Received: 20 November 2025 | Accepted: 22 May 2026

DOI: 10.1111/1365-2435.70376

Functional Ecology

RESEARCH ARTICLE

Nitrogen fertilization promotes wheat–weed coexistence through niche differentiation and fitness equalization

Yizhong Rong[1,2] | Weiqiang Liu[1] | Xiang Liu[3] | Abolghassem Emamverdian[1] | Zhen Zhang[2] | Shengman Lyu[4] | Li Zhang[1]

[1]National Key Laboratory for the Development and Utilization of Forest Food Resources, College of Ecology and the Environment, Bamboo Research Institute, Nanjing Forestry University, Nanjing, P. R. China

[2]College of Resources and Environment, Anhui Agricultural University, Hefei, P. R. China

[3]State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, College of Ecology, Lanzhou University, Lanzhou, P. R. China

[4]Department of Ecology and Evolution, University of Lausanne, Lausanne, Switzerland

Correspondence
Shengman Lyu
Email: shengman.lyu@unil.ch

Li Zhang
Email: zhangl@njfu.edu.cn

Funding information
National Natural Science Foundation of China, Grant/Award Number: 32101260

Handling Editor: Kechang Niu

Abstract

1. Nitrogen fertilization is commonly applied to increase crop yields in agroecosystems. Beyond its direct benefits, nitrogen fertilization may also influence crop production indirectly by altering crop–weed competition. Moreover, nitrogen fertilization can simultaneously threaten the biodiversity of both natural and managed communities, including weed diversity in wheat fields. Such diversity losses may weaken resistance to antagonists (e.g. pests and pathogens), compromising agroecosystem health and crop productivity. However, how nitrogen fertiliation affects crop-weed coexistence in agroecosystems, and the mechanisms underlying these effects, remain unclear.
2. Here, we conducted a competition experiment between wheat and two dominant weeds (i.e. *Avena fatua* L. and *Echinochloa crus-galli* (L.) P. Beauv.) by growing a total of 2490 individuals in a response-surface design with and without nitrogen fertilization. At the end of growing season after 8 months, we harvested one-third individuals to measure individual seed production to parametrize competitive population models, allowing to quantify niche and fitness differences and to predict competitive outcomes. We then measured various functional traits at individual level on the remaining two-thirds at their peak growth, including plant height, three leaf traits (e.g. leaf area, specific leaf area), five root traits (root area, specific root area) with and without nitrogen fertilization.
3. We found that nitrogen fertilization facilitated coexistence between wheat and weeds, but the underlying processes differed for the two weed species with distinct functional strategies. Specifically, fertilization increased the niche differences between wheat and *E. crus-galli*, resulting from amplified root area and length differences between them. In contrast, nitrogen addition reduced the competitive advantage of wheat over *A. fatua* and increased the likelihood of their coexistence by increasing *A. fatua*'s seed mass, specific root area, and length while reducing wheat height.

Yizhong Rong and Weiqiang Liu—contributed to the work equally and should be regarded as co-first authors.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2026 The Author(s). *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

4. *Synthesis*. These findings demonstrate that nitrogen addition can affect coexistence through both niche and fitness difference-related processes and reveal the effect of nitrogen fertilization on plant coexistence is highly species-specific. Our study highlights the importance of trait plasticity for mediating coexistence under varying nutrient conditions and offers practical recommendations for selecting wheat varieties that support sustainable weed management under varying fertilization regimes to balance crop production and biodiversity conservation.

KEYWORDS
competition dynamics, nitrogen fertilization, phenotypic plasticity, plant functional traits, species coexistence, sustainable agriculture, trait-mediated interactions

1 | INTRODUCTION

Nitrogen fertilization is a common practice to enhance yield in agroecosystems, but it can also threaten biodiversity in both natural and managed communities (Hautier et al., 2009; Midolo et al., 2019; Suding et al., 2005; Xiao et al., 2021). Studies in natural ecosystems suggest that nitrogen enrichment can often intensify aboveground competition and drive non-random species loss through competitive exclusion (Midolo et al., 2019). While neutral or even positive effects on coexistence have also been reported (Dostál, 2023). Wheat, a staple crop supporting over 40% of the global population (FAO, 2023), experiences substantial yield losses due to competition with weeds such as *A. fatua* (wild oats) and *E. crus-galli* (barnyard grass) (Nasim & Shabbir, 2012; Zhang et al., 2019), as well as from pests and pathogens, whose impacts may sometimes be mitigated by maintaining weed diversity (Adeux et al., 2019; Wan et al., 2026). Therefore, understanding how nitrogen fertilization influences competition and coexistence between wheat and weeds is essential for developing sustainable weed management strategies and securing crop production (Chesson, 2000; Chesson, 2020; Dostál, 2023; Kraft et al., 2015; Nelson et al., 2025; Van Dyke et al., 2022). However, whether and through which mechanisms nitrogen fertilization alters competitive interactions between wheat and weeds, and the extent to which these effects depend on the ecological strategies of weed species, remain unclear.

Community coexistence theory offers a useful framework for understanding how nitrogen fertilization influences competitive outcomes between wheat and weeds and for assessing the comprehensive effects of nitrogen fertilization on wheat yield (Chesson, 2000). This theory explains species coexistence through stabilizing mechanisms, which reduce interspecific competition and promote niche differentiation, and equalizing mechanisms, which reduce species differences in competitive ability (i.e. fitness differences) (Chesson, 2000, 2020). First, nitrogen addition could potentially drive competitive exclusion if it increases the asymmetry of competitive hierarchy by disproportionately benefiting stronger competitors (e.g. DeMalach et al., 2017) and/or if it reduces the niche differences by limiting the dimensions of niche space (e.g. Harpole et al., 2016). For example, increased nitrogen availability can enhance the growth of fast-growing, nitrogen-responsive species, giving them stronger competitive advantage and leading to the competitive exclusion of other weaker competitors (Liu et al., 2017; Suding et al., 2005). Although nitrogen fertilization is expected to increase wheat yield directly, it may also influence yield indirectly by altering the balance between niche and fitness differences between wheat and weeds. In particular, wheat yield may be reduced if fertilization disproportionately enhances weed competitiveness or intensifies competition by reducing niche differentiation.

Alternatively, nitrogen addition may facilitate stable coexistence by increasing the competitive ability (i.e. fitness in the community context) of weaker competitors by alleviating nutrient limitation (e.g. Granjel et al., 2023). For example, nitrogen fertilization may increase the intrinsic growth or competitive performance of weaker competitors, thereby equalizing fitness difference and promoting coexistence (e.g. Dostál, 2023; Godoy & Levine, 2014; Granjel et al., 2023; Zhao et al., 2021). Under such conditions, nitrogen fertilization may enhance wheat yield if it disproportionately benefits wheat, but may reduce wheat yield if it favours weeds. In addition, nitrogen fertilization may also promote coexistence by increasing niche difference, for instance by intensifying intraspecific or weakening interspecific competition (e.g. Dostál, 2023). In this case, increased niche differentiation may alleviate competitive pressure from weeds and amplify the positive effects of fertilization on wheat yield. Despite these potential pathways, the mechanisms through which nitrogen addition influences coexistence between wheat and weeds remain poorly understood.

Plastic responses of plant functional traits related to resource acquisition and use can mediate the effects of nitrogen addition on coexistence between wheat and weed (McGill et al., 2006). First, nitrogen addition can lead to plastic changes in phenotypes in the absence of competition. For example, alleviating nitrogen limitation may lead to increased plant height, larger leaves and longer roots (Wang et al., 2022; Zhang et al., 2023). Such changes may facilitate coexistence if they enhance the intrinsic growth or competitive ability of weaker species, or increase niche differentiation (Carmona et al., 2019). Second, trait plasticity in responses to nitrogen addition may also alter the trait differences between interacting species, thereby influencing the strength of interspecific competition

(Bennett et al., 2016; Helsen et al., 2017; Turcotte & Levine, 2016; Yang et al., 2021; Yang et al., 2024). Trait differences between plant species have been shown to be closely related to competition and coexistence (Adler et al., 2013; D'Andrea & Ostling, 2016; Ferenc & Sheppard, 2020; Funk & Wolf, 2016; Kraft et al., 2017; Lyu & Alexander, 2024; Wong et al., 2021; Yin et al., 2021). In particular, greater hierarchical differences in fitness-related traits (i.e. trait value of focal species—trait value of competitor species) are often associated with larger relative fitness differences (Kraft et al., 2017; Kunstler et al., 2012; Lyu & Alexander, 2024), whereas greater absolute differences in niche-related traits (i.e. the absolute value of hierarchical differences) are tend to weaken interspecific competition and increase niche differences (Kraft et al., 2017; Lyu & Alexander, 2024). Thus, examining how traits and trait differences respond to nitrogen enrichment and competition can provide key insights into the functional processes underlying its effects on coexistence between wheat and weeds.

In this study, we investigate how nitrogen addition affects coexistence between wheat and weeds, and through which processes (i.e. niche vs. fitness differences) and functional traits these effects arise. We interacted wheat with two weed species (wild oat (*A. fatua*) and barnyard grass (*E. crus-galli*)) and grew a total of 2490 individuals using a response-surface design involving four varied densities (4, 8, 12, and 16 individuals per pot) and five proportions (wheat: weed ratios of 0:1, 0.25:0.75, 0.5:0.5, 0.75:0.25 and 1:0) under both ambient condition and nitrogen addition (Zhang & van Kleunen, 2019). This design allowed us to quantify niche and fitness differences and to predict long-term competitive outcomes for each wheat-weed pair. We also measured various functional traits on individuals under ambient condition and nitrogen fertilization in different densities, including maximum (MH) and natural adult height (NH), plant leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC), species-level root length (RL), root area (RA), specific root length (SRL), area (SRA) and volume (SRV), and root tissue density (RTD) within a pot (Table 1). We selected these traits as they represent key dimensions of resource acquisition and competitive ability, including light capture (height and leaf traits) and nutrient uptake (root traits). Differences in these traits are expected to shape niche and fitness differences and thus competitive outcomes. With this dataset, we specifically ask: (1) Does nitrogen addition lead to competitive exclusion or stable coexistence in wheat-weed communities? (2) How does nitrogen addition alter intrinsic growth, inter- and intraspecific competition, and how do these changes affect fitness and niche differences? (3) How do trait responses to nitrogen addition, including changes in functional traits and trait differences, mediate competition and coexistence between wheat and weeds?

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted a field competition experiment at Hefei High-Tech Agricultural Park, China (31°55′ 28.17″ N, 117°12′ 12.85″ E, 39 m a.s.l.) in which wheat (*Triticum aestivum* L.) competed with two weed species, wild oat (*A. fatua*) and barnyard grass (*E. crus-galli*). Wheat is one of the major crops sustaining global grain production. Our selection of these two weed species was based on local community structure surveys; wild oats and barnyard grass are among the most abundant weeds in wheat fields in the study area (Pourreza et al., 2010; Zhang et al., 2019), together accounting for approximately 90% relative abundance of the weed community (Zhang et al., 2019). Wild oat, a Mediterranean-origin invasive species, and barnyard grass, a native weed, have both undergone human-driven unintentional selection for crop-like traits, representing parallel adaptive evolution in agroecosystems (Ye et al., 2019). Both weed species are annual herbaceous plants and belong to the Poaceae family (Editorial Committee of the Flora of China, 1993). The study site was located in a northern subtropical monsoon climate in China with a mean annual temperature of 15.7°C and precipitation of 1000 mm. The soil is yellow brown soil and classified as alfisols according to the USDA soil taxonomy (Tao et al., 2016).

TABLE 1 Twelve functional traits measured in this research with their units and descriptions.

Trait		Units	Description
Whole plant	Natural height (NH)	cm	Natural height of an individual plant
	Maximum height (MH)	cm	Maximum height of an individual plant
	Seed mass (SW)	g	Total seed weight produced by an individual plant
Leaf	Leaf aera (LA)	cm^2	Area of a single leaf
	Specific leaf area (SLA)	cm^2/g	Leaf area divided by its dry mass
	Leaf dry matter content (LDMC)	g/g	Dry mass of leaf divided by its fresh mass
Root	Root length (RL)	cm	Total root length of an individual plant
	Root area (RA)	cm^2	Total root area of an individual plant
	Specific root area (SRA)	cm^2/g	Root area divided by its dry mass
	Specific root length (SRL)	cm/g	Root length divided by its dry mass
	Specific root volume (SRV)	cm^3/g	Volume of root divided by its dry mass
	Root tissue density (RTD)	g/cm^3	Dry mass of root divided by its volume

2.2 | Field competition experiment

We designed a field competition experiment to quantify the outcomes of competition of two wheat-weed pairs: wheat-wild oat (WO pair, between *T. aestivum* and *A. fatua*) and wheat-barnyard grass pairs (WB pair, between *T. aestivum* and *E. crus-galli*) under ambient condition and nitrogen fertilization. We used a response-surface experimental design to parameterize competitive population models, allowing to quantify pairwise niche and fitness differences and the competition outcomes (Inouye, 2001; Zhang & van Kleunen, 2019). This design included 20 different density and proportion combinations, with the total density ranging from 4, 8, 12, to 16 individuals per pot, and the proportion of wheat ranging from 0, 0.25, 0.5, 0.75 to 1, resulting in 20 competition-pots for each pair. We also grew individuals without neighbours to estimate intrinsic population growth, each species had five pots. We replicated the design three times and pots were arranged using a random blocking design. In total, we grew 330 pots ((2 pairs × 20 competition-pots + 3 species × 5 pots without competition) × 2 nitrogen treatments × 3 replicates), consisting of 2490 individuals (Figure S1). Among the three replicates, one was used for seed collection, and the other two were used for destructive measurements of shoot and root traits.

In October 2021, we soaked seeds in a 5% H_2O_2 solution for 10 min and washed them three times with sterile distilled water to stimulate germination and sterilize seed surface. We first germinated seeds in germinating boxes under benign conditions in a growth chamber at 25°C and transplanted the germinated seedings into pots (22 cm in diameter, 25 cm in height) when seedlings reached 2–4 cm in height according to the experimental design. Pots without nitrogen fertilization were filled with local loess soil obtained from a nearby wheat field, while pots with nitrogen fertilization received a single application of urea solution (1.018 g N per pot), which was applied to the soil and well mixed before transplanting, following local fertilization practices (Zhang et al., 2019). We replaced any dead seedlings within the first two weeks after transplanting with new ones and watered plants regularly throughout the experiment.

2.3 | Estimating plant intrinsic growth rates and competition coefficients

After eight months when plants reached their peak growth (June 2022), we recorded the actual number of surviving individuals within a pot (i.e. establishment rate). We then destructively harvested all individuals and collected seeds from each individual to measure seed number and weight. To prevent seed dispersal, mesh bags were placed over the plant inflorescences at flowering stage. The seed mass was weighed to 0.0001 g, and the seed numbers were counted using a seed-counting plate. To describe competition between wheat and weed species in each competing pair, we fitted the fecundity of individual plants (i.e. seed number) to the following model:

$$ln(F_i) = ln(\lambda_i) + \alpha_{ii}N_i + \alpha_{ij}N_j$$

where F_i represents the individual fecundity of species *i*. To account for seedling mortality due to competition, we adjusted the seed number of species *i* by its actual establishment rate (Alexander & Levine, 2019). N_i and N_j are the real number of individuals of species *i* and *j*, respectively. λ_i is the intrinsic growth rate of species *i*, α_{ii} describes the per capita effect of species *i* on itself (i.e. the intraspecific competition coefficient) and α_{ij} describes the per capita effect of species *j* on species *i* (i.e. the interspecific competition coefficient). Negative values of competition coefficients indicate competition among individuals, and positive values indicate facilitation. Therefore, F_i is affected by the number of conspecific and heterospecific competitors (i.e. N_i and N_j), and equals to λ_i in the absence of competition. This is a linearized version (by taking the natural log of both sides of the equation) of a modified Ricker competition model that were commonly used to study annual plant competition (Hart et al., 2012; Inouye, 2001; Ricker, 1954; Zhang & van Kleunen, 2019).

2.4 | Predicting competitive outcomes

We calculated pairwise niche and fitness differences using parameters obtained from the competition models and predicted competitive outcomes between wheat and weeds according to the community coexistence theory of Chesson (Chesson, 2000; Hart et al., 2018; Saavedra et al., 2017):

$$ND = 1 - \rho = 1 - \sqrt{\frac{\alpha_{ij} \times \alpha_{ji}}{\alpha_{jj} \times \alpha_{ii}}}$$

$$FD = \frac{k_j}{k_i} = \frac{ln\lambda_j}{ln\lambda_i}\sqrt{\frac{\alpha_{ii} \times \alpha_{ij}}{\alpha_{jj} \times \alpha_{ji}}}$$

where ND is the niche difference, and FD is the fitness difference. α_{ii} and α_{jj} are intraspecific competition coefficients, α_{ij} and α_{ji} are interspecific competition coefficients; ρ denotes niche overlap, and $1 - \rho$ is the niche difference; κ_j/κ_i represents species difference in intrinsic growth and sensitivity to intra- and interspecific competition. Species will achieve stable coexistence only if their niche differences are sufficient to overcome fitness differences, namely $\rho < \kappa_j/\kappa_i < 1/\rho$ (Chesson, 2000, 2020). Here, the outcomes of competition were predicted based on the relative magnitudes of niche and fitness differences, reflecting the outcomes of long-term competitive population dynamics.

2.5 | Functional trait measurement and trait differences

We measured twelve functional traits on whole plants, leaves and roots to characterize the different functional strategies of studied species and their responses to nitrogen fertilization and competition following standard protocols (Pérez-Harguindeguy et al., 2013) (Table 1). To ensure measurements were taken on healthy, intact

leaves before they dropped during seed maturation in June, we conducted trait sampling one month before harvest (May 2022). We measured plant standing and maximum (i.e. stretched) height of all individuals. We then harvested plants and separated them into above- and below-ground parts. For each individual plant, we randomly selected at least a quarter of the total number of healthy, mature leaves to measure leaf traits, including fresh weight, leaf area, and dry weight. Leaf area was measured with the Digimizer statistical software (MedCalc Software Ltd., Ostend, Belgium). Traits measured on multiple leaves from an individual were averaged to obtain one single value per individual. We randomly selected one individual of each species from each plot for root trait measurements. Harvested roots were washed under running water, scanned with a graphic art scanner (Expression 12000XL, EPSON) and analysed with WinRHIZO root system analysis software to measure root length, area, and volume. All scanned leaves and roots were dried for 48 h at 65°C and weighed to 0.0001 g to obtain dry mass. We then calculated specific leaf area (SLA), leaf dry matter content (LDMC), specific root area (SRA), specific root length (SRL) and root tissue density (RTD).

For aboveground plant functional traits and seed mass, we first calculated the mean values at the species level within each pot, then determined hierarchical trait difference by subtracting the weed trait values from those of the wheat. For below-ground traits, we directly computed hierarchical trait difference by subtracting the weed traits from the wheat traits. In both cases, absolute trait difference was subsequently quantified as the absolute value of the trait difference within each pot.

2.6 | Replication statement

Inference level	Treatment/factor applied at this level	Number of replicates
Species pair (wheat–barnyard grass, wheat–wild oat)	Pot (competition, experimental unit)	20 pots per species pair (4 densities × 5 proportions)
Species (no competition; wheat, barnyard grass, wild oat)	Pot (no-competition pot, experimental unit)	5 pots per species
Nitrogen treatment	2 levels (with N, without N), applied at pot level	3 replicates per combination
Individual plant traits	Traits measured: leaf, root, seed and height	Total 2490 individuals across all pots

2.7 | Statistical analyses

To estimate intrinsic growth rate ($\ln(\lambda_i)$), and intra-(α_{ii}) and inter-specific competition (α_{ij}) under conditions with and without nitrogen addition, we used the *brms* package to implement a Bayesian approach to fit a linear mixed-effects model for each species pair (Bürkner, 2017). We applied the identical approach to investigate the effects of nitrogen addition and neighbour density on wheat seed mass (as an indicator of crop yield). We set the number of conspecific and heterospecific individuals as fixed effects, with pot as random effects. In these fits, we set the priors for parameters to be estimated as a normal distribution, ran the models with 4 chains and 4000 iterations, of which the first 2000 were discarded. Model parameters were sampled from the 95% posterior confidence intervals to construct our parameter estimates, and the adapt delta was 0.99. The good convergence of the γ and B parameters in all models was evaluated by the $\hat{R}$ statistic ($\hat{R} < 1.01$). To test whether nitrogen addition affected $\ln(\lambda_i)$, α_{ii} and α_{ij}, we compared estimates between the nitrogen addition treatment and the no nitrogen treatment using 95% uncertainty intervals (estimate ±1.96 standard error). An effect was considered significant when the 95% interval for the difference between treatments did not include zero, and not significant when it did.

To evaluate the response of plant aboveground traits and seed mass to nitrogen addition (N), and the effects of conspecific (Intra) and heterospecific (Inter) neighbour densities in each competing pair, we conducted a set of linear mixed-effects models with pot as random effect (*lmer* function in lmer package, $y \sim N + Intra + Inter + N{:}Intra + N{:}Inter + (1|pot)$, Bates et al., 2015). To assess the response of root traits to nitrogen addition and neighbour densities, we used a set of linear models (*lm* function in stats package, $y \sim N + Intra + Inter + N{:}Intra + N{:}Inter$). A significant interaction (N:Intra or N:Inter) indicated that the effect of conspecific and heterospecific neighbour densities depended on nitrogen addition; conversely, non-significant interaction suggested additive and independent effects of nitrogen addition and neighbour densities. If interactions were significant, we further explored these interactions by fitting separate models ($y \sim Intra + Inter + (1|pot)$ for aboveground traits and seed mass, and $y \sim Intra + Inter$ for root traits) both with and without nitrogen addition. Similarly, we analysed hierarchical and absolute trait differences using the same linear model structures to determine their relationships with nitrogen addition and conspecific and heterospecific neighbour densities. All statistical analyses were performed in R 4.3.3 (R Core Team, 2023).

3 | RESULTS

3.1 | Changes in niche and fitness differences with nitrogen addition

Nitrogen addition strongly influenced the competitive outcomes and the two processes determining the outcomes, but its impacts differed for the two species pairs. Specifically, nitrogen addition moved the wheat-barnyard grass pair (the WB pair) from the priority effect zone to the competitive exclusion zone by increasing their niche difference (Figure 1). In contrast, fitness difference for the WB pair were only weakly influenced by nitrogen addition, and the value was

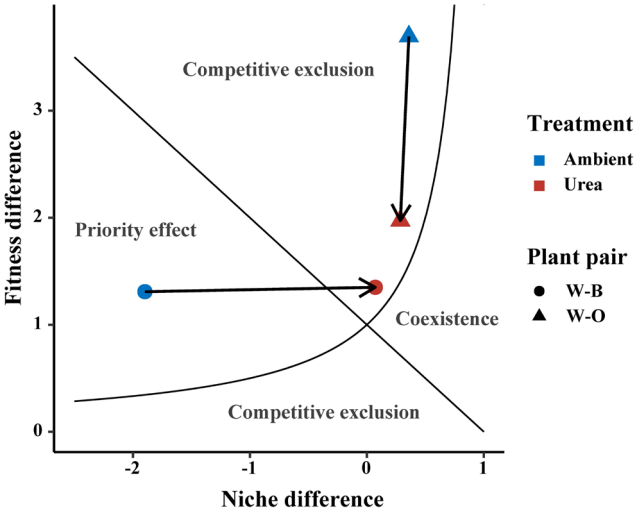


FIGURE 1 Effects of nitrogen addition on niche differences and fitness differences, and predicted coexistence outcomes of competing pairs based on seed number. Fitness differences greater than 1 indicate that wheat is competitively superior to weeds. Pairs coexist when $\rho < \kappa j/\kappa i < 1/\rho$, indicated by the lined region. W-B: Wheat–barnyard grass competition pair; W-O: Wheat–wild oat competition pair.

greater than one, indicating the competitive dominance of wheat over barnyard grass (Figure 1). While the competitive outcome remains unchanged for the wheat-wild oat pair (the WO pair), nitrogen addition resulted in a strong reduction in fitness difference, resulting from decreased competitive dominance of wheat over wild oat, and moved the pair towards the coexistence zone (Figure 1).

3.2 | Changes in intrinsic growth rates and intra- and interspecific competition coefficients with nitrogen addition

For the WB pair, intrinsic growth rate (i.e. fecundity in the absence of competition) and intraspecific competition coefficients of wheat and barnyard grass were not significantly affected by nitrogen addition (Figure 2a,b). The interspecific competition between wheat and barnyard grass were reduced by fertilization (from −0.681 ± 0.425 to −0.17 ± 0.127, Figure 2c). For the WO pair, wheat (4.334 ± 0.204) exhibited a higher intrinsic growth rate compared to wild oat (4.081 ± 0.418) without nitrogen addition (Figure 2d). Nitrogen addition also decreased the intrinsic growth rate of wheat (from 4.334 ± 0.204 to 3.974 ± 0.353) but increased that of wild oat (from 4.081 ± 0.418 to 4.395 ± 0.383) (Figure 2d). Wild oat experienced a reduction in interspecific competition with wheat under nitrogen addition compared to ambient condition (from −0.332 ± 0.058 to −0.165 ± 0.061, Figure 2f). However, the intraspecific competition coefficients for both wheat and wild oat (Figure 2e), as well as the interspecific competition for wheat (Figure 2f), remained stable with nitrogen addition.

3.3 | Changes in plant functional traits with nitrogen addition

Across both WB and WO pairs, nitrogen addition significantly increased root length (from 49.569 ± 8.565 to 77.443 ± 8.495 in WB pair, and from 53.268 ± 7.805 to 84.820 ± 7.939 in WO pair), root area (from 59.525 ± 9.911 to 94.025 ± 9.831 in WB pair, and from 65.666 ± 9.259 to 104.899 ± 9.418 in WO pair), SRA (from 28.888 ± 1.906 to 36.893 ± 1.890 in WB pair, and from 28.115 ± 2.290 to 38.516 ± 2.330 in WO pair), and SRV (from 29.397 ± 1.751 to 36.225 ± 1.737 in WB pair, and from 29.323 ± 1.821 to 39.223 ± 1.853 in WO pair) of wheat in the absence of competition, but significantly decreased its height (from 61.353 ± 1.428 to 54.520 ± 1.348 in WB pair, and from 64.154 ± 1.848 to 56.679 ± 1.872 in WO pair) and RTD (from 35.737 ± 1.686 to 28.927 ± 1.672 in WB pair, and from 35.476 ± 1.690 to 26.398 ± 1.719 in WO pair), and had no significant effects on wheat leaf area, SLA, LDMC, and SRL (Figure 3a,b). Nitrogen addition only significantly increased seed mass of wild oat (from 7.882 ± 3.582 to 18.799 ± 2.876, Figure 3d) and did not significantly affect other traits of wild oats or any traits of barnyard grass (Figure 3c,d).

3.4 | Changes in hierarchical and absolute trait differences with nitrogen addition

For the WB pair, nitrogen addition significantly increased the hierarchical and absolute trait differences in root area (from 0.271 ± 0.031 to 3.926 ± 0.172 in hierarchical difference, and from 0.271 ± 0.031 to 3.926 ± 0.172 in absolute difference) and root length (from 0.258 ± 0.037 to 4.308 ± 0.208 in hierarchical difference, and from 0.258 ± 0.037 to 4.308 ± 0.208 in absolute difference) and had no significant effects on other trait differences (Figure 4a,c). For the WO pair, nitrogen addition significantly decreased the hierarchical and absolute trait differences in height (from 2.424 ± 0.608 to −0.389 ± 0.705 in hierarchical difference, and from 2.183 ± 0.484 to 0.362 ± 0.561 in absolute difference), with no significant effects on other trait differences (Figure 4b,d).

3.5 | Changes in wheat seed mass with nitrogen addition, neighbour density and trait variation

Nitrogen addition significantly reduced wheat seed mass in WO pair (from 39.662 ± 5.818 to 12.609 ± 5.799), but did not change wheat seed mass in the WB pair (from 56.734 ± 7.087 to 49.100 ± 6.775) (Figure 3a,b; Figure 5a). In both species' pairs, wheat seed mass declined as wheat density increased (Figure 5b,c). Nitrogen addition reduced the strength of this negative intraspecific effect in the WO pair (from −0.151 ± 0.021 to −0.041 ± 0.035), but not in the WB pair (from −0.181 ± 0.026 to −0.149 ± 0.034) (Figure 5b,c). Wheat seed mass also declined with increasing weed density in both species' pairs, and nitrogen addition did not alter the interspecific effects

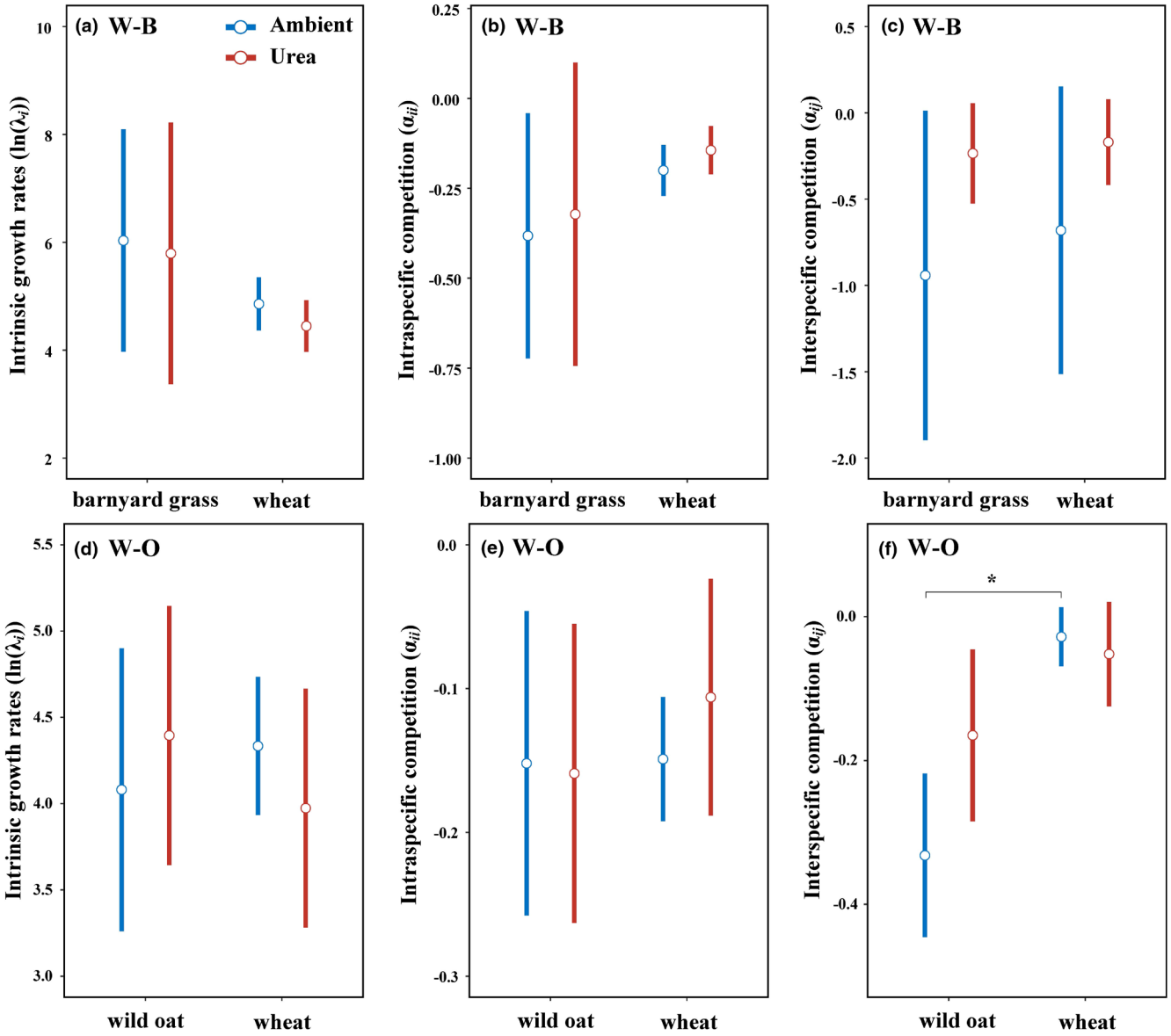


FIGURE 2 Mean intrinsic growth rates ($\ln(\lambda_i)$, a and d) and intra- and interspecific competition coefficients (α_{ii}, α_{ij}, b, c, e and f) of wheat and two weed species (barnyard grass and wild oat) with nitrogen addition, respectively. Error bars represent 95% confidence intervals. Positive values of α_{ii} and α_{ij} indicate facilitation, negative values indicate competition, and values across 0 indicate neutral interaction. W-B: Wheat–wild oat competition pair; W-O: Wheat–wild oat competition pair.

of either weed species (from −0.547 ± 0.347 to −0.125 ± 0.102 in WB pair, from −0.031 ± 0.022 to −0.065 ± 0.052 in WO pair) (Figure 5b,c).

Without nitrogen addition, wheat seed mass in the WB pair increased with wheat height, LA, RL and RA (0.354 ± 0.112, 0.644 ± 0.177, 0.001 ± 0.0001, 0.011 ± 0.001), but decreased with increasing SRA (−0.023 ± 0.010) (Figure S2). In the WO pair, wheat seed mass increased with RL and RA (0.001 ± 0.0002, 0.009 ± 0.001), but decreased with increasing SRA and SRL (−0.012 ± 0.005, −0.001 ± 0.0003) (Figure S3). These relationships were weakened or disappeared under nitrogen addition (Figures S2 and S3).

4 | DISCUSSION

Although negative effects of nitrogen enrichment on diversity are widely documented in natural communities (Hautier et al., 2009; Midolo et al., 2019; Xiao et al., 2021) and also in wheat fields (Zhang et al., 2019), our study found that nitrogen addition facilitated the coexistence of wheat and weed species. By employing a theoretically informed approach, our study further showed that underlying processes differed depending on the interacting species. That is, nitrogen addition facilitated the coexistence of the wheat-barnyard grass pair because it increased their niche differences, while it did

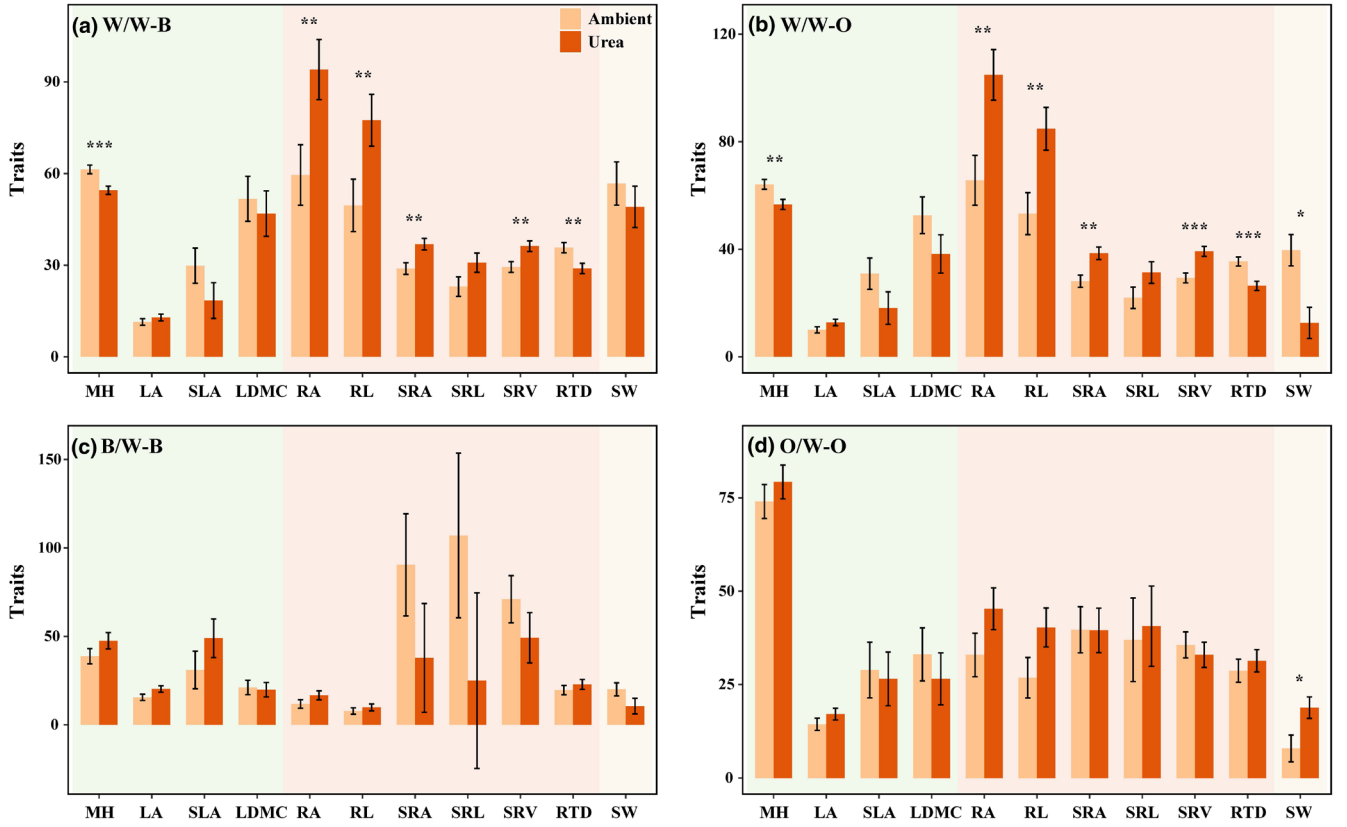


FIGURE 3 Effects of nitrogen addition on the maximum predicted traits of an isolated individual (i.e. without competition) of wheat (a, b) or weed (c, d) in wheat-barnyard grass and wheat-wild oats competing pairs, respectively. The values in histograms were mean ± SE; asterisks indicate significant differences attributable to nitrogen addition. Values in the figure are scaled. To obtain the real values, multiply by the following factors: MH: $\times 10^{0}$, LA: $\times 10^{0}$, SLA: $\times 10^{-1}$, LDMC: $\times 10^{2}$, RA: $\times 10^{-1}$, RL: $\times 10^{-2}$, SRA: $\times 10^{-1}$, SRL: $\times 10^{-2}$, SRV: $\times 10^{1}$, RTD: $\times 10^{2}$, SW: $\times 10^{1}$.

so by equalizing fitness differences of the wheat-wild oat pair. By extensive measurement of a number of ecologically relevant traits, our study also revealed that these shifted outcomes of competition were mediated by plastic responses of various traits related to light and soil nutrient acquisition to nitrogen addition, providing mechanistic insights into the processes underlying the distinct effects of nitrogen fertilization on plant coexistence.

Specifically, for the wheat-barnyard grass pair, nitrogen addition significantly reduced interspecific competition and therefore increased niche differences (Band et al., 2022; Dostál, 2023; Granjel et al., 2023). That was contrast with a previous study which found that nitrogen addition increased barnyard grass competition with wheat (Chauhan & Abugho, 2013). In our system, our result demonstrated that the weakened interspecific competition was likely driven by increased trait differentiation in root length and area between wheat and barnyard grass under fertilization (Figure 4). The greater trait differentiation resulted mainly from the increases in wheat's root area and length with nitrogen addition, while barnyard grass traits remained largely similar (Figure 3). The amplified differences in root traits between these two species likely result in greater partitioning of soil resources, such as nitrogen and phosphorus (Ji et al., 2024). Consistent with this enhanced niche differentiation, our results showed that nitrogen addition did not significantly reduce wheat grain yield when competing with barnyard grass, indicating that resource partitioning effectively protected crop productivity. Therefore, a community with a higher proportion of pairwise interactions among functionally distinct species might be particularly robust to nitrogen addition in the future (Van Dyke et al., 2022). From a management perspective, selecting wheat cultivars that are strong for below-ground competition may help maintain its competitive advantage over barnyard grass and therefore maintain yield in wheat fields heavily dominated by barnyard grass.

For wheat-wild oat pair, nitrogen addition resulted in a reduction in their fitness differences and promoted their coexistence, consistent with a recent study (Granjel et al., 2023). Our research added that this effect was achieved through increased competitive ability of wild oat relative to wheat with nitrogen addition (Figure 3). Wild oat as invasive species became stronger competitor under nitrogen addition because of its increased intrinsic growth rates and weakened interspecific competition (Figure 2). The plastic responses of functional traits to nitrogen addition may help explain their changes. First, we found that seeds mass and various shoot and root traits of wild oat, including root area and length increased under nitrogen addition. Their responses were predicted to enhance fecundity (Figure S4). Furthermore, the weakened competition between wheat and wild oat was likely driven by decreased differences in plant height between them.

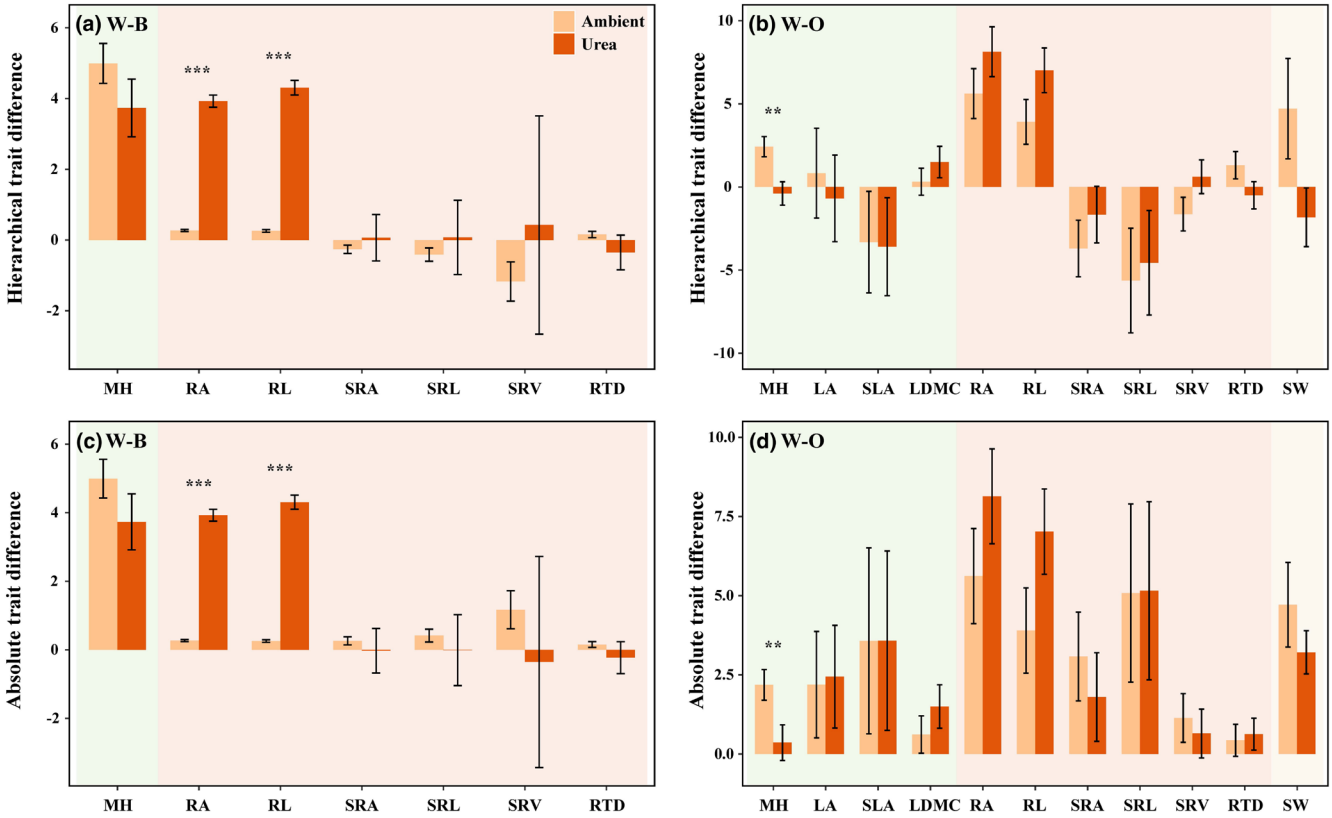


FIGURE 4 Effects of nitrogen addition on the hierarchical and absolute trait differences between wheat and weed in the absence of competition in wheat-barnyard grass and wheat-wild oats competing pairs, respectively. The values were mean ± SE; asterisks indicate significant differences attributable to nitrogen addition. Values in the figure are scaled. To obtain the real values, multiply by the following factors: In panels (a) and (c): MH: $\times 10^{-1}$, RA: $\times 10^{-3}$, RL: $\times 10^{-4}$, SRA: $\times 10^{-4}$, SRL: $\times 10^{-5}$, SRV: $\times 10^{-0}$, RTD: $\times 10^{0}$; in panels (b) and (d): MH: $\times 10^{-1}$, LA: $\times 10^{0}$, SLA: $\times 10^{-2}$, LDMC: $\times 10^{1}$, RA: $\times 10^{-2}$, RL: $\times 10^{-3}$, SRA: $\times 10^{-2}$, SRL: $\times 10^{-3}$, SRV: $\times 10^{0}$, SW: $\times 10^{0}$.

Plant height is closely related to their ability to acquire light, and interacting species with greater differences in height are expected to compete more intensely for light because of its asymmetric nature (DeMalach et al., 2017; Gridzak et al., 2024). Therefore, equalized plant height could have weakened the competitive advantage of wheat over wild oat for light competition, contributing to equalized fitness differences. This reduced competitive advantage of wheat over wild oat also resulted in significant reduction in wheat grain yield under fertilization. In practice, in wheat fields under high wild oat pressure, selecting wheat cultivars that are strong for light competition, such as tall cultivars, may help wheat maintain its competitive advantage over wild oat and facilitate the competitive exclusion of wild oat weeds.

In addition to traits related to light competition, wheat also reallocates resources to its root system to enhance nutrient uptake efficiency after fertilization, resulting in reduced grain yield and plant height but denser roots (e.g., increasing root area, specific root length, and decreasing root tissue density) (Foulkes et al., 2011). Our results also revealed that the strong positive correlations between wheat grain yield and resource-acquisitive traits (e.g. plant height, leaf area and root length) observed under unfertilized conditions were weakened or absent following nitrogen addition. This decoupling shows that traits used for resource foraging no longer provide yield benefits in nutrient-rich environments. Mechanistically, because nitrogen alleviates below-ground stress, the high metabolic costs of growing large roots and leaves outweigh their benefits, particularly under intense light competition from tall weeds like wild oat (Gridzak et al., 2024). In contrast, wild oats primarily increase seed mass while maintaining other traits, as their existing root structure efficiently utilizes additional nutrients. These distinct responses reflect species differences in fundamental ecological strategies. For example, according to Grime's C-S-R model, wheat can be classified as a competitor species, while wild oats are classified as a ruderal species (Grime, 1977). As a result, wild oats are predicted to thrive in frequently disturbed environments through rapid seed production and swift colonization, ensuring persistence despite environmental variability.

The finding that nitrogen addition facilitating coexistence among wheat and the two dominant weed species is consistent with other studies in the same system. For example, a previous study showed that while fertilization reduced weed species richness from six to three, wild oat and barnyard grass persistently coexisted with wheat and even increased their abundance (Zhang et al., 2019). These species-specific responses suggest that the effects of fertilization on coexistence are likely context-dependent (Dostál, 2023). Such shifts in the outcomes of competition suggest that nitrogen addition

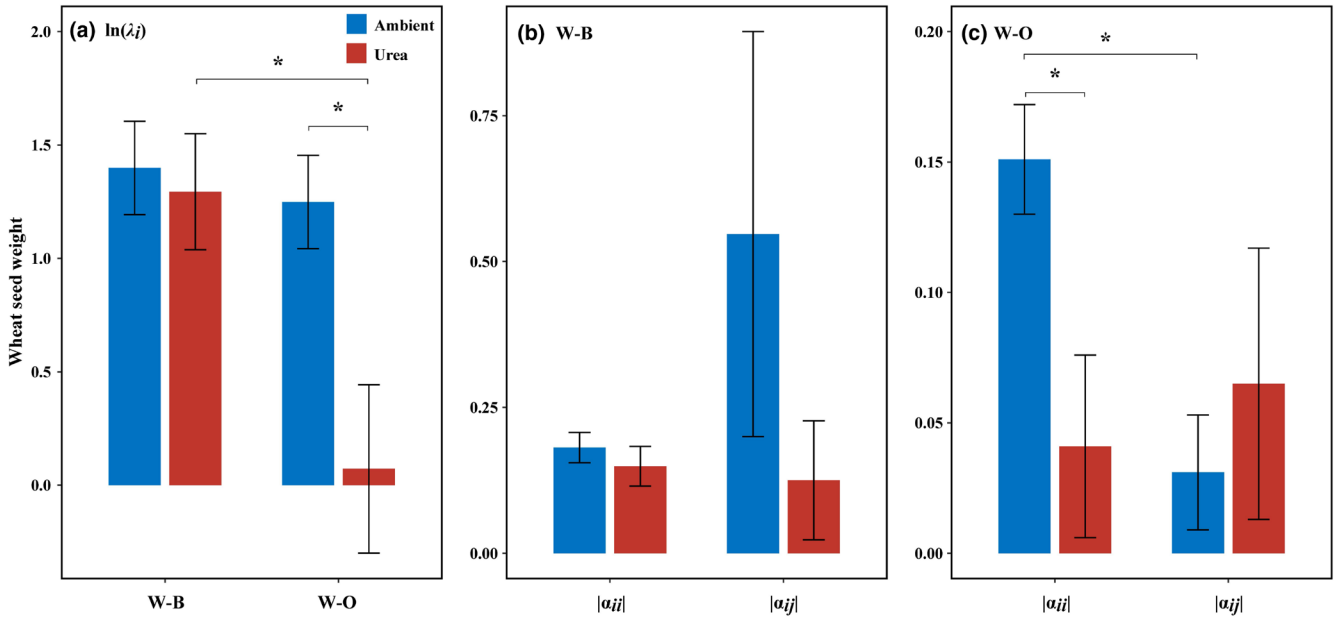


FIGURE 5 Effects of nitrogen addition and neighbour density on wheat seed mass (crop yield), expressed as the intrinsic growth rates ($\ln(\lambda_i)$, a) and the absolute values of the intra- and interspecific competition coefficients ($|\alpha_{ii}|$, $|\alpha_{ij}|$; b, c) for wheat in competition with barnyard grass and wild oat. The competition coefficients were originally negative and are presented here as absolute values for clarity. W-B: Wheat–barnyard grass competition pair; W-O: Wheat–wild oat competition pair.

makes it more difficult to completely eliminate weeds from wheat fields. On the one hand, our experiment shows that, despite its direct fertilization benefits, nitrogen addition can also have unintended negative effects on wheat productivity by intensifying crop–weed competition. In this context, the optimal level of nitrogen application depends on balancing its positive effects on wheat yield against the detrimental effects arising from increased competition with weeds. On the other hand, enhanced coexistence may help maintain weed diversity and improve agroecosystem resistance to antagonists over the long term.

In conclusion, our findings demonstrate that nitrogen addition promotes the coexistence of dominant weeds such as wild oat and barnyard grass with wheat through niche differentiation and fitness equalization driven by trait plasticity. Our study underscores the importance of trait-mediated interactions in shaping competitive outcomes and highlights the context-dependent roles of nitrogen fertilization in modulating plant community dynamics. These context-dependent effects on plant coexistence and underlying functional processes help explain the diverse impacts of nitrogen fertilization on community compositions observed in natural systems. Together, our results provide a more comprehensive understanding of how nitrogen fertilization influences wheat production, encompassing short-term effects driven by direct fertilization and altered crop–weed competition, as well as potential long-term consequences mediated by changes in weed diversity and agroecosystem functioning. Finally, our study suggests that trait-based selection of wheat varieties represents a promising approach for sustainable and effective agroecosystem management that balances crop production and biodiversity conservation.

AUTHOR CONTRIBUTIONS

Li Zhang and Xiang Liu conceived the ideas and designed methodology; Li Zhang, Yizhong Rong and Zhen Zhang collected the data; Yizhong Rong, Weiqiang Liu, and Abolghassem Emamverdian analysed the data; Yizhong Rong, Weiqiang Liu, Li Zhang and Shengman Lyu led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

This study was supported by the National Natural Science Foundation of China (Grants No. 32101260). We thank Junjie Gao, Shushi Cheng, Jiazhen Xi, Jiamei Fan, Yingying He, Xiyun Zhou and Dongxue Ye for their assistance in the planting process, and Zeyu Wang for his assistance in statistical analysis. Open access publishing facilitated by Universite de Lausanne, as part of the Wiley - Universite de Lausanne agreement via the Consortium Of Swiss Academic Libraries.

CONFLICT OF INTEREST STATEMENT

We declare that we have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are available from Figshare (https://doi.org/10.6084/m9.figshare.29994709) (Rong et al., 2026).

ORCID

Yizhong Rong https://orcid.org/0000-0003-4536-4556
Weiqiang Liu https://orcid.org/0009-0005-7921-6852
Xiang Liu https://orcid.org/0000-0003-3914-5824
Abolghassem Emamverdian https://orcid.org/0000-0002-6831-3594

Zhen Zhang https://orcid.org/0000-0002-8205-4154
Shengman Lyu https://orcid.org/0000-0003-0221-5315
Li Zhang https://orcid.org/0000-0003-1512-3137

REFERENCES

Adeux, G., Vieren, E., Carlesi, S., Bàrberi, P., Munier-Jolain, N., & Cordeau, S. (2019). Mitigating crop yield losses through weed diversity. *Nature Sustainability*, *2*(11), 1018–1026. https://doi.org/10.1038/s41893-019-0415-y

Adler, P. B., Fajardo, A., Kleinhesselink, A. R., & Kraft, N. J. (2013). Trait-based tests of coexistence mechanisms. *Ecology Letters*, *16*(10), 1294–1306. https://doi.org/10.1111/ele.12157

Alexander, J. M., & Levine, J. M. (2019). Earlier phenology of a nonnative plant increases impacts on native competitors. *Proceedings of the National Academy of Sciences*, *116*(13), 6199–6204. https://doi.org/10.1073/pnas.1820569116

Band, N., Kadmon, R., Mandel, M., & DeMalach, N. (2022). Assessing the roles of nitrogen, biomass, and niche dimensionality as drivers of species loss in grassland communities. *Proceedings of the National Academy of Sciences*, *119*(10), e2112010119. https://doi.org/10.1073/pnas.211201011

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bennett, J. A., Riibak, K., Tamme, R., Lewis, R. J., & Pärtel, M. (2016). The reciprocal relationship between competition and intraspecific trait variation. *Journal of Ecology*, *104*(5), 1410–1420. https://doi.org/10.1111/1365-2745.12614

Bürkner, P. C. (2017). Brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, *80*, 1–28. https://doi.org/10.1002/ecy.3675

Carmona, C. P., de Bello, F., Azcárate, F. M., Mason, N. W., & Peco, B. (2019). Trait hierarchies and intraspecific variability drive competitive interactions in mediterranean annual plants. *Journal of Ecology*, *107*(5), 2078–2089. https://doi.org/10.1111/1365-2745.13248

Chauhan, B. S., & Abugho, S. B. (2013). Effects of water regime, nitrogen fertilization, and rice plant density on growth and reproduction of lowland weed *Echinochloa crus-galli*. *Crop Protection*, *54*, 142–147. https://doi.org/10.1016/j.cropro.2013.08.005

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*(1), 343–366.

Chesson, P. (2020). Species coexistence. In K. S. McCann & G. Gellner (Eds.), *Theoretical ecology: Concepts and applications* (pp. 5–27). Oxford University Press.

D'Andrea, R., & Ostling, A. (2016). Challenges in linking trait patterns to niche differentiation. *Oikos*, *125*(10), 1369–1385. https://doi.org/10.1111/oik.02979

DeMalach, N., Zaady, E., & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecology Letters*, *20*(1), 60–69. https://doi.org/10.1111/ele.12706

Dostál, P. (2023). Fitness and niche differences are both important in explaining responses of plant diversity to nutrient addition. *Ecology*, *104*(8), e4125. https://doi.org/10.1002/ecy.4125

Editorial Committee of the Flora of China. (1993). *Flora of China*. Science Press.

FAO. (2023). Food and agriculture organization of the United Nations. FAOSTAT. Online Database Retrieved from http://faostat.fao.org/

Ferenc, V., & Sheppard, C. S. (2020). The stronger, the better-trait hierarchy is driving alien species interaction. *Oikos*, *129*(10), 1455–1467. https://doi.org/10.1111/oik.07338

Foulkes, M. J., Slafer, G. A., Davies, W. J., Berry, P. M., Sylvester-Bradley, R., Martre, P., Calderini, D. F., Griffiths, S., & Reynolds, M. P. (2011). Raising yield potential of wheat. III. Optimizing partitioning to grain while maintaining lodging resistance. *Journal of Experimental Botany*, *62*(2), 469–486. https://doi.org/10.1093/jxb/erq300

Funk, J. L., & Wolf, A. A. (2016). Testing the trait-based community framework: Do functional traits predict competitive outcomes? *Ecology*, *97*(9), 2206–2211. https://doi.org/10.1002/ecy.1484

Godoy, O., & Levine, J. M. (2014). Phenology effects on invasion success: Insights from coupling field experiments to coexistence theory. *Ecology*, *95*(3), 726–736. https://doi.org/10.1890/13-1157.1

Granjel, R. R., Allan, E., & Godoy, O. (2023). Nitrogen enrichment and foliar fungal pathogens affect the mechanisms of multispecies plant coexistence. *New Phytologist*, *237*(6), 2332–2346. https://doi.org/10.1111/nph.18689

Gridzak, R., Lavender, T. M., Aarssen, L. W., & Schamp, B. S. (2024). Competition intensity is linked to the co-occurrence status and height differences of plant species found growing together in an old-field community. *Journal of Ecology*, *112*(9), 1967–1977. https://doi.org/10.1111/1365-2745.14363

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, *111*(982), 1169–1194. https://doi.org/10.1086/283244

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Williams, R., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Cleland, E. E., D'Antonio, C., … Wragg, P. D. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, *537*(7618), 93–96. https://doi.org/10.1038/nature19324

Hart, S. P., Burgin, J. R., & Marshall, D. J. (2012). Revisiting competition in a classic model system using formal links between theory and data. *Ecology*, *93*(9), 2015–2022. https://doi.org/10.1890/11-2248.1

Hart, S. P., Freckleton, R. P., & Levine, J. M. (2018). How to quantify competitive ability. *Journal of Ecology*, *106*(5), 1902–1909. https://doi.org/10.1111/1365-2745.12954

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*(5927), 636–638. https://doi.org/10.1126/science.11696

Helsen, K., Acharya, K. P., Brunet, J., Cousins, S. A., Decocq, G., Hermy, M., Kolb, A., Lemke, I. H., Lenoir, J., Plue, J., Verheyen, K., De Frenne, P., & Graae, B. J. (2017). Biotic and abiotic drivers of intraspecific trait variation within plant populations of three herbaceous plant species along a latitudinal gradient. *BMC Ecology*, *17*, 1–12. https://doi.org/10.1186/s12898-017-0151-y

Inouye, B. D. (2001). Response surface experimental designs for investigating interspecific competition. *Ecology*, *82*(10), 2696–2706. https://doi.org/10.1890/0012-9658(2001)082[2696:RSEDFI]2.0.CO;2

Ji, H., Zhou, N., Rengel, Z., Jing, J., & Li, H. B. (2024). Root traits and plasticity differences explain complementarity between co-existing species in phosphorus-limited grassland. *Plant and Soil*, *501*, 611–627. https://doi.org/10.1007/s11104-024-06540-x

Kraft, N. J., Godoy, O., & Levine, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences*, *112*(3), 797–802. https://doi.org/10.1073/pnas.1413650112

Kraft, N. J., Kandlikar, G., Kleinhesselink, A. R., Godoy, O., & Levine, J. M. (2017). One trait fits all? Predicting coexistence of annual plants across spatial and temporal scales. In *2017 ESA annual meeting* (August 6–11). ESA.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N. E., Kattge, J., & Coomes, D. A. (2012). Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: Implications for forest community assembly. *Ecology Letters*, *15*(8), 831–840. https://doi.org/10.1111/j.1461-0248.2012.01803.x

Liu, X., Lyu, S., Sun, D., Bradshaw, C. J., & Zhou, S. (2017). Species decline under nitrogen fertilization increases community-level competence of fungal diseases. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1847), 20162621. https://doi.org/10.1098/rspb.2016.2621

Lyu, S., & Alexander, J. M. (2024). Functional traits predict outcomes of current and novel competition under warmer climate. *Global Change Biology*, *30*(11), e17551. https://doi.org/10.1111/gcb.17551

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*(4), 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Midolo, G., Alkemade, R., Schipper, A. M., Benítez-López, A., Perring, M. P., & de Vries, W. (2019). Impacts of nitrogen addition on plant species richness and abundance: A global meta–analysis. *Global Ecology and Biogeograhy*, *28*(3), 398–413. https://doi.org/10.1111/geb.12856

Nasim, G., & Shabbir, A. (2012). Invasive weed species–a threat to sustainable agriculture. In *Crop production for agricultural improvement* (pp. 523–556). Springer Netherlands.

Nelson, R. A., Sullivan, L. L., Hersch-Green, E. I., Seabloom, E. W., Borer, E. T., Tognetti, P. M., Adler, P. B., Biederman, L., Bugalho, M. N., Caldeira, M. C., Cancela, J. P., Carvalheiro, L. G., Catford, J. A., Dickman, C. R., Dolezal, A. J., Donohue, I., Ebeling, A., Eisenhauer, N., Elgersma, K. J., … Harrison, S. P. (2025). Forb diversity globally is harmed by nutrient enrichment but can be rescued by large mammalian herbivory. *Communications Biology*, *8*(1), 444. https://doi.org/10.1038/s42003-025-07882-7

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*(3), 167–234. https://doi.org/10.1071/BT12225

Pourreza, J., Bahrani, A., & Karami, S. (2010). Effect of nitrogen fertilization application on simulating wheat (*Triticum aestivum*) yield loss caused by wild oat (*Avena fatua*) interference. *American-Eurasian J Agric Environ Sci*, *9*(1), 55–61. https://doi.org/10.5555/20113045364

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada*, *11*(5), 559–623. https://doi.org/10.1139/f54-039

Rong, Y., Liu, W., Liu, X., Emamverdian, A., Zhang, Z., Lyu, S., & Zhang, L. (2026). Nitrogen addition promotes wheat-weed coexistence through niche differentiation and fitness equalization. Figshare, https://doi.org/10.6084/m9.figshare.29994709

Saavedra, S., Rohr, R. P., Bascompte, J., Godoy, O., Kraft, N. J. B., & Levine, J. M. (2017). A structural approach for understanding multispecies coexistence. *Ecological Monographs*, *87*(3), 470–486. https://doi.org/10.1002/ecm.1263

Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional-and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences*, *102*(12), 4387–4392. https://doi.org/10.1073/pnas.0408648102

Tao, X., Cui, J., Dai, Y., Wang, Z., & Xu, X. (2016). Soil respiration responses to soil physiochemical properties in urban different green-lands: A case study in Hefei, China. *International Soil and Water Conservation Research*, *4*(3), 224–229. https://doi.org/10.1016/j.iswcr.2016.08.001

Turcotte, M. M., & Levine, J. M. (2016). Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution*, *31*(10), 803–813. https://doi.org/10.1016/j.tree.2016.07.013

Van Dyke, M. N., Levine, J. M., & Kraft, N. J. (2022). Small rainfall changes drive substantial changes in plant coexistence. *Nature*, *611*(7936), 507–511. https://doi.org/10.1038/s41586-022-05391-9

Wan, N. F., Wang, Y. Q., Fu, L., Liu, J., Woodcock, B. A., Hu, Y. Q., Eskelinen, A., Hector, A., Loreau, M., Hautier, Y., Bardgett, R. D., Kardol, P., Zuppinger-Dingley, D., Fraser, L. H., Bullock, J. M., Nakagawa, S., Shen, S., Xin, F., Shi, D. P., … Scherber, C. (2026). Global evidence that plant diversity suppresses pests and promotes plant performance and crop production. *Nature Ecology & Evolution*, *10*, 293–307. https://doi.org/10.1038/s41559-025-02964-5

Wang, X., Yan, X., Huang, K., Luo, X., Zhang, Y., Zhou, L., Yang, F., Xu, X., Zhou, X., Niu, K., & Guo, H. (2022). Nitrogen enrichment and warming shift community functional composition via distinct mechanisms: The role of intraspecific trait variability and species turnover. *Functional Ecology*, *36*, 1230–1242. https://doi.org/10.1111/1365-2435.14012

Wong, M. K. L., Tsang, T. P. N., Lewis, O. T., & Guenard, B. (2021). Trait-similarity and trait-hierarchy jointly determine fine-scale spatial associations of resident and invasive ant species. *Ecography*, *44*(4), 589–601. https://doi.org/10.1111/ecog.05505

Xiao, Y., Liu, X., Zhang, L., Song, Z., & Zhou, S. (2021). The allometry of plant height explains species loss under nitrogen addition. *Ecology Letters*, *24*(3), 553–562. https://doi.org/10.1111/ele.13673

Yang, J., Song, X., Zambrano, J., Chen, Y., Cao, M., Deng, X., Zhang, W., Yang, X., Zhang, G., Tang, Y., & Swenson, N. G. (2021). Intraspecific variation in tree growth responses to neighbourhood composition and seasonal drought in a tropical forest. *Journal of Ecology*, *109*(1), 26–37. https://doi.org/10.1111/1365-2745.13439

Yang, J., Wang, X., Carmona, C. P., Wang, X., & Shen, G. (2024). Inverse relationship between species competitiveness and intraspecific trait variability may enable species coexistence in experimental seedling communities. *Nature Communications*, *15*(1), 2895. https://doi.org/10.1038/s41467-024-47295-4

Ye, C. Y., Tang, W., Wu, D., Jia, L., Qiu, J., Chen, M., Mao, L., Xu, H., Yu, X., Lu, Y., Wang, Y., Olsen, K. M., Timko, M. P., & Fan, L. (2019). Genomic evidence of human selection on Vavilovian mimicry. *Nature Ecology & Evolution*, *3*(10), 1474–1482. https://doi.org/10.1038/s41559-019-0976-1

Yin, D., Liu, Y., Ye, Q., Cadotte, M. W., & He, F. (2021). Trait hierarchies are stronger than trait dissimilarities in structuring spatial co-occurrence patterns of common tree species in a subtropical forest. *Ecology and Evolution*, *11*(12), 7366–7377. https://doi.org/10.1002/ece3.7567

Zhang, L., Cappelli, S. L., Huang, M., Liu, X., Xiao, Y., Cardou, F., Rong, Y., & Zhou, S. (2023). Intraspecific trait variability mediates the effect of nitrogen addition and warming on aboveground productivity. *Oikos*, *2023*, e09559. https://doi.org/10.1111/oik.09559

Zhang, Z., Cao, Y., Wu, J., Ma, Y., He, J., & Zhou, D. (2019). Effects of different tillage methods on weed community diversity in winter wheat fields. *Journal of Ecology and Rural Environment*, *35*(2), 210–216. https://doi.org/10.19741/j.issn.1673-4831.2018.0106

Zhang, Z., & van Kleunen, M. (2019). Common alien plants are more competitive than rare natives but not than common natives. *Ecology Letters*, *22*(9), 1378–1386. https://doi.org/10.1111/ele.13320

Zhao, N., Xu, Y., Chen, L., Jiang, M., Dong, K., Wang, J., & Gao, Y. (2021). Species identities impact the responses of intensity and importance of competition to the soil fertility changes. *Global Ecology and Conservation*, *27*, e01519. https://doi.org/10.1016/j.gecco.2021.e01519

SUPPORTING INFORMATION

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

Figure S1. Schematic diagram of the experimental design. (a) Individual plants of each species (wheat: W, wild oat: O, barnyard

grass: B) was grown alone under fertilized or unfertilized conditions, totalling 90 pots (3 species × 5 pots without competition × 2 nitrogen treatments × 3 replicates). (b) For each competition pair (wheat–wild oat (W-O), wheat–barnyard grass (W-B)), plants were grown under fertilized or unfertilized conditions. As an example, the panel displays the 20 combinations for W-O pair without fertilization, representing 20 combinations of total plant densities (4, 8, 12, 16 individuals per pot) and wheat proportions (0, 0.25, 0.5, 0.75, 1). Competition experiment comprised 240 pots (2 pairs × 20 competition-pots × 2 nitrogen treatments × 3 replicates).

Figure S2. Relationships between functional traits and seed weight of wheat under varying planting densities (1, 4, 8, 12 and 16) and fertilization (ambient and urea) treatments in wheat-barnyard grass competing pair. Solid and dashed lines denote statistically significant ($p \leq 0.05$) and non-significant ($p > 0.05$) relationships, respectively.

Figure S3. Relationships between functional traits and seed weight of wheat under varying planting densities (1, 4, 8, 12 and 16) and fertilization (ambient and urea) treatments in wheat-wild oat competing pair. Solid and dashed lines denote statistically significant ($p \leq 0.05$) and non-significant ($p > 0.05$) relationships, respectively.

Figure S4. Relationships between functional traits and seed numbers of wild oat under varying planting densities (1, 4, 8, 12 and 16) and fertilization (ambient and urea) treatments in wheat-wild oat competing pair. Solid and dashed lines denote statistically significant ($p \leq 0.05$) and non-significant ($p > 0.05$) relationships, respectively.

How to cite this article: Rong, Y., Liu, W., Liu, X., Emamverdian, A., Zhang, Z., Lyu, S., & Zhang, L. (2026). Nitrogen fertilization promotes wheat–weed coexistence through niche differentiation and fitness equalization. *Functional Ecology*, *40*, 2436–2448. https://doi.org/10.1111/1365-2435.70376