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RESEARCH ARTICLE

Beyond trait distances: Functional distinctiveness captures the outcome of plant competition

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Abstract

1. Functional trait distances between coexisting organisms reflect not only complementarity in the way they use resources, but also differences in their competitive abilities. Accordingly, absolute and relative trait distances have been widely used to capture the effects of niche dissimilarity and competitive hierarchies, respectively, on the performance of plants in competition. However, multiple dimensions of the plant phenotype are involved in these plant–plant interactions (PPI), challenging the use of relative trait distances to predict their outcomes. Furthermore, estimating the effects of competitive hierarchy on the performance of a group of coexisting plants remains particularly difficult since relative trait distances relate to the effects of a focal plant on another.
2. We argue that trait distinctiveness, an emerging facet of functional diversity that characterizes the eccentric position of a species (or genotype) in a phenotypic space, can reveal the unique role played by a given individual plant in a group of competing plants. We used the model crop species *Oryza sativa* spp. *japonica* to evaluate the ability of trait distances and trait distinctiveness to predict the outcome of intraspecific PPI on the performance of single genotype and genotype mixtures. We performed a screening experiment to characterize the phenotypic space of 49 rice genotypes based on 11 above-ground and root traits. We selected nine genotypes with contrasting positions in the phenotypic space and grew them in pots following a complete pairwise interaction design.
3. Relative distances and distinctiveness based on traits associated with light competition were by far the best predictors of the performance of single genotypes—taller

genotypes that acquired resource faster being the best competitors—while absolute trait distances had no effect. These results indicate that competitive hierarchy for light dominates PPI in this experiment. Consistently, trait distinctiveness in plant height and age at flowering had the strongest, positive effects on mixture performance, confirming that functional distinctiveness captures the effects of trait hierarchies and asymmetric PPI at this scale.

4. Our findings shed new light on the role of trait diversity in regulating PPI and ecosystem processes and call for a greater consideration of functional distinctiveness in studies of coexistence mechanisms.

KEYWORDS
biodiversity–ecosystem functioning, competitive dominance, crop genotype mixtures, functional rarity, symmetric and asymmetric plant–plant interactions

1 | INTRODUCTION

Can we predict the outcome of plant–plant interactions (PPIs) from functional traits? Although this question has long been investigated in ecology (Goldberg, 1997; Grime et al., 1989; Keddy, 1989; Tilman, 1988), there is still no consensual response. The environmental context dependency of PPI (Florianova et al., 2022; Maestre et al., 2009; Suding et al., 2004), coupled with the multifaceted nature of PPI (Mayfield & Levine, 2010; Weiner, 1990) and the fact that the match between traits and PPI varies depending on the particular species concerned (Goldberg & Landa, 1991; Wagg et al., 2017), can explain this lack of consensus. Furthermore, competition studies most often use the performance of single plants in terms of survival, biomass production or reproductive output as the currency of the outcome of PPI (Aarssen & Keogh, 2002), but more rarely examine the performance of the community (e.g. productivity). As a result, while PPIs play a key role in the regulation of species coexistence and ecosystem functioning in both natural and managed communities (Grime et al., 1989; Keddy, 1989; Tilman, 1988), the promise of functional traits to ultimately predict community assembly and ecosystem-level properties (Adler et al., 2013; Lavorel & Garnier, 2002; McGill et al., 2006) remain elusive.

Historically, comparative approaches that screen the diversity of functional trait values across species or genotypes (Figure 1a) aimed at identifying proxies of their competitive abilities (Goldberg & Landa, 1991; Grace, 1990). Some traits were convincingly associated with the effects of plants on resource depletion (e.g. plant height; Gaudet & Keddy, 1988), with subsequent negative impact on the fitness of neighbours (Violle et al., 2009). Other traits were associated with the response of plants submitted to resource depletion by neighbours (e.g. specific leaf area [LA], relative growth rate; Goldberg, 1997; Keddy et al., 1998; Violle et al., 2009). Nevertheless, findings from these comparative approaches varied from one study to another (Navas & Violle, 2009; Wang et al., 2010), which limits their applications in different contexts. More importantly, they were mostly based on the hypothesis that PPIs are hierarchic due to the asymmetric nature of resource depletion (mostly light) at play (Schwinning & Weiner, 1998; Weiner, 1990). Accordingly, better competitors (e.g. taller plants) have disproportional probabilities to outcompete weaker ones through a limitation of resources for the latter. This hierarchy in competitive abilities of species can be captured by the *relative* trait distance between them (trait of plant A − trait of plant B, also known as *hierarchical trait distance*; Figure 1b; Kunstler et al., 2012). However, such a view of PPI is partial since it ignores symmetric interactions among plants (Weiner, 1990), which, under the niche dissimilarity hypothesis, is expected to lead to weaker PPI among distantly related species (or genotypes; Cahill et al., 2008; Macarthur & Levins, 1967; Stubbs & Bastow Wilson, 2004; Violle et al., 2011). In that case, the *absolute* trait distance (|trait of plant A − trait of plant B|) should explain the outcome of symmetric PPI (Figure 1b), plants A and B being hardly impacted by competition if the trait dissimilarity between them is large enough (Kunstler et al., 2012). However, while symmetric PPIs are expected to dominate when competition comes from below-ground resources (Schwinning & Weiner, 1998) but see (Fort et al., 2014), they have been most frequently approached using above-ground trait distances (e.g. Ferenc & Sheppard, 2020; Gross et al., 2007; Kraft et al., 2014). Several root traits are expected to reflect plants' ability to capture and use soil resources (e.g. root length density, specific root length), and as such are good candidates for markers of below-ground PPI (Bergmann et al., 2020; Weigelt et al., 2021). The fact that plants experience both asymmetric and symmetric resource depletion throughout their life cycle (Weiner, 1990), and that different phenotypic dimension can drive both types of PPI, stresses the need to characterize multiple trait dimensions to elucidate the role of trait distances in driving PPI (Kraft et al., 2015).

Using trait distances to capture the effects of symmetric and asymmetric competition on the performance of a group of coexisting plants (e.g. community-level productivity) is a grand challenge in ecology, as illustrated in biodiversity–ecosystem functioning research (de Bello et al., 2021; Garnier et al., 2016). Depending on the nature of PPI, we can make several predictions. Under symmetric PPI, all plants are expected to grow on average better in mixtures than in pure stands provided that niche dissimilarity is

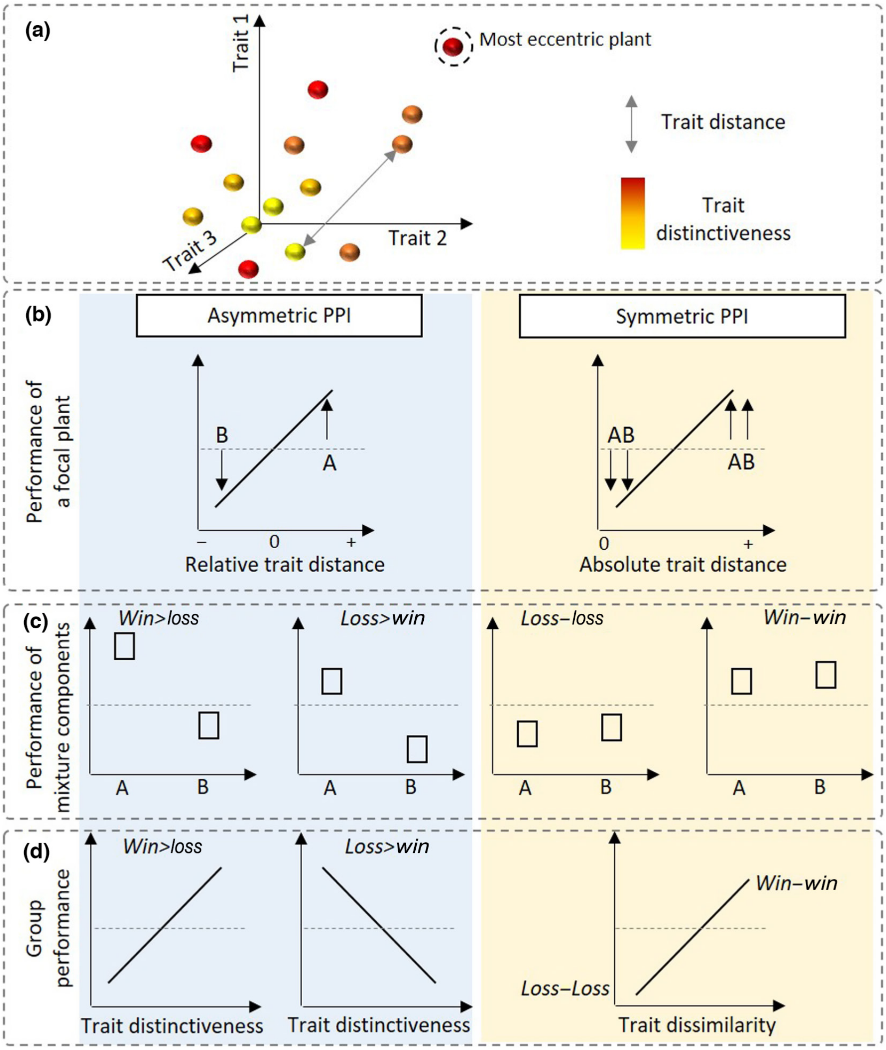

FIGURE 1 Analytical framework to capture the outcomes of symmetric and asymmetric PPIs from trait distances and trait distinctiveness. (a) Characterization of the multidimensional phenotypic space of a plant species. Differences between two plants are captured by Euclidean distances computed on a multidimensional basis (grey arrow as an example). Trait distinctiveness defines the position of each plant compared to all others within the phenotypic space. Notably, it highlights plants having eccentric positions (yellow colour on the yellow-red colour scale) within this space. (b) The effects of asymmetric (blue box) and symmetric (yellow box) PPI on the performance of a focal plant A in interaction with plant B can be captured by relative (trait plant A − trait plant B; 'competition-trait-hierarchy' hypothesis) and absolute (|trait plant A − trait plant B|; 'competition-trait-similarity' hypothesis) trait distances respectively. Under asymmetric PPI, the plant with the most favourable trait value (here plant A) performs better in association with another plant than with itself, while the other plant performs worse in this situation than in association with itself (plant B). Under symmetric PPI, the more different trait values the plants display, the greater their performances when growing together, relative to the performances expected when growing in pure stands. (c) Expected effects of asymmetric and symmetric PPI on the performance of the competing plants A and B. Under asymmetric PPI, the stronger competitor (plant A) produces more biomass than in pure stand (dotted line) while the weaker competitor (plant B) produces less. Plant A wins more biomass than plant B loses (win>loss scenario) or plant B loses more biomass than plant A wins (loss>win scenario). Under symmetric PPI, both plants can be winners (win–win scenario) or losers (loss–loss scenario), depending on the strength of competitive interactions. (d) Expected effects of asymmetric and symmetric PPI on group performance. In the case of asymmetric PPI, trait distinctiveness is expected to capture trait hierarchy at the group level. Under the win>loss scenario, the presence of a plant displaying high value of trait distinctiveness is expected to promote group performance while it should reduce group performance under the loss>win scenario. In the case of symmetric PPI, group performance should increase with trait dissimilarity among coexisting plants.

large enough to allow an optimal partitioning of resources (win-win scenario, Figure 1c), as depicted by the so-called 'complementarity effect' (Loreau & Hector 2001). Conversely, in case of weak niche dissimilarity, mixed genotypes can produce less in mixture than in pure stands due to strong competitive interactions (loss–loss scenario, Figure 1c). Accordingly, greater trait dissimilarity between two plants should lead to greater performance of the mixture (Figure 1d). Under asymmetric PPI, the mixture can produce more biomass than expected from pure stands as soon as the best competitor wins more biomass than the weaker competitor loses (win>loss scenario, Figure 1c). Conversely, differences in competitive abilities can impair mixture performance if the loss of the weaker competitor is not counterbalanced by the gain of the stronger (loss>win scenario, Figure 1c). However, deciphering the role of asymmetric PPI on the performance of plant mixture is particularly challenging given that relative trait distance is a directional, individual-centred metrics. Furthermore, the outcome of competitive hierarchy is under the control of many traits (e.g. plant height, phenology, Freckleton & Watkinson, 2001). The fact that relative distances cannot be computed on a multi-trait basis limits their use to predict the effects of asymmetric PPI.

In this study, we argue that functional trait distinctiveness, an emerging facet of trait diversity (Munoz et al., 2023; Violle et al., 2017), can help capture the outcomes of PPI on the performance of both individual plants and groups of coexisting plants. Trait distinctiveness corresponds to the average trait distance between a given species (or genotype) and all the components of a given species pool (Grenié et al., 2018). Although related, it differs from the absolute trait distance (or trait dissimilarity) by giving a measure of the species position in the phenotypic space (Figure 1a): the higher the distinctiveness, the most distant the species from all others and the more eccentric position it displays in the phenotypic space (Grenié et al., 2018). Furthermore, trait distinctiveness can account for multiple traits differences between plants, unlike relative trait distances. For these reasons, we expect that computing maximal trait distinctiveness within a group of competing plants can quantify the effect of asymmetric PPI on mixture performance, plants with the highest distinctiveness being the best (e.g. taller, fast growing) or the weakest (e.g. shorter, slow growing) competitor among a given pool of plants (Figure 1d).

A better understanding of the relationship between traits, PPI, and performance is finally crucial from an applied perspective, and more notably in agricultural sciences, where it can bring crucial insights for the establishment of generic assembly rules for crop genotype mixtures (Litrico & Violle, 2015). Indeed, although genotype mixtures are on average more productive than their mono-genotypic stands, not all combinations of genotypes result in such overyielding (Kiaer et al., 2009; Reiss & Drinkwater, 2018). Identifying the best performing genotype mixtures from trait distances is therefore becoming a pressing issue (Barot et al., 2017; Litrico & Violle, 2015). In that perspective, we used the model crop species *Oryza sativa* L. ssp. *japonica* to examine the links between trait distances, trait distinctiveness and the associated nature of intraspecific PPI (i.e. asymmetric vs. symmetric). To that end, we screened the phenotypic diversity of 49 rice genotypes based on key below-ground and above-ground functional traits. We conducted a competition experiment by growing nine of those genotypes in pots under conditions of pairwise interaction with themselves or with other genotypes. We expect trait distinctiveness to be the main driver of the performance of mixtures dominated by asymmetric PPI (Figure 1d). Conversely, absolute trait distance is expected to be the main driver of mixture performance in pots where symmetric PPI dominates (Figure 1d). We further expect that plant traits depicting plant competition for light (e.g. plant size, photosynthesis efficiency, leaf N concentration) relate more to asymmetric PPI while traits related to below-ground resource acquisition (e.g. specific root length, root diameter [RD], root N concentration [RN]) are preferentially linked to symmetric PPI.

2 | MATERIALS AND METHODS

2.1 | Experimental design

We built two experiments: a first screening experiment of the trait diversity of 49 temperate rice genotypes (*Oryza sativa* subsp. *japonica*) and a second experiment dedicated to the evaluation of the role of trait distance in driving the outcome of PPI using a subset of nine contrasted genotypes out of the 49 genotypes. Both experiments were conducted at the CEFE-CNRS (Montpellier, France) from June to September 2021, in outdoor conditions (mean daily temperature from 18.7 to 28.1°C). Plants were grown in 8.8 L plastic pots (15 cm diameter; 50 cm depth) filled with a mixture of 50% quartz sand (volume based) and 50% soil (62% sand, 27% silt and 11% clay). Pots were amended with 3.5 $g\,L^{-1}$ of NPK fertilizer (Basacote® High K 6M NPK 13-5-18) and 5.9 $g\,L^{-1}$ of Fe fertilizer (Ferveg® 6; 6% Fe EDDHA). Plants were watered every day with a drip irrigation system, with approximately 150 mL of tap water.

2.2 | Genotype selection

For the screening experiment, we selected 49 temperate rice genotypes from the European Rice Germplasm Collection (Courtois et al., 2012; listed in Table S1) to characterize the phenotypic space of a large panel of rice genotypes. The selection was based on previously acquired trait data coming from greenhouse for root traits and field experiment for above-ground traits (Biscarini et al., 2016; Frontini et al., 2021; Volante et al., 2017; details in Supporting Information) to a priori maximize phenotypic diversity. Within this pool of genotype, we also chose a subset of nine contrasted genotypes to assess the role of trait distance and trait distinctiveness in driving the outcome of PPI in a second competition experiment. Among these nine genotypes, seven were chosen according to their multi-trait distinctiveness (details of calculation below) using preliminary trait data for its computation (Table S1). More precisely, we selected two genotypes with low distinctiveness values (LIDO and MARATELLI), two with intermediate ones (BALDO and SESIA) and three with high values (GRITNA, LUXOR and OTA). In addition, in order to increase the functional spectrum of this subset of genotypes, we selected two additional distinct genotypes commonly used in rice ecophysiological studies (NIPPONBARE and KITAAKE), both genotypes displayed the highest level of multi-trait distinctiveness among the 49 genotypes (Table S1). Importantly, multi-trait distinctiveness calculated a priori based on these preliminary trait data was highly correlated with multi-trait distinctiveness calculated a posteriori based on the trait data acquired in this experiment ($r=0.72$).

2.3 | Screening experiment

We grew the 49 genotypes as single plants in pots (four replicates per genotype) until the flowering stage, for 196 pots. We quantified above-ground and root biomass of each plant and measured traits related to plant size (plant height and LA), light acquisition [(photosynthesis efficiency, leaf nitrogen (N) and phosphorus (P) concentrations)] and below-ground resource acquisition (specific root length, RD, root tissue density [RTD] and RN). We further quantified plant phenology (age at flowering) as it can relate to both symmetric and asymmetric PPI (Kraft et al., 2015) as well the root/shoot ratio, the latter being a broad proxy of plant competitive ability (Goldberg, 1997). A detailed description of trait measurements can be found in de Tombeur et al. (2023).

We estimated the age at flowering (hereafter Flower, in growing degree-days) by the sum of growing degree-days from germination to the appearance of the top first panicles, and considering a base temperature of 10°C . We measured plant height as the distance between the soil surface and the base of the spikes of the main stem. Photosynthesis efficiency was estimated by quantifying the chlorophyll fluorescence in mature leaves exposed to full sunlight using a pulse-amplitude-modulated fluorimeter (Mini-PAM II; Walz). We then collected the same leaf and scanned at 600 dpi to calculate the LA (m^{-2}) with WinFOLIATM (Regent Instrument). After drying at 60°C for 72 h and grinding, we determined leaf N concentration with a CN elemental analyser. Three additional N-1 adult leaves were then sampled, dried at 60°C for 72 h, and grinded to quantify the concentration of P with a portable X-ray fluorescence spectrometer (Reidinger et al., 2012). Roots were carefully cleaned with tap water, and two to three well-developed representative root axes (i.e. non-degraded and mature axes) were selected on each individual plant. They were scanned at 600 dpi to measure mean RD (in mm) and the proportion of fine roots (diameter < 0.1 mm; PFR in %), root length and root volume using WinRHIZOTM Pro (Regent Instrument). They were then dried at least 48 h at 60°C and weighted to calculate the specific root length (SRL, in $m\,g^{-1}$) and the RTD (in $g\,cm^{-3}$). After grinding, RN (in % DW) were determined by a CHN Elemental analyser (CHN model EA 1108).

2.4 | Competition experiment

A subset of nine genotypes were grown according to two modalities: (i) in mono-genotypic stands, that is, two individuals of the same genotype planted together within one pot (hereafter monoculture) and (ii) in binary intergenotypic mixtures by making all possible pairwise combinations. We used a randomized block design using four blocks, with each mixture and monoculture replicated one time in each block for a total of 208 pots (36 individual pots, 36 monoculture and 144 pairwise mixtures). Monocultures and mixtures were harvested after grain maturation. The panicles of each individual plant were clipped and dried for at least 72 h at 60°C. We weighed plant panicles to estimate the performance of each plant in terms of grain yield.

2.5 | Performances of single genotype and genotype mixture

We computed the relative grain yield (RY) of genotype *i* grown in genotype mixtures to estimate the effect of the neighbour on the focus plant performance relatively to its performance grown in monoculture following Equation (1):

$$\mathrm{RY}_i = \frac{Y_{i_{\mathrm{mixt}}}}{Y_{i_{\mathrm{monoc}}}}, \qquad (1)$$

where $Y_{i_{\mathrm{mixt}}}$ is the biomass of the grains produced by genotype *i* in mixture and $Y_{i_{\mathrm{monoc}}}$ is the biomass of the grains produced by genotype *i* grown in pure stand. $\mathrm{RY} > 0.5$ indicates higher genotype performance in the mixture than in the monoculture.

We calculated the total relative yield (RYT) to assess the performance of the mixture composed of genotype *i* and *j* following Equation (2):

$$\mathrm{RYT}_{i,j} = \frac{\frac{Y_{i_{\mathrm{mixt}}}}{Y_{i_{\mathrm{monoc}}}} + \frac{Y_{j_{\mathrm{mixt}}}}{Y_{j_{\mathrm{monoc}}}}}{2}. \qquad (2)$$

$\mathrm{RYT} > 1$ indicates higher mixture yields than expected from the average yield of the mono-genotypic stands (i.e. overyielding).

In addition, we quantified the transitive overyielding of each mixture ($D_{\max}$ index; Hooper & Dukes, 2004) to evaluate whether a given mixture performs better or worse than the most productive genotype in monoculture following Equation (3):

$$D_{\max_{i,j}} = \left[Y_{i,j} - \max\left(Y_{i_{\mathrm{monoc}}}, Y_{j_{\mathrm{monoc}}}\right)\right] / \max\left(Y_{i_{\mathrm{monoc}}}, Y_{j_{\mathrm{monoc}}}\right), \qquad (3)$$

where $Y_{i,j}$ is the observed total yield of a mixture made of genotypes *i* and *j*. $D_{\max} > 0$ indicates higher grain yield in the mixture than expected from the maximal yield of the mono-genotypic stands (i.e. transgressive overyielding).

Because a significant block effect was observed on the biomass production of mono-genotypic stands and genotype mixtures, we used mono-genotypic productivity within blocks, rather than using mean mono-genotypic values across blocks, to estimate RY, RYT and $D_{\max}$.

Finally, we classified each mixture pot according to the RYs of its components. Pots were the RYs of the two competing genotypes were >0.5 and <0.5 corresponded to win–win and loss–loss pots respectively. Pots with one genotype having $\mathrm{RY} > 0.5$, the other $\mathrm{RY} < 0.5$ and $\mathrm{RYT} > 1$ corresponded to win>loss pots while pots with one genotype having $\mathrm{RY} > 0.5$, the other $\mathrm{RY} < 0.5$ but $\mathrm{RYT} < 1$ were classified as loss>win pots.

2.6 | Trait distances and trait distinctiveness

We quantified relative trait distances (i.e. hierarchical trait distance) between two competing genotypes as $t_i - t_j$ where t_i and t_j were the functional trait values of genotype *i* and *j* respectively. Absolute trait distance, a proxy of niche similarity, was calculated as the Euclidean distance between trait values $|t_i - t_j|$.

We further calculated the trait distinctiveness of each genotype. Trait distinctiveness is the average trait distance of a genotype from a given pool of other genotypes (Grenié et al., 2018), and is computed according to the following equation:

$$D_i = \frac{\sum_{i\neq j}^{N} d_{i,j}}{N-1}, \tag{4}$$

where D_i is the trait distinctiveness of genotype *i*, *N* the total number of genotypes considered and $d_{i,j}$ the Euclidian distance between genotype *i* and genotype *j*. We computed trait distinctiveness for each of the 49 genotypes used in the screening experiment (Table S1).

We calculated absolute trait distance (i.e. Euclidean distance) and distinctiveness for each trait separately and for all traits considered together (i.e. multidimensional approach) as the role of niche dissimilarity could be best captured by a multi-trait rather than by a single-trait approach (Kraft et al., 2015).

2.7 | Statistical analysis

We quantified the mean trait values of each genotype while accounting for block effects using the lsmeans function of the lsmeans R library (Lenth, 2018). We used a principal component analysis (PCA) to characterize the phenotypic space covered by the 49 rice genotypes based on these mean trait values.

Then, we evaluated the respective influence of absolute trait distance, relative trait distance and trait distinctiveness on single plant performance (RYs) using separate linear models. These trait metrics were standardized so that the estimated coefficient of regression can be directly compared and ranked to identify the stronger effects (Schielzeth, 2010). Similarly, we deciphered the roles of trait distance and trait distinctiveness in driving the performance of genotype mixture expressed by both RYT and $D_{\max}$ using separate linear models. At the mixture scale, trait distances can only be quantified by absolute distances (also called 'trait dissimilarity' in Figure 1d) between the competing genotypes. For each mixture pot and trait, we calculated the maximum of trait distinctiveness between the two competing genotypes. Trait metrics were standardized to allow the direct comparison between models' outputs. Finally, we tested for differences in RYT, $D_{\max}$, trait distance and trait distinctiveness between the four types of mixture (i.e. win>loss, loss>win, win–win and loss–loss pots) using ANOVA and Tukey HSD tests. RYT and $D_{\max}$ were log-transformed to satisfy normality. All analyses were conducted using R version 4.2.2 (R Core Team, 2022).

3 | RESULTS

3.1 | Phenotypic space of the 49 studied rice genotypes

The first three principal components (PCs) explained approximately 72% of the total variance (Figure 2a,b; Table S2). The first PC (PC1) depicted a slow-fast continuum in resource use that opposed

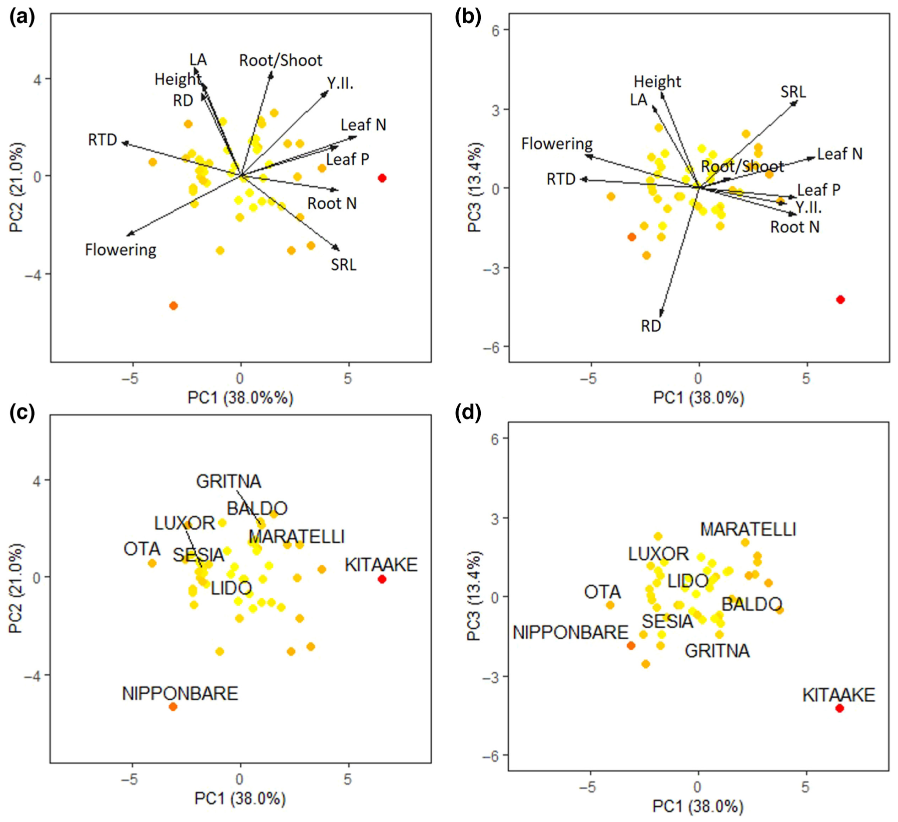

FIGURE 2 Phenotypic space of the studied 49 rice genotypes. (a, b) Projection of genotypes (dots) on the phenotypic space defined by PC axes PC1, PC2 and PC3. (c, d) Positions of the nine rice genotypes used for the subsequent pairwise competition experiment. Arrows indicate the direction and weighing of vectors representing the 10 traits considered. The colour gradient indicates genotypes with lowest (yellow) to highest (red) multi-trait distinctiveness. Flowering, age at flowering; LA, leaf area; RD, root diameter; RTD, root tissue density; SRL, specific root length; Y.II., photosynthetic efficiency.

genotypes with high nutrient concentrations (leaf and root N, leaf P), high photosynthetic efficiency (Y.II.) and high SRL to late flowering genotypes, with high RTD. PC2 mostly depicted the size of rice genotypes, high and positive PC2 coordinates corresponding to taller plants with larger leaves. Taller plants were also characterized by high root/shoot ratio, indicating that they allocated a larger amount of biomass to their roots compared to shorter plants. PC3 revealed a trade-off between higher SRL and lower RD (Figure 2b).

The nine genotypes selected for the competition experiment displayed contrasting traits and covered the full range of PC1, PC2 and PC3 values (Figure 2c,d). KITAAKE and NIPPONBARE, the most functionally distinct genotypes (Table S1) were the shortest genotypes of the collection and displayed the extreme values of age at flowering (Figure S1). NIPPONBARE had the latest flowering date while KITAAKE flowered earlier than the other genotypes (Figure S1).

3.2 | Performance of individual plants

The level of trait distinctiveness of a genotype was the best predictor of its individual performance in response to competition, explaining between 2% and 15% of the variance of RY's (Table 1). The more distinct a genotype in terms of plant height, LA, age at flowering, leaf N and root/shoot ratio, the worse it performs in mixture while when grown in pure stand. Conversely, distinctiveness based on root N, SRL, RD and RTD had positive effects on RY. Relative trait distances between a focal genotype and its neighbour also significantly explained variation in genotype relative yields (between 2% and 11% of the variance of RY's; Table 1). As expected, RYs increased with the relative distance of traits that depicted plant size (i.e. height and LA). It also increased with relative distance based on root/shoot ratio, photosynthetic efficiency, leaf N and P concentrations. Conversely, RYs decreased with the relative distance based on age at flowering, indicating that genotypes which flower later than their neighbours had lower RYs. Relative distances based on root traits had no significant effects on RYs. Finally, absolute trait distances poorly influenced the performance of genotypes in response to competition (between 0.0% and 2.0% of explained variance; Table 1).

3.3 | Performance of genotype mixtures

Over all mixtures, average RYT equalled 2.22, meaning that mixtures produced on average twice as much grain than expected from single genotypes (Figure S2). However, RYT variation was high, with values ranging from 0.05 to 11.5 (Figure S2), meaning that some mixtures performed poorly while others were far better than expected from the performance of their genotypes when grown in pure stand. Beneficial effects of genotype mixtures can be further assessed by the $D_{\max}$ metrics that characterizes transitive overyielding (i.e. a situation where a mixture produces more grains than the most productive genotype when grown in pure stand). Average $D_{\max}$ was 0.35 (SD = 1.57) and significantly differed from 0 (Figure S2). In addition, the distribution of the 144 mixture pots in the four types of mixture performance (i.e. win–win, loss–loss, win>loss and loss>win pots) was not random, with more pots producing above the average of their mono-genotypic stands (i.e. overyielding) than pots with lower grain yields than the mono-genotypic stands ($\chi^2 = 13.6$, $p = 0.003$). Specifically, we observed 32.3% (i.e. 88 pots) of win>loss, 29.4% (i.e. 80 pots) of win–win, 26.5% (i.e. 72 pots) of loss–loss and 11.8% (i.e. 32 pots) of loss>win pots. We reported significant differences in RYT (ANOVA, $F = 58.2$, $p < 0.001$) and $D_{\max}$ (ANOVA, $F = 54.7$, $p < 0.001$) between the four types of mixture performance (Figure 3). RYT and $D_{\max}$ were highest in win–win pots than in win>loss, loss>win and loss-loss pots (Figure 3).

We reported almost no significant effect of absolute trait distances and trait distinctiveness on the RYT of genotype mixture (Table 1). By contrast, trait distinctiveness had significant impacts on transitive overyielding; $D_{\max}$ increased with increasing multi-trait distinctiveness, as well as with distinctiveness in plant height, LA, age at flowering and leaf N content (Table 1). However, the % of explained variance remained low (i.e. between 3% and 4%; Table 1).

Finally, testing for differences in trait dissimilarity and trait distinctiveness between the four types of mixtures indicated that pots where asymmetric PPI dominated (i.e. win>loss and loss>win pots) displayed the highest level of multi-trait distinctiveness (Figure 4). This was notably due to high distinctiveness in above-ground trait, and more notably in plant height, LA, age at flowering and leaf N content in those pots (Figure 4). However, loss>win pots had the lowest SRL (Figure 4). On the contrary, win–win pots had the highest SRL distinctiveness but the lowest distinctiveness in photosynthesis efficiency (Figure 4). Loss–loss pots displayed the lowest multi-trait distinctiveness as well as the lowest distinctiveness in height, LA, age at flowering and leaf N content (Figure 4). We found no significant difference in trait dissimilarity among the four types of mixture pots (Table S4).

4 | DISCUSSION

The primary aim of this study was to evaluate the potential of different facets of trait distances between competing plants to predict the outcome of symmetric and asymmetric intraspecific competition on the performance of genotypes and genotype mixtures. We showed that trait distinctiveness as well as relative distances in traits that related to light competition, such as plant height, LA, photosynthesis efficiency and leaf N concentration, were the best predictors of the performance of genotypes when grown in mixtures. This confirms that genotypes which are taller than their neighbours and which have faster resource-use strategies display higher performance under competition (Gaudet & Keddy, 1988; Violle et al., 2009; Zhang et al., 2020). By contrast, absolute trait distances poorly explained the performance of genotypes in pairwise mixtures. These results provide strong evidence that, in this experiment, intraspecific PPIs are dominated by asymmetric competition for light. They

TABLE 1 Effects of relative trait distances, absolute trait distances and trait distinctiveness on the performance of each individual genotype grown in mixtures (RY) and on the performance of each genotype mixture (RYT: nontransitive overyielding; $D_{\max}$: transitive overyielding). Relative trait distances cannot be calculated on the basis of multiple traits or at the mixture level. Significant effect ($p < 0.05$) are highlighted in grey.

	Relative trait distance			Absolute trait distance			Trait distinctiveness		
	Estimate	SD	r^2	Estimate	SD	r^2	Estimate	SD	r^2
RY									
All traits	–	–	–	−0.08	0.11	<0.01	**−0.29**	**0.11**	**0.02**
Height	**0.60**	**0.11**	**0.10**	−0.13	0.11	<0.01	**−0.28**	**0.11**	**0.02**
Leaf area	**0.48**	**0.11**	**0.06**	0.01	0.11	<0.01	**−0.43**	**0.11**	**0.05**
Y.II.	**0.28**	**0.11**	**0.02**	−0.10	0.11	<0.01	−0.19	0.11	0.01
Flower date	**−0.35**	**0.11**	**0.04**	−0.08	0.11	<0.01	**−0.32**	**0.11**	**0.03**
Leaf N	**0.48**	**0.11**	**0.06**	**−0.25**	**0.11**	**0.02**	**−0.55**	**0.11**	**0.09**
Leaf P	**0.25**	**0.11**	**0.02**	−0.09	0.11	<0.01	0.09	0.11	<0.01
Root/shoot	**0.62**	**0.11**	**0.11**	**−0.34**	**0.11**	**0.03**	**−0.73**	**0.11**	**0.15**
Root N	−0.10	0.11	<0.01	**0.28**	**0.11**	**0.02**	**0.30**	**0.11**	**0.03**
SRL	0.03	0.11	<0.01	−0.03	0.11	<0.01	**0.47**	**0.11**	**0.06**
RD	0.14	0.11	0.01	0.07	0.11	<0.01	**0.34**	**0.11**	**0.03**
RTD	−0.10	0.11	<0.01	0.07	0.11	<0.01	**0.22**	**0.11**	**0.01**
RYT									
All traits	–	–	–	0.03	0.10	<0.01	0.09	0.10	0.01
Height	–	–	–	0.04	0.10	<0.01	0.09	0.10	0.01
Leaf area	–	–	–	0.07	0.10	<0.01	0.03	0.10	<0.01
Y.II.	–	–	–	−0.02	0.10	<0.01	0.06	0.10	<0.01
Flower date	–	–	–	0.03	0.10	<0.01	0.10	0.10	0.01
Leaf N	–	–	–	0.01	0.10	<0.01	0.12	0.10	0.01
Leaf P	–	–	–	−0.01	0.10	<0.01	0.13	0.10	0.01
Root/shoot	–	–	–	−0.08	0.10	0.01	−0.03	0.10	<0.01
Root N	–	–	–	0.13	0.10	0.01	**0.19**	**0.09**	**0.03**
SRL	–	–	–	−0.02	0.10	<0.01	0.13	0.10	0.01
RD	–	–	–	0.06	0.10	<0.01	0.15	0.10	0.02
RTD	–	–	–	−0.02	0.10	<0.01	0.04	0.10	<0.01
$D_{\max}$									
All traits	–	–	–	0.13	0.09	0.01	**0.20**	**0.09**	**0.03**
Height	–	–	–	0.15	0.09	0.02	**0.22**	**0.09**	**0.04**
Leaf area	–	–	–	0.13	0.09	0.01	**0.19**	**0.09**	**0.03**
Y.II.	–	–	–	0.01	0.10	<0.01	0.10	0.10	0.01
Flower date	–	–	–	0.13	0.10	0.01	**0.20**	**0.09**	**0.03**
Leaf N	–	–	–	0.09	0.10	0.01	**0.22**	**0.09**	**0.04**
Leaf P	–	–	–	0.01	0.10	<0.01	0.08	0.10	0.01
Root/shoot	–	–	–	0.07	0.10	<0.01	0.13	0.09	0.01
Root N	–	–	–	0.12	0.10	0.01	0.18	0.09	0.03
SRL	–	–	–	−0.01	0.10	<0.01	0.08	0.10	0.01
RD	–	–	–	0.09	0.10	0.01	0.09	0.10	0.01
RTD	–	–	–	0.03	0.10	<0.01	0.09	0.10	0.01

Abbreviations: Flower, age at flowering; LA, leaf area; r^2: coefficient of determination estimated by linear models; RD, root diameter; RTD, root tissue density; RY, relative grain yield; RYT, total relative yield; SD: standard deviation; SRL, specific root length; Y.II., photosynthesis efficiency.

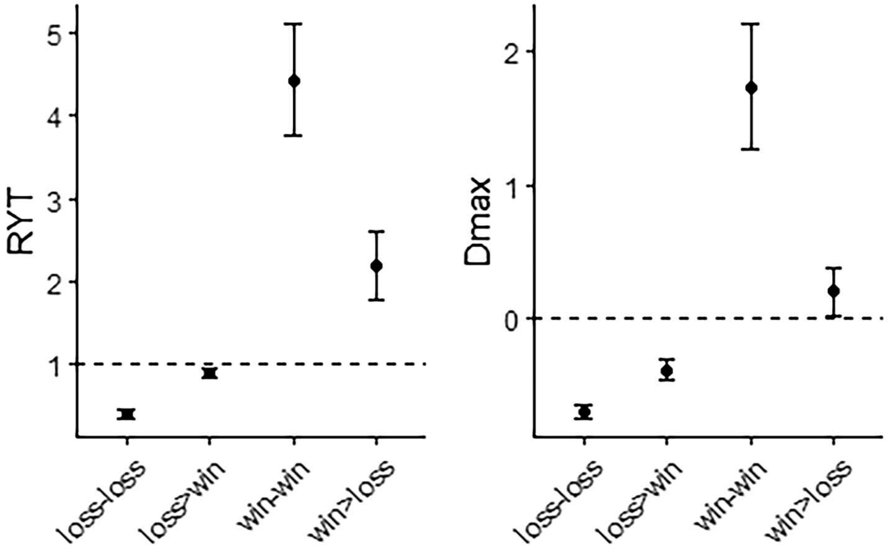

FIGURE 3 Average performance of the four types of genotype mixture. Left: Total relative yield (RYT). Right: transitive overyielding (D_{max}). Vertical bars show confidence intervals ($\alpha = 0.05$). Dotted lines indicate the limit above which overyielding is positive. Loss–loss and win–win are mixtures where the two competing genotypes produce respectively less and more grains than in their mono-genotypic stand. Loss>win and win>loss are mixtures where one genotype produces more and the other less grain than in their mono-genotypic stand.

complete previous findings from interspecific competitive experiments (Gaudet & Keddy, 1988; Goldberg & Landa, 1991; Kraft et al., 2014; Kunstler et al., 2012; Zhang et al., 2020) by emphasizing that intraspecific trait variability can deeply affects the outcomes of PPI (Carmona et al., 2019). However, the predominance of asymmetric competition over symmetric competition among crops has not been reported so often (but see Montazeaud et al., 2018). Our findings are all the more important as the theoretical basis of crop diversification, which has gained traction in recent years, is implicitly rooted on symmetric competition and complementarity rather than on asymmetric competition (Barot et al., 2017; Litrico & Violle, 2015).

Our results highlighted the key role that trait distinctiveness exerts on the outcomes of asymmetric PPI on the performances of genotype mixtures. First, and as expected, the highest values of trait distinctiveness, notably in terms of plant height, LA and age at flowering, are observed in win>loss and loss>win pots, that is, those pots where asymmetric PPI dominates. Second, distinctiveness based on plant height, LA, phenology and leaf N content exerted the strongest positive effects on the performance of genotype mixtures. Although the trait distinctiveness of a genotype (or a species) is relative to the pool of genotype (or species), it has been shown that the values of trait distinctiveness of species are strongly correlated when computed from local to larger scales (Gauzere et al., 2023). These results confirm that trait distinctiveness is a good candidate to capture the outcomes of asymmetric PPI at the community level, unlike relative distances that can only capture the effects of asymmetric PPI on a focal plant.

Distinctiveness based on plant size and phenology also have negative effects on the performance of single genotypes, suggesting that the more distinct genotypes were weakest competitors in the pool of genotypes considered. These genotypes are KITAAKE and NIPPONBARE—which have a different genetic background than the other genotypes considered—and are the shortest genotypes in our collection. As such, they probably suffer more strongly than others from asymmetric competition for light (Gaudet & Keddy, 1988; Weiner, 1990), which explains the negative relationships between trait distinctiveness and the performance of single genotypes. However, even if these functionally distinct genotypes have lower performance in mixtures due to asymmetric PPI, their presence generally promotes the performance of the genotype mixture. Indeed, their reduced stature implies that they have very limited influence on the growth of their taller neighbours. The latter can in turn produce more biomass than in mono-genotypic stands due to the release of competitive interactions with themselves (Mahaut et al., 2020). The fact that the number of win>loss pots exceeds by far the number of loss>win pots indicates that most of the time, biomass win of the best competitors counterbalances biomass loss of the weaker competitors. Asymmetric PPI can therefore result in positive overyielding in genotype mixtures, as previously observed (e.g. Montazeaud et al., 2018, 2020). However, this conclusion can be refined by considering the role of plant phenology distinctiveness. KITAAKE, which is more frequently observed in win>loss pots (Figure S3), also displays the earliest flowering time. It could therefore partly escape the competitive constraints imposed by taller neighbours thanks to a rapid life cycle, so that its biomass loss in genotype mixtures stays relatively low. Conversely, NIPPONBARE, which is more frequently observed in loss>win pots (Figure S3), displays the latest flowering time. This combination of traits (i.e. being the shortest with the latest flowering) makes the genotype very sensitive to competition induced by taller neighbours, so that its loss of biomass in genotype mixtures is too important to be outweighed by biomass gains of its taller neighbours. Therefore, asymmetric competition between genotypes with different competitive abilities does not always guarantee a better productivity of genotype mixtures.

The fact that asymmetric PPI seems to dominate in our experiment does not preclude the fact that symmetric PPI can operate. As evidence, one third of the genotype mixtures are win–win pots, a scenario that suggests the existence of complementarity mechanisms in the way genotypes use resources. In theory, complementarity arises when trait dissimilarity between competing plants enhances the partitioning of resources (Adler et al., 2013; Macarthur & Levins, 1967), notably water and nutrients for which PPIs are expected to be mostly symmetric (Schwinning &

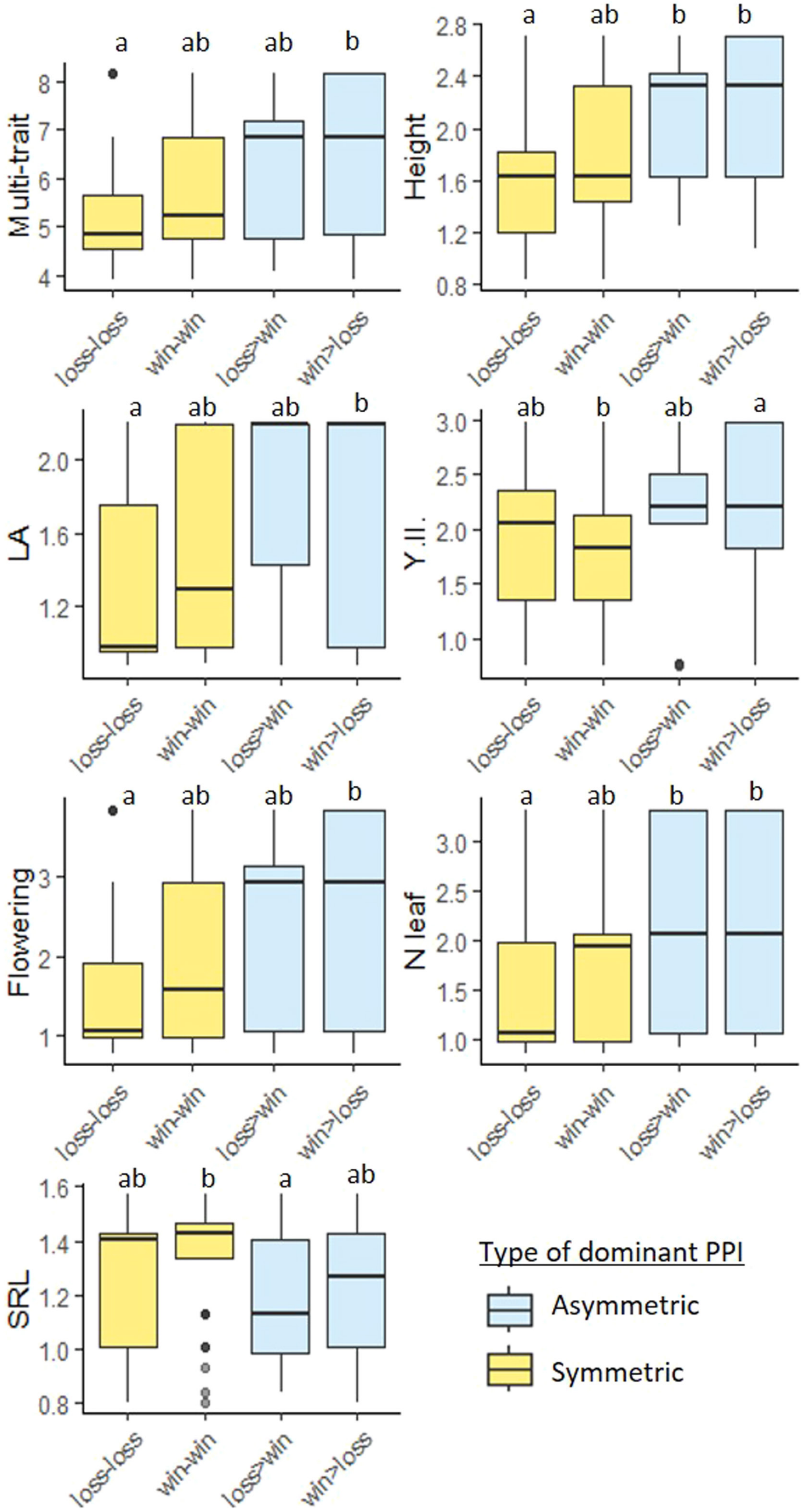

FIGURE 4 Differences in trait distinctiveness between mixtures where symmetric PPI (loss–loss and win–win pots) and asymmetric PPI (win > loss and loss > win pots) dominated. Differences between types of mixtures are evaluated through ANOVA and Tukey HSD tests. Only significant differences are reported ($p < 0.05$). Type of mixtures with different letters had different trait distinctiveness. Flowering, age at flowering; LA, leaf area; PPI, plant–plant interaction; SRL, specific root length; Y.II., photosynthetic efficiency.

Weiner, 1998). However, while we consider numerous root traits that are directly linked to the use of below-ground resources (Bergmann et al., 2020; Carmona et al., 2021; Weigelt et al., 2021), we find almost no significant, positive effect of absolute trait distance (or trait dissimilarity) on the performances of single genotype and genotype mixture. One possible explanation is that water and nutrients are not limiting in our experiment, contrary to the space available for root development, which could have limited the establishment of complementarity in soil exploration strategy. Yet, while niche complementarity and its related 'competition-trait-similarity' hypothesis is a central theory in ecology (Abrams, 1983), an unequivocal relationship between trait dissimilarity and niche complementarity remains particularly scarce in the ecological literature. Nonetheless, these win-win mixtures display the highest level of distinctiveness based on SRL. In addition, root trait-based distinctiveness has effects on the performance of individual genotypes. Taken together, these results suggest that distinctiveness based on root traits might capture the effect of symmetric PPI for belowground resources. This is also supported by the fact that absolute multi-trait distance and multi-trait distinctiveness are strongly related, although nonlinearly (Figure S4). Conversely, mixtures where competitive interactions impair the performance of both genotypes (i.e. loss–loss pots) display the lowest level of distinctiveness. Mixing genotypes that display very common trait values, and therefore which are likely to share the same trait values, should therefore lead to strong competitive interactions that limit the performance of each competitor, as predicted by the limiting similarity hypothesis (Macarthur & Levins, 1967). Giving more attention to trait distinctiveness thus holds great promise to reconcile functional traits and niche theory.

Finally, combining phenotypes in varietal mixtures to optimize crop performance represents a major challenge for plant breeding (Litrico & Violle, 2015). Our results show that growing varieties in mixtures lead, on average, to higher grain yields than expected from monocultures considering both the mean (RYT) and the maximum (D_{max}) monoculture performance. However, the benefit of mixing rice varieties for grain production strongly varied from one mixture to another, as observed elsewhere (e.g. Montazeaud et al., 2020; Reiss & Drinkwater, 2018). Our results reveal that higher performance of genotype mixtures occurs when the two genotypes perform better in the mixture (i.e. win–win pots) or when the gains of one genotype overcome the losses of the other (i.e. win>loss pots). Interestingly, these two scenarios are equally likely in our experiment, although both D_{max} and RYT are by far higher in win–win pots. This new finding suggests that minimizing competitive interactions, so that each genotype will produce more in mixture than in monoculture, leads to greater mixture performance than do interactions between genotypes that have different competitive abilities. Deciphering the role of plant traits and trait distances in driving symmetric PPI will therefore be all the more crucial for the development of high-performing crop mixtures.

To conclude, our study shed new light on the role that functionally distinct plants play as drivers of competitive interactions within plant communities. Such an in-depth analysis of the mechanisms by which functionally rare species can affect community dynamics hold great promise to understand why functionally distinct species are key for ecosystem functioning (Bagousse-Pinguet et al., 2021; Brun et al., 2022; Delalandre et al., 2022). We focused on pairwise interactions between genotypes of a given species to avoid dealing with an interaction milieu (sensu McGill et al., 2006) that is too complex to decipher the mechanisms at play. In the future, a critical challenge will be to assess the role of trait distinctiveness in driving PPI in richer communities and where intransitive competition can dominate PPI (Soliveres & Allan, 2018).

AUTHOR CONTRIBUTIONS

Florian Fort, Cyrille Violle, Delphine Luquet and Elsa Ballini conceived the ideas and designed the methodology; Ammar Shihan, Koloina Rahajaharilaza, Felix de Trombeur, Denis Fabre, Susan Hartley and SJT collected the data, Lucie Mahaut analysed the data, Lucie Mahaut, Cyrille Violle and Florian Fort led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Cyrille Violle is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.95x69p8qc.

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SUPPORTING INFORMATION

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

Figure S1. Mean genotype traits measure from the screening experiments.

Figure S2. Distribution of non-transitive (total relative yield) and transitive (D_{max}) mixture overyielding.

Figure S3. Association between individual genotype and type of mixture performance.

Figure S4. Relationship between multi-trait (absolute) distance and maximal distinctiveness.

Table S1. Multi-trait distinctiveness of 49 rice genotypes.

Table S2. Trait-by-trait distinctiveness of the nine genotypes used in the competition experiment.

Table S3. Results of the principal component analysis based on a correlation matrix of the main plant traits for 49 rice genotypes, as shown in Figure 2.

Table S4. Mean absolute trait distance and maximal trait distinctiveness in four type of genotype mixtures.

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