocultures, the increasing number of TE lines within the mixtures did not affect their functioning (i.e. neither productivity nor performance of competitors). In other words, mixtures of two TE lines had comparable functioning to most diverse mixtures (Figure 2b). The alternative analysis testing the number of lines with *ONSEN* insertions (i.e. excluding lines 4, 7 and 15 to 20) provided a similar result, which is just presented in the Supporting Information (Model 7 in Table S4 and Figure S4B,C).

As expected, phenotypic variability of populations increased with increasing numbers of TE lines (Pearson correlation between

the number of TE lines and functional diversity, $r=0.67$, $p<0.001$; Figure 3a and Figure S4A just considering the number of lines with *ONSEN* insertions). Thus, the effect of functional diversity on productivity and competitor performance (Figure 3b,c) was comparable to the effect of the number of lines (Figure 2b,d). In fact, models using either the number of TE lines or functional diversity explained a very similar proportion of the variance (Models 1 vs. 2 in Table S4; for productivity: $R^2=0.77$ using either the number of TE lines or functional diversity; and for competitor's performance: $R^2=0.19$ using the number of lines as a quantitative predictor or $R^2=0.21$ using functional diversity).

3.3 | Effect of specific TE lines and their traits on population functioning (T3)

We assessed whether individual TE lines or their specific traits affected population performances by adding specific lines and population trait means to the models, alone and together with the corresponding diversity estimates (number of lines or functional diversity, respectively). Generally, the inclusion of specific lines slightly improved predictions for both *Arabidopsis* productivity and competitor's performance (Models 3 and 5 in Table S4). Specifically, lines 8 and 15 (control) had, respectively, a negative and positive significant effect on *Arabidopsis* productivity, while lines 2 and 5 had a positive and line 11 a negative effect on the competitor's performance (Model 5 in Table S4). The inclusion of functional traits in the populations, however, only improved predictions for *Arabidopsis* productivity (Models 4 and 6 in Table S4). *Arabidopsis* populations formed by TE lines with lower SLA tended to produce more biomass, but competitors' performance was not affected by the functional characteristics of *Arabidopsis* populations (Models 4 and 6 in Table S4).

4 | DISCUSSION

We investigated the ecological role of phenotypic variation in *Arabidopsis thaliana* populations attributed to experimental *ONSEN* retrotransposon bursts. Such intraspecific functional diversity showed different effects on the functioning of populations. We show that TE-generated variation is mostly responsible for shifts in ecologically important functional traits such as plant biomass (both above- and below-ground) and other traits associated with the so-called plant economic spectrum (e.g. SLA and SRL, see Figure 1). Importantly, we showed that an increasing number of TE lines, that is, lines with differing numbers of *ONSEN* retrotransposon copies integrated at different places in the genome, increased functional diversity (see Figure 3b) as well as total population productivity (see Figure 2b). Moreover, higher functional diversity in *Arabidopsis* populations reduced the performance of their competitors (see Figure 2d), meaning that more diverse populations were more resistant to interspecific competitors.

Our investigation indicates that the transpositions of the *ONSEN* retrotransposon within individual TE lines predominantly shaped various functional traits aligned with the plant economic spectrum (Díaz et al., 2016; Reich, 2014), reflecting the resource-use strategies of plants. While this is the case, we acknowledge that other genetic variations, possibly related to the construction of TE lines, such as SNPs or indels brought about by chemical and heat stress mutagenic effects, could also contribute to the variation of functional traits. However, the impact of such non-*ONSEN* related-variations on trait variation was not found to be significant, leading us to infer that TE-generated variation, more so than SNP- or indel-generated variation, drove the functional divergence among individuals for traits such as SLA, SRL or biomass. This variation fostered niche and resource partitioning between TE lines, which in turn amplified the productivity of mixtures by

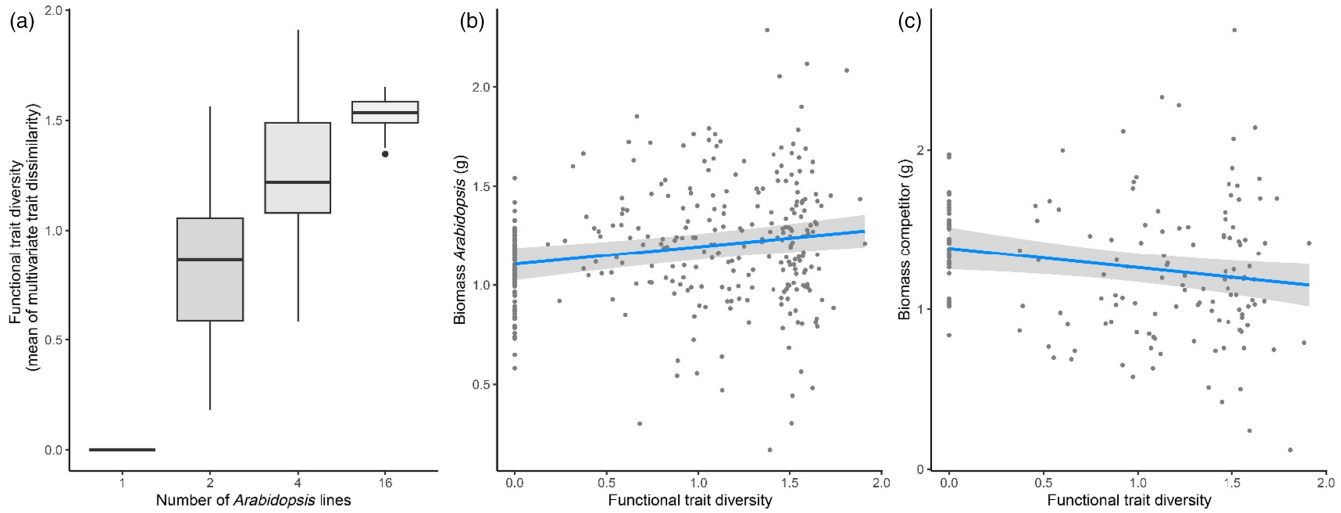

FIGURE 3 (a) Corresponding functional diversity of each of the populations resulting from mixing differing numbers of transposable element lines. (b and c) Partial effect of diversity, measured as functional diversity, on the biomass of *Arabidopsis* (b) and the biomass of the competitors (c). In regression plots, solid coloured lines represent the slope estimate and 95% confidence intervals predicted by the selected models.

optimizing the use of limited resources—a mechanism commonly referred to as 'complementarity' (Hooper et al., 2005). Nevertheless, we emphasize that, although potentially less crucial, other genetic variations such as SNPs or indels should not be completely disregarded in their contribution to functional trait variation.

Although the observed diversity effect seems to be mainly driven by functional diversity, pointing in the direction of complementarity (Díaz et al., 2007), we also identified specific TE lines and traits that had significant effects on the productivity of mixtures. This indicates that the probability of including a key TE line in mixtures (specifically TE lines 8 and 15, the latter a control line without additional *ONSEN* insertions; Table S1), the so-called selection effect (Loreau & Hector, 2001), also played a role in the observed diversity effects. However, only characteristics of TE line 8 strongly deviated from the rest (i.e. smallest and highest SLA; Figure S3), suggesting that although many traits linked to resource foraging strategy and competitive ability of the plants were measured, they were insufficient to completely characterize niche differences among TE lines (Cadotte, 2017; Kraft et al., 2015; Kunstler et al., 2016). Nevertheless, we were able to detect an effect on population productivity by the average SLA of the population, which is a trait known to be related to the resource foraging strategy of the plant (i.e. niche segregation), as well as to the fitness or competitive ability of individuals (Kraft et al., 2015; Puy et al., 2021).

Besides increasing population productivity, it is generally acknowledged that increased phenotypic diversity usually increases the resistance of populations to environmental stress (e.g. Grime, 2001 or Tilman et al., 2006). This was, however, not the case for our study, as we did not observe a significant interaction between diversity level and treatment. This means that, although our treatments of contrasting abiotic and biotic environments (drought, competition and both in combination) were clearly stressful for the populations of *Arabidopsis* (i.e. biomass production decreased by more than 50% compared to control conditions), diversity did not ameliorate the negative effect of stressors when compared with monocultures. In other words, all populations were similarly affected by stressors despite their different levels of diversity. However, what we did find is that interspecific competitors produced less biomass in mixtures than when grown in *Arabidopsis* monocultures, irrespective of whether mixtures were formed by 2, 4 or 16 TE lines (see Figure 2d). This decreased performance of competitors, although not translating into an ameliorating effect of competition on the productivity of *Arabidopsis* populations, may indicate that diversity enhances the resistance to invasion by competitors and population performance.

In nature, small and/or declining populations are often at risk of losing genetic diversity due to inbreeding or random genetic drift. Low genetic diversity is inevitably connected with an increased risk of populations' extinction (Buckley & Puy, 2022). Our study outlined that TEs can be beneficial to plant populations by creating functional diversity that promotes population functioning and stability in addition to generating heritable (epi)genetic variation on which selection can act (Lisch, 2009). This indicates that commonly reported maladaptive phenotypic consequences of TEs on individuals (e.g. Vinogradov, 2003) can be, in particular situations, ameliorated or even overturned at the population level by the functional diversity effect. Moreover, considering that challenging situations, including genomic or environmental stress, trigger transpositional bursts, TEs can be seen as an insurance mechanism for populations to dramatically increase their functional diversity in response to stressors, allowing rapid adaptation to changing ecological conditions (Baduel et al., 2021; Belyayev, 2014). This mechanism might be especially crucial for the persistence of populations with limited dispersal capacity at the trailing edge of their distribution or suitability range. TE-generated functional diversity can thus provide the necessary time for adaptation in threatened populations, which ultimately can facilitate their survival.

In summary, our proof-of-principle study underscores the potential of TE-generated functional diversity to influence population functioning akin to effects observed in genetically diverse populations (Crutsinger et al., 2006; Ehlers et al., 2016). However, it's essential to note that not all the diversity effects we observed can be solely accredited to *ONSEN* insertions. As disclosed by comprehensive genome screening, the TE lines exhibited variations at the SNPs and indels level—referred to as non-*ONSEN* variation—which are likely the result of the mutagenic effects of zebularine, α-amanitin and heat stress (Belfield et al., 2021; Liu et al., 2015; Lu et al., 2021). Despite this, our analysis identified the influence of non-*ONSEN*-driven genetic variation on trait variation in TE lines as minimal and statistically non-significant (Supporting Information, Tables S2 and S3). Moreover, control lines (lines 15–20) and lines 4 and 7, which lacked additional *ONSEN* copies in their genome (Figure 1 and Figure S2), exhibited comparable phenotypes (Figure 1 and Figure S2). This suggests a limited effect of non-*ONSEN*-driven genetic variation on the functional traits of TE lines. Interestingly, *ONSEN* transposition shows a pronounced preference for exons and regions rich in the histone variant H2A.Z (Quadrana et al., 2019; Roquis et al., 2021), an attribute anticipated to yield significant phenotypic implications. Additionally, several studies underscore *ONSEN's* direct role in generating transcriptomic and phenotypic variation in *A. thaliana* (Baduel et al., 2021; Ito et al., 2011, 2016; Quadrana et al., 2019; Roquis et al., 2021; Thieme et al., 2017, 2022). Given these findings, we deduce that the *ONSEN* effect, inclusive of its influence on epigenetic variation, was likely the central driver in generating functional diversity in our experimental populations. Our investigation sheds light on the essential ecological role of *ONSEN* transpositions. Yet, the extent to which the diversity effects of transposons are general in other plant species remains uncertain. Consequently, we encourage more extensive research in this area to increase our understanding of how transposons affect population functioning and ultimately ecosystems as a whole.

AUTHOR CONTRIBUTIONS

Vít Latzel and Javier Puy designed and performed the study. Javier Puy, Francesco de Bello, Lars Gotzenberger and Michael Thieme

analysed the data. Michael Thieme and Etienne Bucher provided plant material. Vít Latzel and Javier Puy wrote the first draft of the manuscript and all authors contributed substantially to revisions. Vít Latzel and Javier Puy made equivalent contributions and should be considered joint first authors.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest. Francesco de Bello is an Associate Editor for the *Journal of Ecology* but took no part in the peer review or decision-making process for this manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available at Figshare: https://doi.org/10.6084/m9.figshare.23816931.v1 (Latzel et al., 2023).

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SUPPORTING INFORMATION

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

Table S1. The number of unique *ONSEN* insertions, unique SNPs and unique indels of TE lines. Unique non-*ONSEN* variation is a sum of SNPs and indels.

Table S2A. The effect of the number of *ONSEN* versus non-*ONSEN* insertions on trait dissimilarity using a PERMANOVA test. The dissimilarity between lines is based on the Gower distance approach.

Table S2B. The effect of the number of *ONSEN* versus non-*ONSEN* insertions on trait dissimilarity using a PERMANOVA test. The dissimilarity between lines is based on the Euclidean distance approach.

Table S3. The effect of the number of *ONSEN* versus non-*ONSEN* insertions on trait dissimilarity using a PERMANOVA test. The dissimilarity between lines is based on the PCA scores of the first two axes (see Figure 1).

Table S4. Summary of performances of all the models conducted to predict *Arabidopsis* productivity and competitor's performance based on treatment, population diversity measured as the number of lines (Model 1), functional diversity (Model 2) or the number of lines with *ONSEN* mobilization (Model 7) and the presence of specific TE lines (Model 3), population trait means (Model 4) or average number of private insertions (Model 8) and their respective combinations (Model 5, 6 and 9).

Figure S1. Variance partitioning of trait variation explained by *ONSEN* vs. non-*ONSEN*.

Figure S2. Trait correlations between functional traits using TE lines means.

Figure S3. Difference between pairs of TE lines in the different functional traits measured.

Figure S4. (A) Corresponding functional diversity of each of the populations resulted from mixing just the number of TE lines with *ONSEN* insertions. (B and C) Partial effect of diversity, measured as a number of TE lines in the population with *ONSEN* insertion, on the biomass of *Arabidopsis* (B) and biomass of the competitors (C).

Figure S5. Effect of treatment and number of TE lines on overyielding of the mixtures (how much better mixtures perform than monocultures) calculated as net diversity effect following Loreau and Hector, 2001 (i.e. for a given mixture, net diversity effect is the difference between the observed productivity and the expected productivity, the latter being the productivity of the different TE lines that comprise the population in the corresponding monoculture).

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