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Phenotypic limits of crop diversity: a data exploration of functional trait space

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Summary

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- Relationships between crop genetic and functional diversity are key to addressing contemporary agricultural challenges. Yet, there are few approaches for quantifying the relationship between genetic diversity and crop functional trait expression. Here, we introduce ‘functional space accumulation curves’ to analyze how trait space increases with the number of crop genotypes within a species.
- We explore the potential for functional space accumulating curves to quantify genotype–trait space relationships in four common annual crop species: barley (*Hordeum vulgare*), rice (*Oryza sativa*), soybean (*Glycine max*), and durum wheat (*Triticum durum*). We also employ these curves to describe genotype–trait space relationships in the wild annual *Arabidopsis thaliana*, which has not been subjected to artificial selection.
- All five species exhibited asymptotic functional space accumulation curves, suggesting a limit to intraspecific functional crop diversity, likely due to: dominant phenotypes represented by several genotypes; or functional redundancy that might exist among genotypes. Our findings indicate that there is a diminishing return of functional diversity with increasing number of genotypes.
- Our analysis demonstrates the efficacy of functional space accumulation curves in quantifying trait space occupancy of crops, with implications for managing crop diversity in agroecosystems, and genetic diversity in crop breeding programs.

Introduction

The intentional cultivation of greater crop diversity both within and among agricultural systems is a crucial strategy for addressing the complex challenges faced by modern agriculture including food security, environmental sustainability, and resilience to global change (Kremen *et al.*, 2012; Jones *et al.*, 2014; Renard & Tilman, 2019; Beillouin *et al.*, 2021; Rasmussen *et al.*, 2024). Crop genetic resources play a critical role in achieving these outcomes associated with crop diversification (McCouch & Riesberg, 2023), and in influencing whether or not greater crop diversity ultimately fulfills a suite of functions in an agricultural system (Garnier & Navas, 2012; Wood *et al.*, 2015; Isaac *et al.*, 2021). With many advances in understanding the role of crop genetics in breeding, we still lack a clear conceptualization of the point at which a genotypic pool can still be improved in terms of functional diversity. Achieving the goals of crop diversification therefore requires a deeper understanding of the

correspondence between genetic and functional diversities within crop populations.

Genetic diversity within crop species is largely assessed on the basis of the number of varieties, alleles, or genes (Perales & Golicher, 2014; Thormann *et al.*, 2016). Crop functional diversity is broadly quantified as the variability in proxies of plant functions, or ‘functional traits’ (Martin & Isaac, 2015; Milla *et al.*, 2015; Wood *et al.*, 2015; Khoury *et al.*, 2022). Functional traits encompass a multitude of phenotypic characteristics related to plant performance in response to the environment as well as plant effects on ecosystem processes (Lavorel & Garnier, 2002; McGill *et al.*, 2006; Violle *et al.*, 2007; Garnier *et al.*, 2016; Shipley *et al.*, 2016; Sobral, 2021). Due to their close dependence on environmental conditions and ecological contexts, functional traits can also serve as meaningful indicators of the range of environmental conditions to which species are exposed, or ‘niche breadths’ (Violle & Jiang, 2009; Schellenberger Costa *et al.*, 2018). Following this, quantifying functional trait variation

within and among crop populations can contribute to our understanding of how specific traits influence various agroecological outcomes, including crop performance (Murphy *et al.*, 2008; Rolhauser *et al.*, 2022), resource utilization (Vicente *et al.*, 2019; Borden *et al.*, 2020), and adaptability to changing environmental conditions (Reynolds *et al.*, 2005; Martin *et al.*, 2017). While all traits are functional within particular contexts (Sobral, 2021), traits have rarely evolved in isolation from one another due to pleiotropy and/or ecophysiological and biomechanical trade-offs, cumulatively leading to phenotypic integration (Ackerly *et al.*, 2000; Denison, 2012). As such, a more comprehensive view of plant trait variation is offered through analyses of multi-trait functional spaces, which reflect both within-trait variation and between-trait covariation (Cornwell *et al.*, 2006; Blonder *et al.*, 2014; Laughlin & Messier, 2015; Carmona *et al.*, 2016).

Functional spaces of crop species are determined by the structure of trait variation and covariation in wild ancestors, and the subsequent influence of domestication (Wood *et al.*, 2015; Nimmo *et al.*, 2023). During domestication, crops undergo intentional selection for specific performance traits including increased yield, uniformity, and adaptation to cultivation practices (Gaut *et al.*, 2018). These selection pressures, when applied for specific growing conditions, can result in the fixation of favorable alleles and a decrease in genetic variation within crop populations, and as a result, this process potentially decreases the range of phenotypic trait values (Streit Krug *et al.*, 2023). Alternatively, the introduction and adaptation of crops to new growing environments can result in the emergence of distinct phenotypes within crop species that expand trait ranges (Ross-Ibarra *et al.*, 2007). Such increases in phenotypic diversification have been achieved through several processes, such as regional adaptation or the incorporation of wild relatives in breeding programs (Streit Krug *et al.*, 2023). Instead, trait covariation, unlike trait ranges, has been largely overlooked in plant breeding, particularly in biotechnological applications (Denison, 2012).

Quantifying how the functional trait space of crops changes with greater crop genetic diversity is therefore a key challenge in agriculture. Here, we propose characterizing 'functional space accumulation curves' to explore the potential for phenotypic diversification within crop populations, as a means to further extend our understanding of the functional consequences of crop genetic diversification and/or erosion. These curves specifically quantify how the accumulation of functional trait space changes as a function of the number of genotypes within a crop species (Fig. 1). Functional space is measured here as the size of the n -dimensional trait space or 'hypervolume': a multivariate quantification of the total trait space for a given set of organisms (Blonder *et al.*, 2014). These curves are constructed by randomly selecting subsets of genotypes from a species and calculating the n -dimensional hypervolumes occupied by each subset. Similar approaches have been used for identifying the number of individual samples (i.e. the number of individual plants or farms) necessary to achieve a detailed understanding of crop functional diversity across multiple spatial scales (Isaac & Martin, 2019), but have yet to be tested as a means of quantifying

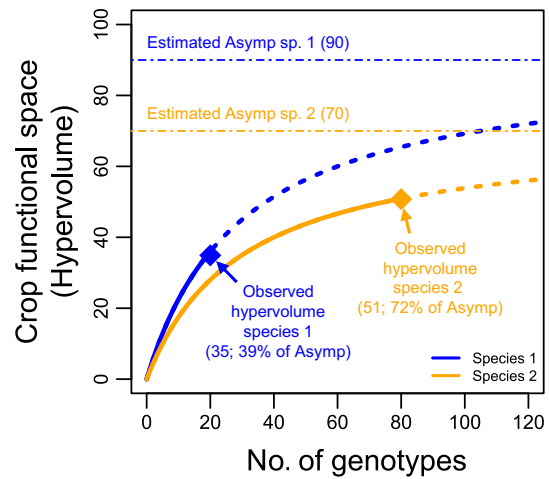


Fig. 1 Functional space accumulation curves describe the relationship between the size of crop functional spaces (or hypervolumes; a unitless metric of multivariate trait space) and the number of genotypes. Gradients of genotype numbers are created by drawing random subsets of different sizes from a pool of genotypes. In this example, the hypervolume of crop species 1 (blue) is 35 with 20 genotypes, while the hypervolume of crop species 2 (orange) is 51 with 80 genotypes (continuous lines and diamonds). The extrapolated portion of the curves (dashed lines) indicates that the potential diversity of crop species 1 (the one with smaller observed hypervolume) is higher than that of crop species 2, as the estimated hypervolume asymptotes are 90 and 70 (dot-dashed lines along the y-axis). Indeed, observed hypervolumes (diamond points along the y-axis) account for 39% and 72% of their respective asymptotes, or total theoretical crop trait diversity. Furthermore, both species would require 120 genotypes to reach 80% of their respective asymptotes. This exercise shows that asymptote calculation can reveal patterns that could not be seen based on differences in observed hypervolumes alone.

genotype–phenotype diversity relationships in crops. Here we show that functional space accumulation curves can be used to: evaluate whether additional genetic diversity indeed results in a trait expression that occupies novel functional space; assess the effectiveness of different sampling strategies for capturing functional diversity in crops and agroecosystems; and quantify the size of a genotypic pool necessary to meet a certain functional diversity target (Fig. 1).

We test our ideas by employing published datasets of four key crop species including barley (*Hordeum vulgare* L.), rice (*Oryza sativa* L. subsp. *japonica*), soybean (*Glycine max* (L.) Merr.), and winter durum wheat (*Triticum turgidum* ssp. *durum* (Desf.) Husn.). We then use these datasets to quantify functional space accumulation curves for each species, based on phenotypic traits associated with crop growth, development, and resource-use efficiency: time to reproduction, plant height, specific leaf area, and leaf N concentration (Table 1). These species were chosen due to their agricultural significance, contributing to *c.* 38.5% of agricultural lands globally (Martin *et al.*, 2019), along with a wealth of available genotype and trait data. We also estimate functional trait space accumulation curves of *Arabidopsis thaliana* (L.) Heyhn, an annual species commonly employed as a model species in plant eco-evolutionary research (Koornneef *et al.*, 2004) which has not been subjected to artificial selection pressures. We

Table 1 Ecological and agronomic significance of the four traits considered here to characterize functional trait space accumulation.

Trait (Units)	Ecological significance	Agronomic significance
Plant height, H (cm)	Taller plants possess a competitive advantage in light acquisition. However, tall plants necessarily invest resources in nonphotosynthetic supporting organs, thereby generating a trade-off between growth and survival in closed canopies (Westoby <i>et al.</i> , 2002)	Breeding for taller plant varieties leads to higher yield potential, as greater H allows for greater light interception and photosynthetic capacity. However, excessive height can lead to lodging (stem breakage), which negatively affects crop productivity. Also, height at the stand level can compromise yield (Anten & Vermeulen, 2016)
Time to reproduction or heading (degree-days)	A key phenological trait, determines the timing of reproduction and seed production (Wolkovich <i>et al.</i> , 2014). Influences the interactions of reproductive parts with the abiotic environment, as well as other organisms such as pollinators, herbivores, and seed dispersers	Knowledge of heading guides farmers in crop management and planning, by informing optimized planting schedules, estimates of time required for crop maturation, and synchrony of planting with favorable environmental conditions. This trait is used to improve the yield and quality of agricultural produce (Egli, 2011)
Specific leaf area, SLA (m ² kg ⁻¹)	Quantifies light capture per unit investment in leaf biomass. High SLA enables rapid growth, although high SLA is hypothesized to relate to greater vulnerability to abiotic stress, herbivory, and other forms of damage (Poorter <i>et al.</i> , 2009). Therefore, SLA represents a trade-off between resource acquisition and conservation	Crops with higher SLA can potentially achieve higher photosynthetic rates and growth rates. Farmers can choose cultivars with specific SLA values to match their production goals and environmental conditions. However, high SLA can also increase the susceptibility of crops to water stress, pests, and diseases (Zhou <i>et al.</i> , 2020)
Leaf nitrogen concentration, LNC (%)	A key indicator of plant nutrient status that influences plant–environment interactions (Chapin III, 1980). N is an essential nutrient for plant growth and can limit primary production. Leaf N concentrations are closely correlated with photosynthetic rates, plant growth rates, and the availability of nutrients to other organisms such as herbivores and decomposers	Measuring LNC helps determine crop nutritional status. This trait therefore aids in diagnosing nutrient deficiencies, optimizing fertilizer applications, and ensuring efficient use of N-based inputs. Balancing LNC is crucial to avoid excessive fertilization, which can lead to environmental issues (Gastel & Lemaire, 2002)

take advantage of the extensive genetic and phenotypic information available for this wild species (Przybylska *et al.*, 2023) to broadly explore if functional trait space accumulating curves may also inform our understanding of the role domestication plays in shaping functional trait space occupancy. Our analysis specifically asks: (1) do functional space accumulation curves of crops exhibit saturating asymptotic shapes? If so, (2) what percentage of this theoretical maximum trait space is occupied by the available genotypic pools of these crops; and (3) how many genotypes are needed to account for a high and biologically meaningful percentage of the asymptotic space among species? We also ask (4) are functional trait space accumulation curves able to capture the influence of domestication on plant trait expression? Finally, we ask (5) do theoretical maximum trait spaces vary across species in relation to trait ranges and trait covariation?

Materials and Methods

Target species and data gathering

We assembled a trait dataset for a total of $n = 324$ genotypes belonging to barley ($n = 73$), rice ($n = 47$), soybean ($n = 25$), and winter durum wheat ($n = 179$). Based on most recent (2021) data from the Food and Agricultural Organization (FAO) of the United Nations (FAO, 2021) barley, rice, soy, and wheat contribute to *c.* 48.9, 165.3, 129.5, and 220.8 million ha, respectively, of agricultural land globally (though note that the FAO does not differentiate wheat types). Therefore, our analysis was designed to inform an understanding of phenotypic trait variation across the primary crops in 3.3%, 11.3%, 8.8%, and 15.1% of

agricultural land globally, for a total of 38.5%. In addition to their importance in the global food system, these crops have long been among the most intensively studied in terms of crop responses to environmental change (e.g. Liu *et al.*, 2019) and agricultural management (e.g. Cartter & Hartwig, 1962). By extension, these crops represent model systems for research surrounding crop biology and ecology (e.g. Izawa & Shimamoto, 1996; Dawson *et al.*, 2015), and receive among the most attention in large-scale crop breeding programs (e.g. Wissuwa *et al.*, 2016; Loskutov & Khlestkina, 2021).

Winter durum wheat is an annual cereal crop that exhibits a considerable range of environmental adaptability. Different wheat varieties are cultivated in various regions world-wide including those in temperate, Mediterranean, and semi-arid climates (Mariani *et al.*, 2021). We gathered trait data for 179 winter durum wheat genotypes that are publicly available in Montazeaud *et al.* (2020) and Lemoine *et al.* (2023). The 179 inbred lines of durum wheat derived from a diversified evolutionary prebreeding population, built from the crossing between the different compartments of the domestication history of durum wheat, from wild and primitive *Triticum turgidum* sub-species to elite types (David *et al.*, 2014). The experiment was set up on the field in randomly arranged single-genotype plots in November 2017 at Manguio, southern France (INRAE – UE DIASCOPE). Each plot consisted of six 1.5 m long rows with 20 cm between rows (i.e. plot width was 1.2 m) and 2–3 cm between plants of the same row, which resulted in a planting density of 240 plants m⁻². Plant height (H) was measured at heading (i.e. when the spikes began to form) on three plants per plot as the distance (in cm) between soil surface and the highest spike using a low-cost

ultrasonic device for semi-automated measurements (Montazeaud *et al.*, 2021). Leaf traits including specific leaf area (SLA) and leaf nitrogen concentration (LNC) were measured at the end of the tillering stage. For SLA and LNC, one foliar disk with a diameter of 6-mm (surface area 28.27 mm²) was collected from each of four healthy and mature leaves from randomly sampled individuals within each plot (Montazeaud *et al.*, 2020; Lemoine *et al.*, 2023). The disks were dried for a minimum of 48 h at 60°C and weighted to calculate SLA as area/mass. Leaf nitrogen concentration was estimated using spectral reflectance measurements of the foliar disk obtained with a LabSpec 4 Spectroradiometer (Analytical Spectral Devices Inc., Boulder, CO, USA) following in-house calibration (Ecarnot *et al.*, 2013); see further details in Montazeaud *et al.* (2020). A base temperature of 0°C was used to calculate degree-days to heading, and heading date was defined as the date at which spikes become visible in 50% of the plants within a plot (Lemoine *et al.*, 2023).

Barley is an annual cereal crop that can grow in diverse climates, ranging from cool temperate to subtropical regions, with variations in temperature, rainfall, and day length (Verstegen *et al.*, 2014). We gathered trait data for 73 barley genotypes from an unpublished trial that had the purpose of screening these genotypes based on their functional traits (e.g. see Díaz *et al.*, 2016) for further experiments. These genotypes represent all the malting barley genotypes maintained by the French 'Small grain cereals Biological Resources Centre' (https://www6.clermont.inrae.fr/umr1095_eng/Organisation/Experimental-Infrastructure/Biological-Resources-Centre), which is a reference list for Europe. These genotypes included 61 modern varieties, seven landraces, and six breeding lines. The 73 genotypes were grown in February–July 2021 in Montpellier, France, in controlled glasshouse conditions. Single plants were grown in 4-l pots, with four pots (replicates) per genotype. Temperature was maintained between 18°C and 25°C, and plants were irrigated twice a week. Plant height and leaf traits were measured at heading on each plant. Plant height was measured as the distance (in cm) between soil surface and the base of the spike borne by the tallest tiller. A mature N-1 leaf (i.e. that below the flag leaf) was collected from each plant, rehydrated overnight, scanned, weighed, and then dried at 60°C for 72 h. The pictures of scanned leaves were then measured using the IMAGEJ software (Wayne Rasband; National Institute of Health, Bethesda, MD, USA) to calculate SLA. Then LNC was determined on the same leaf after grinding using a CN Elemental Analyser (CHN model EA 1108; Fisons Instruments, Glasgow, UK). The heading date was measured for each plant and converted to degree-days using a 0°C base temperature.

Rice is a staple annual cereal crop primarily grown in tropical and subtropical regions (Chauhan *et al.*, 2017). We gathered trait data for 47 rice genotypes that are publicly available from de Tombeur *et al.* (2023). These genotypes were selected from the European Rice Germplasm Collection (Courtois *et al.*, 2012) to maximize phenotypic and genotypic diversity (de Tombeur *et al.*, 2023). The experiment was conducted in 8.8-l pots in outdoor conditions in an experimental field of the Centre d'Ecologie Fonctionnelle et Evolutive (CEFE, Montpellier, France), from

June to September 2021, with one plant per plot and four pots (replicates) per genotype. Traits were measured at the beginning of the flowering stage. Plant height was measured as the distance (in cm) between soil surface and the base of the spike borne by the tallest tiller. A mature N-1 leaf (i.e. that below the flag leaf) was collected from each plant, rehydrated overnight, scanned, weighed, and then dried at 60°C for 72 h. The pictures of scanned leaves were then measured using IMAGEJ software (Wayne Rasband; National Institute of Health) to calculate SLA. Then, LNC was determined on the same leaf after grinding using a CN Elemental Analyser (CHN model EA 1108; Fisons Instruments). A base temperature of 10°C was used to calculate degree-days to heading for each plant.

Soybean is a leading annual oilseed crop predominantly cultivated in warm temperate to subtropical regions (Wilcox, 2004). We gathered trait data for 25 soybean genotypes from a field experiment conducted by Rotundo *et al.* (2014). Elite soybean cultivars from maturity groups IV–V were evaluated on a Vertic Argiudoll located in Zavalla, Santa Fe, Argentina. Planting was carried out in November 2009 and December 2010, with the plants placed in plots measuring 5.5 by 0.52 m at a density of 38 plants m⁻², with three replicates per genotype. Traits were measured at the beginning of the flowering stage (R1), which was defined at the plot level when at least 50% of the plants reached that stage (Fehr & Caviness, 1977). A base temperature of 10°C was used to calculate degree-days to reproduction (R1, generically referred to here as heading). Plant height was measured as the distance from the soil surface to the tallest node in the main stem having an expanded leaf (as defined in Fehr & Caviness, 1977). In each plot, the height of 10 consecutive plants was measured and a mean per plot was recorded. After height measurements, plants were hand clipped from 0.5 m of the two central rows in each plot (c. 20 plants). Upon sampling, plants were kept in water to avoid dehydration. Leaves were detached from the plants and total sample leaf area was measured using a LICOR 3100 leaf area meter (LICOR Biosciences, Lincoln, NE, USA). After this, leaves were dried at 60°C for at least 96 h and weighed, and this was used to calculate SLA. Leaf N concentrations in leaves were obtained on ground subsamples using a TruSpec N Analyzer (LECO Corp., St. Joseph, MI, USA).

Arabidopsis thaliana is a winter–spring annual native to Europe and central Asia, but it has expanded and naturalized across the world (Koornneef *et al.*, 2004). *Arabidopsis thaliana* is known for its broad ecological distribution and adaptability to various environments, resulting in a large latitudinal range from North Scandinavia to central Africa (Koornneef *et al.*, 2004). We compiled data on the four target traits for 75 *A. thaliana* genotypes by intersecting two data sources. Time to heading, SLA, and LNC was extracted from the AraDiv database (publicly available; Przybylska *et al.*, 2023), which contains information on a total of 730 accessions selected to maximize the geographic and genetic coverage of *A. thaliana*. Plants were grown between February and July 2021 in 80-ml pots (one plant per plot and three replicates per genotype) in a glasshouse under controlled conditions in the experimental field of CEFE, Montpellier, France (Przybylska *et al.*, 2023). For SLA, one leaf per plant was cut and

photographed, and the one-sided projected leaf area was measured using IMAGEJ software (Wayne Rasband; National Institute of Health). Harvested leaves were then dried at 60°C for at least 72 h to calculate SLA. Leaf nitrogen concentration was estimated using a predictive model developed by Vasseur *et al.* (2022) that is based on near-infrared spectroscopy measurements; see further details in Przybylska *et al.* (2023). Time to flowering (generically referred to here as heading) was calculated for each plant as the number of degree-days between sowing and the appearance of the first flower using a base temperature of 4°C. Plant height data was extracted from Vasseur *et al.* (2018), such that height corresponds to the length of the main flowering stem measured with a ruler at the end of reproduction after the plant was fully dried. In this experiment, plants were grown in four replicates (300-ml pots, one plant per plot) per accession in a glasshouse between December 2015 and May 2016.

Across all datasets, the target traits employed in our final analysis were all quantified using methods outlined in trait collection handbooks (Pérez-Harguindeguy *et al.*, 2013), therefore facilitating the first conversion into common units (Table 1). Moreover, all traits were collected at similar plant growth stages, across similar replication levels among studies. Therefore, while direct cross-species comparisons were not the main focus of our analysis here, our datasets remain comparable in a manner consistent with meta-analyses of functional trait variation within and among plants (e.g. Díaz *et al.*, 2016).

Data analysis

Before analysis, we first pooled together the five trait datasets, averaged the replicates to obtain one mean value per trait per genotype, and then standardized this resulting trait data to zero mean and unit variance. Standardizing after this merging of datasets allows plotting accumulation curves on the same, common scale across datasets. We then used a principal components analysis (PCA) based on these data to: visualize observed functional spaces occupied by each species; and select uncorrelated traits for hypervolume calculations. Based on this analysis, plant height, SLA, and LNC (all standardized to zero mean and unit variance) were selected for hypervolume calculations and estimation.

Then, for each species individually, we selected 1000 random subsets of sizes 4 to n genotypes and calculated hypervolume sizes for each subset using the 'hypervolume_box' function in the HYPERVOLUME R package (Blonder *et al.*, 2014, 2018). The hypervolume_box function creates a kernel density estimate by placing box-shaped kernels on each data point and then generating random points within each kernel. The density of the kernel at each point is calculated by performing a range query on a tree that divides the data recursively. This density information is then used to resample the random points, making their density uniform and fixing their number. The function then estimates the n -dimensional hypervolume (unitless) from this resampled set of points. This procedure was used to calculate the mean hypervolume and associated 95% confidence intervals for each subset size.

The relationship between trait hypervolume and subset size was analyzed using tools developed for the analysis of

species–area relationships contained in the SARS R package (Matthews *et al.*, 2019). Specifically, we used the cumulative beta-P distribution in this package – a highly flexible 4-parameter sigmoid function – to estimate an asymptote in the number of genotype–hypervolume relationship, usually fitting data sets closely and showing good extrapolation accuracy (Tjørve, 2003; Dengler, 2009). Specifically, the cumulative beta-P distribution is given by the following equation:

$$\text{Hypervolume} = d \left(1 - \left(1 + \left(\frac{n}{c} \right)^z \right)^{-f} \right) \quad \text{Eqn 1}$$

where n is the number of genotypes, d is the theoretical asymptotic maximum hypervolume, c affects the shape and scaling of the curve, z determines the curve steepness, and f influences the curvature (such that higher values of f result in a more concave shape). According to our own analyses, the beta-P model indeed fitted our data consistently better than the other 10 asymptotic models available in the 'SARS' R package (Supporting Information Table S1). From the fitted functions for each species, we estimated the asymptotic hypervolumes (parameter d), and calculated both the percentage of the asymptotic space that is represented in the available genotypic pools, and how many genotypes are needed to account for a given percentage of the estimated asymptote. For the latter, we are interested in relatively high percentages that, while nearly saturating the asymptotic space, would be accounted for a reasonable number of genotypes, since the number of genotypes necessary to reach the asymptote is infinite by definition. Thus, we rearranged Eqn 1 to obtain.

$$n = c \left((1-p)^{\frac{1}{f}} - 1 \right)^{\frac{1}{z}} \quad \text{Eqn 2}$$

where p is the target proportion of the asymptote, d . Here, we used 0.8 (or 80%) as the target proportion to interpret as

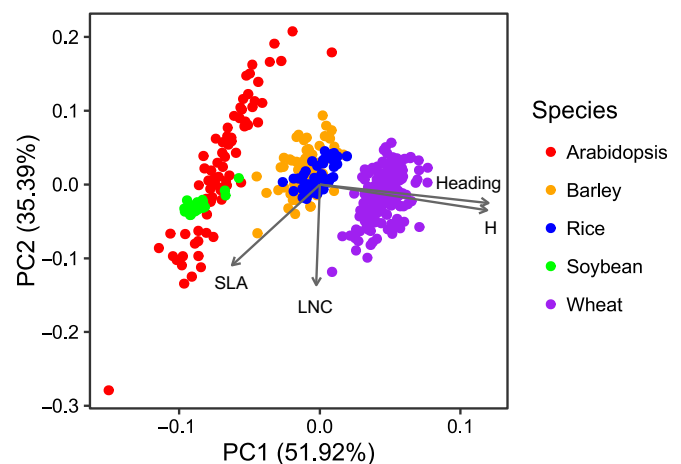


Fig. 2 Principal components analysis (PCA) summarizing the trait distribution of the five study species including *A. thaliana*, barley, rice, soybean, and wheat. The PCA is based on four traits: time to heading (Heading, number of degree-days), plant height (H, cm), specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$), and leaf nitrogen concentration (LNC, %).

an approximate for ecologically meaningful diversity from functionally and farmer-relevant traits (Khoury *et al.*, 2022), and we rounded up the estimations to the nearest whole

number. Eqn 2 (or the equivalents for other underlying models) can be used to calculate genotype numbers for other proportions.

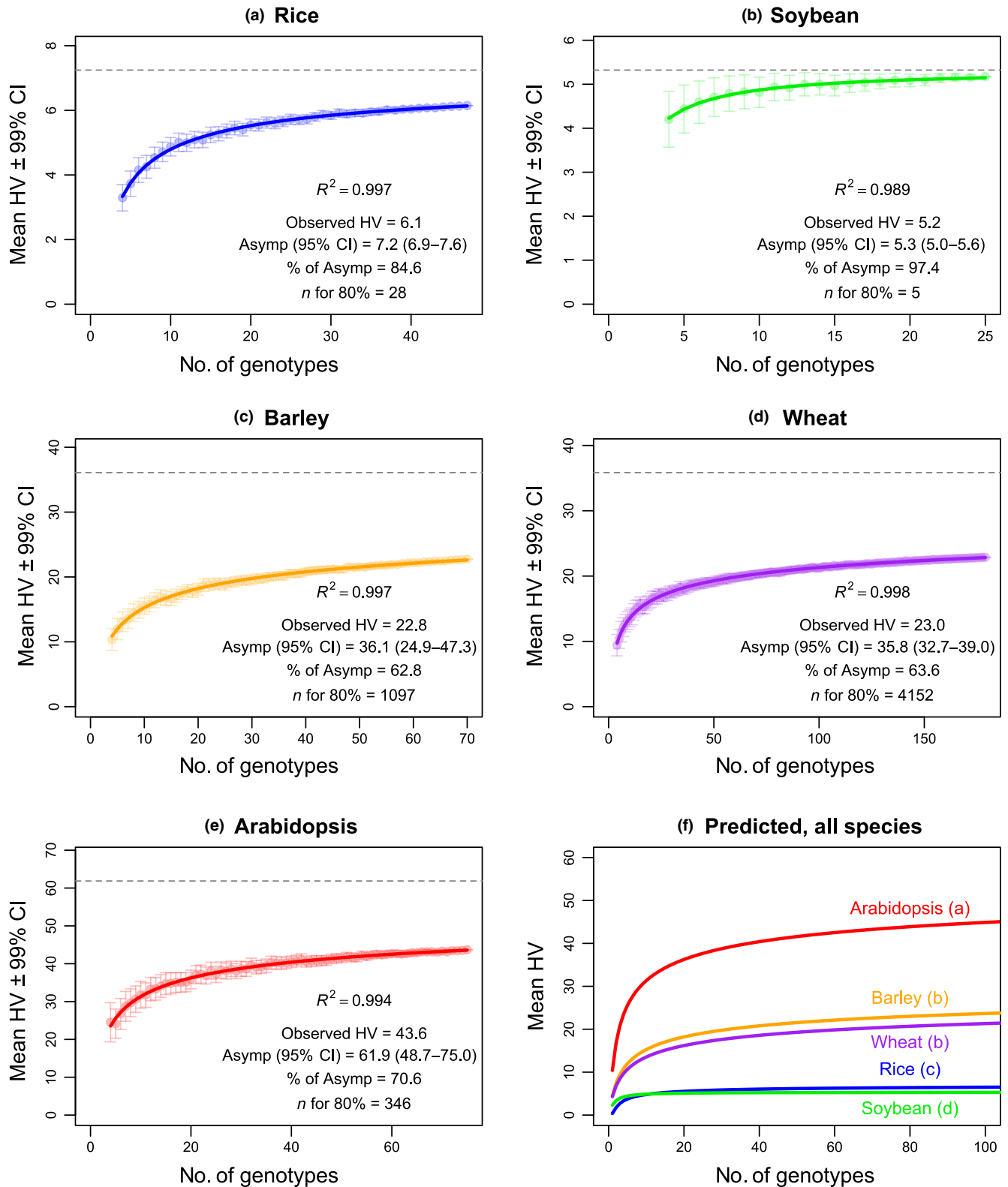
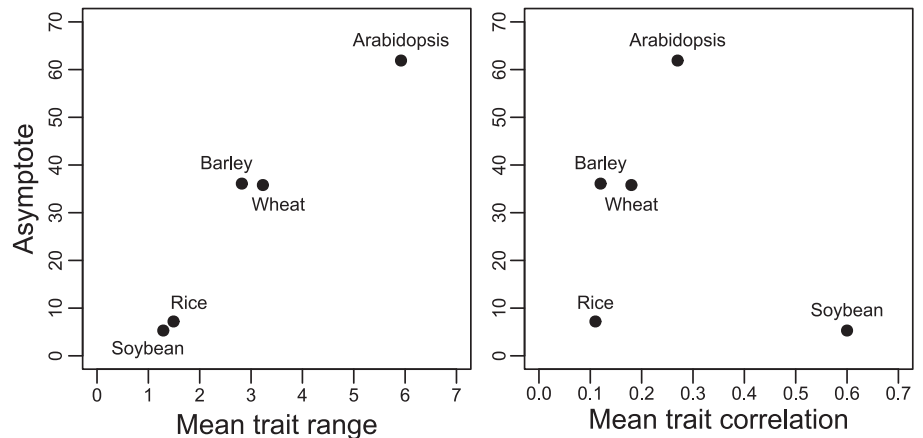


Fig. 3 Randomization tests evaluating variation in estimated three-dimensional hypervolumes for rice (a), soybean (b), barley (c), wheat (d), and *A. thaliana* (e) as a function of the number of genotypes. Hypervolumes (HV) were calculated based on plant height, specific leaf area, and leaf nitrogen concentration. Data points represent the mean hypervolume calculated for 1000 randomized datasets for varying number of genotypes. Error bars correspond to 95% confidence interval based on the normal distribution. Cumulative beta-P models were fitted to mean hypervolume data (continuous line); gray horizontal dashed lines show the asymptote estimated by these models. Results shown inside panels are model's goodness of fit (R^2), the observed hypervolume (corresponding to the rightmost data point), the estimated asymptotic hypervolume (Asymp), the percentage of the asymptote represented by the observed hypervolume (% of Asymp), and the number of genotypes needed to account for at least 80% of the asymptote (n for 80%). Scales in (a–e) are adjusted proportionally to estimated asymptotes and are therefore not equal. Panel (f) shows all the predicted curves together, and letters in parenthesis show significant differences between species in terms of asymptotic hypervolume based on their 95% confidence intervals.

Fig. 4 Relationships between mean trait range, mean trait correlation, and estimated asymptotes from accumulation curves for the five species. Mean trait ranges are the means across the three traits that were used to estimate hypervolumes (plant height, specific leaf area, and leaf nitrogen concentration), while mean trait correlations are the means of the three bivariate Pearson correlations between these traits, all of them calculated for each species separately.



Results

Functional trait spaces of the five species differentiated along a heading–height gradient depicted by PCA axis 1, which explained 51.9% of the total trait variance across our pooled dataset (Fig. 2; see also mean trait values in Table S2). Along this gradient, soybean and *A. thaliana* were the shortest species which were the quickest to reach the reproductive stage, while durum wheat represented the tallest species that is slowest to reproduction; barley and rice were generally intermediary between these two end points. PCA axis 2 accounted for 35.4% of the total variance and mostly reflected intraspecific variability in LNC and, to a lesser extent, SLA which was also associated with axis 1 (Fig. 2). We selected height, LNC, and SLA for further hypervolume calculations since these traits represent the first two PCs and their bivariate correlations are relatively low (i.e. $r < 0.5$; Table S3).

All functional trait space accumulation curves showed a saturating asymptotic shape with extremely high model fits ($R^2 \geq 0.989$ in all five cases; Fig. 3). In our datasets, rice and soybean were very close to reaching their modelled potential trait space asymptotes, reaching *c.* 84.6% (with 47 genotypes) and 97.4% (with 25 genotypes) of estimated maximum hypervolume space, respectively (Fig. 3a,b). By comparison, barley (70 genotypes), durum wheat (179 genotypes), and *A. thaliana* (75 genotypes) only attained between 60% and 65% of their potential estimated maximum trait space in our datasets (Fig. 3c–e). Rice and soybean were also similar in that only a relatively small number of genotypes (i.e. 28 and 5, respectively) accounted for 80% of their respective theoretical maximum trait space values (Fig. 3a,b). This number of genotypes was orders of magnitude

greater for the other species in our analysis. Specifically, 346, 1097, and 4152 genotypes are needed to attain 80% of the maximum trait space for *A. thaliana*, barley, and durum wheat, respectively (Fig. 3c–e). Plotting all curves together shows a clear pattern of separation between species (Fig. 3f). Overall, estimated asymptotes across the five species were positively and significantly correlated with mean trait ranges ($R = 0.97$; $t = 7.07$, $DF = 3$, $P = 0.006$), but not with mean trait correlations ($R = -0.31$; $t = -0.57$, $DF = 3$, $P = 0.607$; Fig. 4). Furthermore, there was no clear correlation between asymptotes and genotypic pool size ($R = 0.44$; $t = 0.85$, $DF = 3$, $P = 0.457$) or between mean trait ranges and genotypic pool size ($R = 0.35$; $t = 0.64$, $DF = 3$, $P = 0.565$) across the five species (Fig. S1).

Discussion

The observed saturating asymptotic shape of the functional space accumulation curves for all species in our study indicates that there is a diminishing return of functional diversity with increasing genetic diversity. That is, the increment in functional trait space occupied due to the addition of a single genotype becomes progressively smaller as we increase the number of genotypes. Importantly, this implies a degree of functional redundancy that exists among different genotypes, and further, that there exists a limit to intraspecific functional crop diversity despite progressive increases in the number of genotypes added to our analysis.

Asymptotic functional accumulation curves resemble the role of species dominance in determining an asymptotic relationship between species diversity and ecosystem function (Schwartz *et al.*, 2000; Loreau *et al.*, 2001). In this context, our results

suggest that there are single phenotypes represented by several genotypes within each species. This phenotypic dominance may be unexpected and rather undesirable given the breeding efforts on these major crops. However, it should be noted that such breeding efforts have largely targeted yield rather than functional traits (Milla *et al.*, 2015). Crop diversification therefore requires careful selection of genotypes that capture a substantial portion of the functional diversity (Moore *et al.*, 2023). For plant breeders, this implies that strategic selection and breeding of genotypes with distinctive trait values (*sensu* Violle *et al.*, 2017) can lead to significant gains in functional diversity and move crop curves to higher asymptotes, but that these gains may nevertheless decrease in terms of overall potential crop functional biology. For farmers, particularly those interested in crop diversification via variety mixtures (Kjær *et al.*, 2009; Barot *et al.*, 2017; Reiss & Drinkwater, 2018; Wuest *et al.*, 2021), asymptotic functional accumulation curves imply that the greatest gains in intraspecific functional diversity can be expected when farms transition from extremely limited genetic diversity, like genetic monocultures, to genotype mixtures with strategically distinctive trait values.

The identification of a small number of genotypes that can account for a high percentage of the asymptotic space has important implications for plant breeding. For instance, in rice and soybean, only a few genotypes were necessary to capture 80% of their respective asymptotic spaces (28 and 5 genotypes, respectively). Targeted selection and breeding efforts focused on genotypes with favorable functional traits can result in substantial gains in functional diversity. However, achieving a high percentage of the asymptotic space would require a much larger number of genotypes in crops such as barley and durum wheat (1097, and 4152, respectively) and to a lesser extent, *A. thaliana* (346). This suggests that species like barley and durum wheat may possess a higher potential for functional diversification, but realizing a significant portion of that potential would necessitate more extensive efforts in terms of genotype selection and breeding.

A full cross-species comparison of functional accumulation curves across species is not the main goal of this analysis, as datasets emerged from studies that employed different designs and methods. Biases could also potentially arise from differences in genotypic pool size, although our results do not show striking biases in this regard. Rather, asymptotes correlated better with trait ranges, a correlation that (only arguably, given the small number of datasets analyzed) seems at least in part related to biological differences in terms of niche breadth. Under more homogeneous data collection conditions, however, our methodological approach would allow such comparisons of cross-species patterns in genotype–trait space relationships. For instance, *A. thaliana*, the only noncultivated species in our study, showed a distinctively higher asymptote compared with crops, which is consistent with the hypothesis that domestication has narrowed crop phenotypic space. Among crops, barley and wheat displayed higher asymptotes compared with rice and soybean. The former two are relatively cool-season species (base temperature 0°C) and were domesticated *c.* 10 000 yr ago in the Fertile Crescent, western Asia (Haas *et al.*, 2019). The other two are considered warm-season species (base temperature 10°C) that were

domesticated around the same time in eastern Asia (Molina *et al.*, 2011; Sedivy *et al.*, 2017).

Moreover, the calculation of asymptotes and the extrapolation of curves revealed patterns that could not be seen based on differences in observed hypervolumes alone. For instance, the observed hypervolume for the *A. thaliana* genotypic pool (75 genotypes) was almost twice as that of barley (70 genotypes), while the difference inverted for *n* for 80%, being more than three times larger for barley. This result stresses that the requirements for a given genotypic pool to achieve a certain desired level of functional space occupation cannot be directly inferred from observed hypervolumes and highlight the utility of functional space accumulation curves. In sum, when paired with our functional trait space accumulation curve method, a larger sample containing species with contrasting domestication histories and from different biogeographic regions will allow to test the role of these important factors on crop functional diversity, as well as the mechanistic roles of niche breadth and ecophysiological trade-offs in structuring genotype–trait space relationships.

Our approach can also be applied at different spatial scales. At large scales which are relevant to breeding programs, asymptotes can inform on the potential of genotypic pools to increase functional diversity. This may be particularly relevant to prioritize and compare crops with different levels of domestication, from existing crops, to underutilized ones and wild species with cropping potential (Streit Krug *et al.*, 2023). Furthermore, as calls for transformation in agriculture gain momentum (Wezel *et al.*, 2020), a more complete understanding of how expanding crop portfolios, in terms of enhanced genotypes on farms, will impact agroecosystem function is essential. Our analytical approach can be extended to consider multiple crop species in order to guide the design of maximally diverse farms. For instance, root trait space analysis has been used to determine coordination between crop species (Nimmo *et al.*, 2023), and by extension, our functional trait space accumulation curves can help assess questions related to the species and genotypes required to saturate root trait space to enhance nitrogen acquisition.

Our study underscores the importance of functional ecology in the context of crop diversity management and plant breeding, where our analytical framework can be used to: identify the minimum set of genotypes to achieve desired trait expression outcomes; and/or design parsimonious phenotyping experiments. The application of functional space accumulation curves enables quantitative assessments of the potential and limitations of functional trait space occupation within and across crop populations. This knowledge can guide the selection, breeding, and combination of genotypes with desirable functional traits, ultimately leading to the development of more resilient and sustainable agricultural systems. Furthermore, our findings highlight the significance of considering species-specific characteristics when designing diversification strategies, as different crops exhibit distinct patterns of functional diversity and potential for diversification.

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Competing interests

None declared.

Author contributions

AGR contributed to the conceptualization, formal analysis, and writing – original draft. MEI contributed to the conceptualization, funding acquisition, supervision, and writing – review and editing. CV contributed to the conceptualization, supervision, and writing – review and editing. ARM contributed to the conceptualization and writing – review and editing. FV contributed to conceptualization, investigation, and writing – review and editing. TL and LM contributed to the investigation and writing – review and editing. FF and DV contributed to the conceptualization. JLR contributed to the investigation.

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Data availability

The data used in this manuscript are available in Dataset S1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Species, genotype and traits (heading, height (H), specific leaf area (SLA), leaf nitrogen concentration (LNC)) data.

Fig. S1 Relationship between available genotypic pool size, mean trait range, and estimated asymptotes from accumulation curves for the five species.

Table S1 Goodness-of-fit statistics.

Table S2 Species mean trait values.

Table S3 Bivariate trait correlations.

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