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Early human selection of crops' wild progenitors explains the acquisitive physiology of modern cultivars

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32

33 **Abstract**

34 Crops have resource-acquisitive leaf traits, which is usually attributed to the process of

35 domestication. However, early choices of wild plants amenable for domestication may

36 also have played a key role in the evolution of crops' physiological traits. We compiled

37 data on 1,034 annual herbs to place the ecophysiological traits of 69 crops' wild

38 progenitors in the context of global botanical variation, and conducted a common-garden

39 experiment to measure the effects of domestication on crop ecophysiology. Our study

40 found that crops' wild progenitors already had high leaf nitrogen, photosynthesis,

41 conductance, transpiration, and soft leaves. After domestication, ecophysiological traits

42 varied little and in idiosyncratic ways. Crops did not surpass the trait boundaries of wild

43 species. Overall, the resource-acquisitive strategy of crops is largely due to the inheritance

44 from their wild progenitors rather than to further breeding improvements. Our study

45 concurs with recent literature highlighting constraints of crop breeding for faster

46 ecophysiological traits.

47   **Main text**

48   **Introduction**

49   Modern civilisation relies on a small number of the world's *ca.* 354,000 flowering plants

50   for its nourishment [1,2]. Food crops evolved under cultivation from their respective wild

51   progenitors over the last millennia [3]. During this process, crops tended to converge in

52   some traits, such as large seeds with low dormancy and dispersal ability, high plant vigour

53   and yield potential, and synchronous phenologies [4]. However, plant growth rates and

54   other physiological traits evolved inconsistently after domestication [5,6]. This is puzzling,

55   as cultivated plants typically exhibit faster growth and carbon fixation rates than wild

56   species that were never domesticated [7,8]. An alternative hypothesis is that the wild

57   progenitors of crops were physiologically distinct. Indeed, crop domestication may have

58   already started with distinctive wild species, as proto-farmers may have consciously or

59   unconsciously selected for cultivation wild species with particular traits [9–12]. However,

60   the relative importance of 'early human selection' *vs.* 'evolution under cultivation' to

61   explain the fast physiological rates of crops is largely unknown.

62   Ecophysiological traits (*i.e.* traits that influence resource use and acquisition) are

63   key determinants of plant growth and performance and play an important role in

64   environmental adaptation [13]. The ecophysiological traits of crops are a non-random

65   representation of those of wild plants. For example, agricultural species tend to have

66   higher net photosynthesis, higher stomatal and mesophyll conductances, more leaf

67   nitrogen, and softer leaves than wild herbs [7,8,14–16]. Other attributes related to the

68   acquisition of resources in the soil, such as root tissue density, specific root length or root

69   mass fraction, also differ between crops and non-crop species [17]. This suggests that the

70   ability to thrive successfully under productive and fertile conditions is a common

71   characteristic of crops [16]. Despite the lack of detailed empirical evidence, the acquisitive

72   strategy of crops has typically been attributed to selection forces operating under

73   cultivation [18].

74   Before the advent of agriculture, hunter-gatherers harvested and used a wide array

75   of wild food plants, but only a few of these wild foods were domesticated and made it to

76   current-day agricultural systems [19,20]. This subset of wild foods are the wild progenitors

77   of modern crops. Whether crops' wild progenitors share a number of common traits that

78   can differentiate them from other wild species has recently been a matter of study. For

79   example, wild progenitors of barley, einkorn and emmer wheat have larger seedlings,

80   faster germination and greater seed mass, growth rate, height, and yield than other wild

81 grasses common in the Fertile Crescent [10]. In addition, seeds of cereal and legume crops'

82 wild progenitors are larger than those of other wild species [11,21,22]. The fine roots of crops´

83 wild progenitors are also noticeably acquisitive compared to other wild herbs, suggesting

84 that the roots of crops´ progenitors were already preadapted to cultivation before

85 domestication [17]. Although there are hints that the choices of early farmers could have a

86 major impact on the phenotypic profile of modern crops, a comprehensive screening

87 comparing the ecophysiology of crops' wild progenitors with global botanical diversity

88 is currently lacking.

89   In addition to early selection, the acquisitive strategy of crops could also be

90 explained by later evolution under cultivation. Initial domestication and subsequent plant

91 breeding have resulted in crop varieties that are phenotypically different from their wild

92 progenitors due to several selection forces [4]. First, agricultural environments are resource-

93 rich habitats (high availability of nutrients, light and water) that typically select for

94 acquisitive, fast-growing plants [15,23,24]. Second, artificial selection and modern breeding

95 programmes have promoted high-yielding and less stress-tolerant plants, which may have

96 led to indirect changes in correlated traits such as those related to allocation and

97 physiological response [25,26]. However, the effects of domestication on ecophysiological

98 traits appear to be inconsistent or variable among crops [5]. For example, photosynthetic

99 rates decreased with domestication in wheat and bean [27,28], but increased in cassava and

100 cotton [29,30], while stayed steady in rice [31,32]. Even when comparisons are performed across

101 several crop species grown simultaneously under the same conditions, the effects of

102 domestication on ecophysiological traits tend to vary within and among crops [33,34].

103 Therefore, the evolution of ecophysiological traits under cultivation remains to be

104 investigated across a wider range of crops and accessions, and a distinction needs to be

105 made between the effects of initial domestication and of modern plant breeding.

106   Here, we addressed the question of which of the two processes –early human

107 selection and/or evolution under cultivation– has led to crops having a more acquisitive

108 ecophysiology than wild species. Both processes may have pushed crops out of the

109 phenotypic boundaries defined by the global pool of wild species [15]. Therefore, we also

110 wondered whether the acquisitive strategy of crops is so distinct as to push them outside

111 the boundaries of the ecophysiological trait spectra of wild species (Fig. 1). To carry out

112 the research, we first compiled a dataset (hereafter referred to as the *global dataset*) of

113 five leaf ecophysiological traits related to carbon-water economics: net photosynthetic

114 rate per unit area (A_{area}), stomatal conductance to water vapour (g_{wv}), mass-based leaf

nitrogen concentration ($[N_{mass}]$), specific leaf area (SLA), and ^{13}C isotopic composition (δ^{13}C). Using phylogenetically informed analyses, we compared the ecophysiological traits of crops' progenitors with those of other wild annual herbs. Second, we set-up a glasshouse experiment with 11 annual herbaceous crops, including progenitor, landrace and improved accessions of each crop, and measured the same ecophysiological traits that were considered in the *global dataset* (hereafter, the *experimental dataset*). By comparing wild progenitors with landraces, and landraces with improved cultivars under common-garden conditions, we addressed the effects of domestication and modern breeding, respectively. Finally, we computed the phenotypic spaces of crops and wild species, based on their ecophysiological traits, and measured their size, uniqueness and degree of overlap. Specifically, we asked: i) Do the ecophysiological traits of crops' progenitors tend to exhibit a more acquisitive strategy than other wild herbs?; ii) How have domestication and modern plant breeding impacted crop ecophysiology?; and iii) Do the ecophysiological traits of domesticated plants extend beyond the global trait variation observed in wild species?

Results

Our *global dataset* included ecophysiological trait data on 1,146 annual herbs, including domesticates, crops' wild progenitors and wild species (Extended Data Table 1). These species belonged to 515 genera and 65 angiosperm families. The set of crops retrieved in this compilation accounts for the crop species grown in 75% of global croplands (http://faostat.fao.org, 2021 data). Each leaf trait varied by up to two orders of magnitude and was dependent on photosynthetic pathway and phylogenetic history (Fig. 2, Extended Data Table 1 and Extended Data Fig. 1). On average, wild C_4 species had lower g_{wv} (PGLS estimate = -135.3 mmol m^{-2} s^{-1}, $P = 0.05$), lower [N_{mass}] (PGLS estimate = -0.43 %, $P = 0.02$), and higher $\delta^{13}C$ (PGLS estimate = 14.3 ‰, $P < 0.001$) than wild C_3 species (Fig. 2, Extended Data Table 2a and Extended Data Fig. 1). The pattern of trait correlations also differed by photosynthetic pathway (Extended Data Fig. 2).

Crops' wild progenitors differed from other wild annual herbs for all five ecophysiological traits studied, irrespective of their phylogenetic context (Fig. 2 and Extended Data Table 2a). The wild progenitors of crops had 3.73 higher A_{area} ($P = 0.04$), 93.7 higher g_{wv} ($P = 0.05$), 0.85 higher [N_{mass}] ($P < 0.001$), 58.7 higher SLA ($P < 0.001$), and 1.39 lower $\delta^{13}C$ ($P = 0.01$) in comparison with the data from other annual herbs (Fig. 2 and Extended Data Table 2a). The same pattern was observed when domesticates were compared to wild herbs (Extended Data Fig. 1). When field studies were excluded to control for confounding environmental factors, crops' progenitors also exhibited more acquisitive ecophysiological traits than other wild species (except for [N_{mass}]; Extended Data Table 2b). The higher acquisitive profile of crops' wild progenitors was more prominent in some functional groups (*e.g.* forbs) than in others (*e.g.* cereals; Extended Data Table 3) and was dependent on human selection purposes (*i.e.* wild progenitors selected for leaf production showed greatest differences in A_{area} (PGLS estimate = 9.16 μmol m^{-2} s^{-1}, $P < 0.001$) and g_{wv} (PGLS estimate = 286.2 mmol m^{-2} s^{-1}, $P < 0.001$), those selected for fruit/flower production, in $\delta^{13}C$ (PGLS estimate = -3.73 ‰, $P < 0.001$), and those selected for seed production, in SLA (PGLS estimate = 50.6 cm^2 g^{-1}, $P = 0.004$); Extended Data Fig. 3).

The range of ecophysiological traits in our *experimental dataset* encompassed a small-to-average portion of the variation in these plant traits found in the *global dataset* (15% for A_{area}, 28% for g_{wv}, 3% for [N_{mass}], 20% for SLA, and 55% for $\delta^{13}C$). The effects of domestication were small in magnitude and diverse among crops and accessions within crops (Fig. 3 and Extended Data Fig. 4). Most crops showed no domestication effects;

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only lettuce showed a modest decrease in A_{area} and g_{wv}, while tomato a slight increase in A_{area} and SLA (Extended Data Fig. 4). Domestication tended to decrease [N_{mass}] (LMM estimate = -0.33 %, P = 0.01) and increase $\delta^{13}C$ (LMM estimate = 0.37 ‰, P = 0.04) (Extended Data Table 4), but with a small effect size, so that none of the specific landraces differed from their wild progenitors when compared pairwise by species (Extended Data Fig. 4). We found no effect of modern breeding (*i.e.* no differences between landraces and modern cultivars) for any of the ecophysiological traits (Fig. 3, Extended Data Table 4 and Extended Data Fig. 4).

Crops took almost half of the phenotypic space of wild species, with Jaccard indices ranging from 38 to 50 % (Fig. 4 and Extended Data Table 5). However, trait combinations differed between plant types, with crops occupying the acquisitive end of the wild-type phenotypic spaces (Fig. 4 and Extended Data Table 5). Crops had smaller phenotypic spaces in seven of the ten trait combinations that included A_{area} and g_{wv} (Fig. 4 and Extended Data Table 5). The unique fractions of crop trait spaces were small and not significantly different from null expectations, except for [N_{mass}] and $\delta^{13}C$ (Extended Data Table 5). C_4 crops showed the most unique trait combinations, with distinct [N_{mass}] and $\delta^{13}C$ values as compared to the phenotypic space of wild herbs (Extended Data Fig. 5).

Discussion

The comparative analysis of 1,103 wild herbaceous species showed that the direct progenitors of major food crops have a more acquisitive ecophysiology than other wild annual herbs that never became domesticated. On average, crops' wild progenitors had higher photosynthetic rates, stomatal conductances, leaf nitrogen, softer leaves, and lower water use efficiency (*i.e.* higher $\delta^{13}C$) than other wild herbs. Further evolution under cultivation did not consistently change ecophysiological traits. Domesticated plants have maintained the variation of ecophysiological traits within the range already set by their wild progenitors. Accordingly, the phenotypes of domesticates laid within the trait space occupied by wild annuals, but tended to cluster at the acquisitive end of the spectra of variation. Overall, our findings highlight the importance of early human selection over further breeding improvements for the prevalence of acquisitive strategies in modern cultivars. This has important implications for current debates concerning the origins of agriculture and for research on the ecological strategies of wild progenitors, as well as for attempts to breed crops with improved photosynthetic performance.

We found that crops' wild progenitors tend to have more acquisitive ecophysiological traits compared to other wild species. Acquisitive strategies had previously been described as a distinctive characteristic of crops *vs*. wild species [7,8,16,18,23]. However, these studies included a limited number of crop species and traits, did not distinguish between crop progenitors and other wild species, and/or only considered growth form as a factor that could influence leaf economics. Ecophysiology also depends on life cycle, photosynthetic pathway and phylogeny, and shows high sensitivity to environmental conditions [35–37]. In contrast to other studies, our analyses were restricted exclusively to annual species, which include the progenitors of most major food crops, to account for differences in growth according to life cycle. In addition, they controlled for photosynthetic pathway and phylogeny, and distinguished between plants grown in the field and under controlled conditions. Based on more targeted comparisons and a global-scale data compilation, we found that domesticated plants do have an acquisitive physiology and are less efficient in water use, but this profile was already in their wild progenitors. The magnitude of trait differences between crop progenitors and other wild species differed according to functional group affiliation and human selection purposes. There are several explanations for the diversity between functional groups, including differences in growth habit, habitat preference and plant stature, which covary with physiological traits [38]. The organ under selection could also explain the ecophysiological

216 differences between crops' wild progenitors, because vegetative vigour or fleshy fruiting
217 tend to require a higher source capacity to meet the demand for assimilates and water than
218 high seed production [39]. Thus, in addition to the generalized acquisitive profile of crops'
219 wild progenitors, other characteristics that differ between functional groups and crop
220 types also had an influence on why certain wild species were chosen by early farmers.

221   The acquisitive physiology of crops' wild progenitors may reflect their pre-
222 adaptation to early anthropogenic environments. This hypothesis was first proposed by
223 Engelbrecht in 1916 [40], who suggested that early human selection may have favoured
224 traits that were advantageous in the nutrient-rich and moist habitats around human
225 settlements (the so-called 'dump heap hypothesis' [41]). If so, crops' wild progenitors would
226 be either ruderal or competitive plants characterised by relatively rapid growth and high
227 resource uptake rates [42]. In support of this hypothesis, some studies have shown that
228 crops' progenitors germinate earlier, grow faster and have more acquisitive traits
229 compared to other wild species [10,17], but the results are diverse in terms of reproductive
230 allocation and phenology, *i.e.* traits that distinguish ruderal from competitive plants
231 [10,11,43,44]. Our study places crops' wild progenitors on the fast end of the leaf economics
232 spectrum [45], which, together with earlier literature, supports that wild progenitors tend to
233 be either competitors or ruderals. However, some wild progenitors thrive in stressful
234 environments, such as cold and high-altitude steppes or poor calcareous soils with arid
235 climates [46,47]. In these environments, species can follow a conservative stress-tolerant
236 strategy or an acquisitive stress-escape strategy. 'Stress-escapers' have evolved a rapid
237 acquisition of maximum physiological carbon uptake capacity and an earlier phenology
238 that ensures growth occurs during seasons when stress is absent [48,49]. Further studies
239 encompassing a wider range of phenotypic traits would be needed to establish whether
240 wild progenitors are predominantly ruderals or competitors, and a distinction between
241 'stress-tolerator' and 'stress-escaper' would be crucial to ensure a correct interpretation
242 of plant strategies in crops' wild progenitors.

243   The acquisitive physiology of crops' wild progenitors may also be a consequence
244 of choosing more palatable and/or nutrient-rich wild plants. Defence strategies depend on
245 complex structural traits (such as sclerophylly) and chemical composition (leaf carbon
246 nitrogen ratios), some of which are also related to leaf economics traits [50]. Since both
247 structural and chemical defences are physiologically costly, investment in defence often
248 trades-off with ecophysiological traits promoting growth and yield [51,52], although many
249 factors may obscure this relationship, such as plant ontogeny or trait multi-functionality

250   [53,54]. In addition, food quality is associated with higher nitrogen and water contents in

251   plant tissues and lower levels of non-digestible compounds [55,56]. By choosing more

252   palatable or nutrient-rich plants, early farmers could therefore have indirectly selected for

253   plants with more acquisitive ecophysiology. Indeed, wild species of genera with crops'

254   wild progenitors have lower levels of secondary compounds than genera without them [57].

255   In the case of chickpea, for example, taste and nutritional value were the main

256   determinants in the decision-making of early farmers [58]. However, further experimental

257   evidence looking at plant defence and nutritional quality traits is needed to test this

258   hypothesis.

259   Our results showed small and generally non-consistent effects of domestication

260   and improvement on ecophysiological traits, suggesting that evolution under cultivation

261   has not substantially changed crop ecophysiology. The few experiments that grew sets of

262   crops and their wild progenitors in common gardens, and measured photosynthesis and

263   other ecophysiological traits, tended to concur with our results [33,59]. Variation in

264   ecophysiological traits is often constrained by covariation with other phenotypic traits at

265   the leaf- and whole-plant levels. For example, crops tend to be larger and have larger

266   leaves than their wild progenitors [60]. An increase in leaf size is associated with higher

267   construction and maintenance costs per unit leaf area, at the expense of lower investment

268   in photosynthetic machinery [61]. Larger leaves and plants also require more supporting

269   tissues such as petioles and stems, diverting resources from source tissues [62]. Moreover,

270   in herbaceous crops, photosynthetic capacity is already very high within the context of

271   botanical variation [7] and is limited by three factors: stomatal, mesophyll conductance, and

272   photochemistry, whose contribution to photosynthetic regulation is very well-balanced

273   implying a complex co-regulatory scenario [37]. Scaling this complexity has proven

274   difficult and could constrain the evolution of higher photosynthetic rates in crops [63]. For

275   example, a more even distribution of stomata between both leaf sides after domestication

276   (*i.e.* improved conductance) did not lead to an increase in photosynthesis, which may be

277   due to a trade-off with other limiting factors (*e.g.* reduced water use efficiency [64]) or a

278   saturation of effective stomatal conductance [65]. Further, domestication started with

279   acquisitive species, *i.e.* crops´ wild progenitors, which might have prevented further

280   improvements in crop ecophysiology [66]. Therefore, breeding for ever more acquisitive

281   ecophysiological traits in crops may be compromised by the complex regulation between

282   the factors that limit photosynthetic capacity when it is already optimised.

283   Domesticated plants clustered at the acquisitive end of ecophysiological trait co-
284   variation spaces. Thus, there is segregation in trait space between crop and wild plants
285   for ecophysiological traits, in line with findings for other traits [15,18,67–69]. We also found
286   differences in the size of phenotypic spaces between crops and wilds. Crops tended to
287   have smaller ecophysiological spaces, suggesting that crops are not only highly
288   acquisitive species, but also have less variable phenotypes than wild species. Reductions
289   in crop phenotypic variability have also been observed in other studies [70], as well as in
290   genetic diversity (the so-called 'bottleneck effect' [71–73]). Even studies that have
291   considered factors promoting evolutionary diversification of crops, such as phylogenetic
292   origins, geographic spread and diversity in domestication purposes, have found that crops
293   have low internal phenotypic diversity [6]. We found the same trend here after comparing
294   the crop- and wild-phenotypic spaces at equal sample sizes, controlling the effect of
295   species richness. We suggest that the constrained phenotypic spaces of crops and their
296   acquisitive strategy may be a consequence of phenotypic canalization due to inheritance
297   from their wild progenitors, which already harboured reduced phenotypic variance in
298   their ecophysiological traits. Although intraspecific variation was not considered here,
299   the study of trait spaces within species and the processes that shaped them should also be
300   further explored to understand the evolutionary potential of ecophysiological traits.

301   Finally, the phenotypic spaces of crops did not extend beyond the
302   ecophysiological boundaries observed in the wild plants. In other words, crops did not
303   overcome the constraints and trade-offs that determine trait-trait correlation patterns and
304   limit phenotypic diversity in wild species. This is consistent with previous studies
305   suggesting that artificial selection has limited potential to shift phenotypes beyond those
306   observed in the wild [16,57,74,75]. However, these studies focused on intraspecific variation
307   or a limited number of traits and did not explicitly analyse trait spaces using probability
308   density functions and weighted sample sizes. By quantifying unique fractions, our results
309   support this general trend, but also highlight that the only crops that have explored new
310   phenotypic regions within the leaf economics spectra of wild species are those with C_4
311   physiology. The events that led to the CO_2-concentrating mechanism of C_4 species
312   occurred relatively recently [76], and this evolutionary innovation may have provided
313   greater scope for improvements in leaf-level nitrogen and water use efficiencies.

314   Our findings shed light on how early human choices acted on wild herbs and
315   influenced the later evolution of crop progenitors into domesticated plants. A global
316   screening of ecophysiological traits of wild annual herbaceous species showed that crops'

317   wild progenitors were already acquisitive and fast-growing species regarding other wild

318   species that were never domesticated. This phenotypic differentiation suggest that an

319   acquisitive physiology was one of the aspects that led to certain wild plants becoming the

320   progenitors of crops. Similarly, a comparison of the ecophysiological traits of

321   domesticated plants with their wild progenitors showed that domestication and

322   subsequent plant breeding have not favoured a further evolution of the acquisitive

323   strategy. Moreover, our results show almost no tendency for the ecophysiological traits

324   of domesticated plants to fall outside the range limits set by wild species. Artificial

325   selection for acquisitive traits may be compromised by inherent trade-offs between traits

326   at different plant organizational levels, by factors limiting photosynthetic capacity in

327   acquisitive plants, and by the lower physiological diversity of crops and their progenitors

328   compared to other wild species. These results serve as a cautionary lesson for efforts to

329   shift physiological traits during modern breeding, whether in existing crops or in wild

330   species targets for neo-domestication, and call for redirecting future breeding efforts

331   towards other traits more likely to change, such as those related to biomass allocation and

332   seed/plant size.

Methods

Data compilation

We compiled a *global dataset* of 1,146 annual herbs, including domesticates, crops' progenitors and other wild herbs, based on ecophysiological data from diverse databases, published articles, and measured data from an experiment. The ecophysiological traits considered in this compilation were net photosynthetic rate per unit area (A_{area}; µmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapour (g_{wv}; mol H_2O m^{-2} s^{-1}), mass-based leaf nitrogen concentration ([N_{mass}]; %), specific leaf area (SLA; cm^2/g), and ^{13}C isotopic composition ($\delta^{13}C$; ‰). The selection of ecophysiological traits was based on the following criteria: i) previous evidence of differences between wild and domesticated species in these traits [7,8]; ii) functional relevance to plant physiology and resource use; and iii) data availability for both wild and domesticated species. The vast majority of data were compiled from the TRY plant trait database [77] (request no. 21571, accessed June 2022; www.try-db.org), the Botanical Information and Ecology Network (BIEN) database [78] (accessed March 2023; https://bien.nceas.ucsb.edu/bien/), the AusTraits database [79] (accessed March 2023; www.austraits.org), the China plant trait database [80] (accessed June 2022), and the LEDA database [81] (accessed March 2023; www.leda-traitbase.org). The dataset was supplemented by published data not included in the former databases [6–8,16,33,44,82–87] and from data of our own experiment (see section 'Glasshouse experiment' below).

Data were filtered to include only herbs and grasses, but not bamboos, carnivores, climbers, epiphytes, geophytes, helophytes, lianas, parasites, shrubs, succulents, trees, and vines, based on growth form information from the above databases or from the Plants of the World Online (POWO) database (www.plantsoftheworldonline.org). We also excluded non-food crops, based on the Crop Origins database [88], as the literature supporting wild progenitor assignment and differences in ecophysiology between crop and wild plants mainly refers to food crops [7,8,89]. For food crops and their wild progenitors, we also collected data on the primary organ under selection (either fruits/flowers, leaves/shoots, roots, or seeds) from the same database. Finally, we focused on annual plants because most major food crops are annuals, and comparisons with wild species of other life cycles might be misleading.

From this list, we distinguished between plant type (*i.e.* domesticate, crop's wild progenitor and another wild species), functional group (*i.e.* cereal, legume and forb), photosynthetic pathway, and indoor and outdoor studies. 'Crop's wild progenitor' is the

extant wild taxa most closely related to the crop's ancestor, and 'another wild species' is that species that was never domesticated. 'Forb' is an herbaceous flowering plant that is neither a cereal (*i.e.* not a graminoid) nor a legume (*i.e.* not a pulse). We recorded information on photosynthetic pathway (C_3 *vs*. C_4), as it determines very distinct patterns of ecophysiological traits [36], based on the above databases and published literature [90,91]. The search was oriented to papers on ecophysiological traits of plants grown in the field or under controlled environmental conditions. In case of experimental studies, we only considered control treatments (*i.e.* without light, water, nutrient, grazing, or competition stress) and plants growing under atmospheric [CO_2]. The species compiled for each ecophysiological trait and associated reference/database can be found in Supplementary Table 1. Plant taxonomy was standardised according to the Leipzig Catalogue of Vascular Plants (LCVP) as the most up-to-date and comprehensive reference dataset currently available for vascular plants, using the 'LCVP' and 'lcvplants' R packages [92].

Glasshouse experiment

Plant material

We built the *experimental dataset* by setting up a glasshouse experiment and collecting the same ecophysiological traits as in the *global dataset*, but over the domestication history of 11 annual herbaceous crops. The studied crops belong to nine botanical families: Amaranthaceae, Asteraceae, Boraginaceae, Brassicaceae, Fabaceae, Malvaceae, Pedaliaceae, Poaceae and Solanaceae, and have different photosynthetic pathways: C_3 and C_4 (Supplementary Table 2). For each crop, we distinguished three domestication statuses: wild progenitors, landraces, and improved cultivars. Landraces are domesticated genotypes that have not been intensively bred in the last centuries, and improved cultivars are the last improved domesticated plants resulting from intensive breeding programmes since the decade of the 1950s, with the onset of the Green Revolution. For each domestication status and crop, we obtained seeds from two accessions, for a total of 66 accessions. The selection of species and accessions attempted to take into account both intra- and interspecific variability, including phylogenetically diverse plant lineages, different types of food crops (grain, vegetable and fruit crops), and accessions from different geographical origins. Accession identifiers and seed donors can be found in Supplementary Table 2.

In May 2020, ca. 30 seeds of each accession were sown on cell-pack flats. After germination, four seedlings per accession were randomly selected and transplanted to

401   single-plant pots (3.6 L; 15 × 15 × 20 cm). Pot size was chosen to minimize growth

402   restriction for the largest species [93]. All pots were filled with washed sand and supplied

403   with 18 g of a slow-release fertiliser (5 g L^{-1}; Basacote Plus 6 M, Compo, Barcelona,

404   Spain). The amount of fertiliser was set according to the manufacturer's recommended

405   dose for high nutrient availability conditions. Plants were grown indoors in the CULTIVE

406   lab glasshouse at Universidad Rey Juan Carlos (Móstoles, Spain) from May to July 2020.

407   To minimize any spatial variability in the glasshouse, plants were arranged randomly

408   using a randomised block design. Plants were irrigated to field capacity daily and grown

409   with ambient light at mean photosynthetically active radiation (PAR) of 900 ± 200 μmol

410   m^{-2} s^{-1} during light hours, with day/night temperatures of $28/20 \pm 4$ °C, and a relative

411   humidity of $56 \pm 15\%$. The sample size of the experiment was 264 plants (66 accessions

412   × 4 replicates).

413

414   *Trait measurements*

415   We took leaf-level measurements of gas exchange, morphology and chemistry. First, gas

416   exchange was measured between 10 am and 1 pm on three consecutive sunny days in

417   June, before the plants reached the reproductive stage. This time criterion was used to

418   reduce methodological variability. Eight randomly chosen plants per crop were measured

419   on each day, following a fixed order by species (cabbage, amaranth, sesame, borage,

420   tomato, faba bean, peanut, oat, millet, lettuce, and okra). For each plant, A_{area} (μmol CO_2

421   m^{-2} s^{-1}), g_{wv} (mol H_2O m^{-2} s^{-1}), intrinsic water-use efficiency (iWUE = A_{area}/g_{wv}, μmol

422   CO_2 mol^{-1} H_2O), electron transport rate (ETR, μmol electrons m^{-2} s^{-1}), and

423   photochemical efficiency (Fv'/Fm') were measured using an infrared gas analyser (LI-

424   6400; Li-Cor Inc., Lincoln, NE, USA). We used the youngest, unshaded, fully expanded

425   leaf from each individual. Measurements were repeated five times on the same leaf and

426   were made under standardized conditions: ambient [CO_2] (C_a = 400 ppm), saturating

427   irradiance (PAR = 1000 μmol m^{-2} s^{-1}), and a flow gas of 500 μmol s^{-1}. The relative

428   humidity (RH) and air temperature (T) inside the chamber were kept constant and close

429   to ambient conditions (RH ~ 55%; T~25°C). Measurements were recorded only when the

430   stability criteria were met (LI-6400 User's Manual, Li-COR Inc.). If the leaf did not

431   completely cover the chamber (*e.g.* for oats), leaf fragments were scanned and the area

432   calculated using Photoshop software (CS6; Adobe Systems, Inc., San Jose, CA, USA) to

433   recalculate gas exchange values.

434   Second, we measured SLA (cm^2/g) as a leaf morphological trait. Two discs (5 mm

435   diameter) of leaf laminae without major veins were taken from the same leaf used for the

436   gas exchange measurements, using a paper punch. All discs were oven-dried at 60 °C for

437   three days and then weighed on a microbalance (accuracy 1 μg; Mettler Toledo,

438   Columbus, OH, USA) to obtain leaf discs dry mass. SLA was calculated as the ratio of

439   leaf discs area to leaf discs dry mass. Net photosynthetic rate per unit mass (A_{mass}; μmol

440   CO_2 g^{-1} s^{-1}) was then calculated as the product of SLA and A_{area}.

441   Third, we collected data on leaf chemistry. For each individual plant, the two leaf

442   discs were sealed in a tin capsule. Total leaf C and N content (μg) and the ratio of stable

443   isotopes $^{13}C{:}^{12}C$ ($\delta^{13}C$, ‰) and $^{15}N{:}^{14}N$ ($\delta^{15}N$, ‰) per sample were measured using an

444   elemental analyser coupled to a stable isotope mass spectrometer (IRMS; Stable Isotope

445   Facility, University of California, Davis, USA). To determine leaf C content per unit mass

446   (C_{mass} μg/μg) and leaf N content per unit mass (N_{mass}, μg/μg), their total content was

447   divided by the leaf discs dry mass. Leaf C content per unit area (C_{area}) and leaf N-content

448   per unit area (N_{area}) were calculated as the product of SLA and C_{mass} or N_{mass}, respectively.

449   We also computed leaf CN stoichiometry (CN, μg/μg) as the ratio of C_{mass} to N_{mass}, and

450   mass-based leaf N concentration ($[N_{mass}]$, %) by multiplying N_{mass} by 100. Finally,

451   photosynthetic N use efficiency (PNUE, μmol CO_2 mol^{-1} N s^{-1}) was calculated by

452   dividing A_{mass} by N_{mass}.

453

454   **Data analyses**

455   Five individuals from the experimental dataset that did not reach the adult stage were

456   excluded from the analyses. No data were excluded from the global dataset. All analyses

457   were performed in R v.4.2.0. [94].

458

459   *Question 1*

460   To assess whether the ecophysiological traits of crops' wild progenitors differ from those

461   of other wild herbaceous species, we performed phylogenetic generalized least squares

462   (PGLS) models, using the *global dataset*. PGLSs include phylogenetic correlation

463   structure in model residuals to account for species' non-independence due to phylogenetic

464   relatedness [95]. Ecophysiological traits were included as response variables and plant type

465   (categorical variable: crop's wild progenitor *vs*. other wild annual herb) and

466   photosynthetic pathway (categorical variable: C_3 *vs*. C_4) as predictors. These analyses

467   were also performed separately for each functional group to analyse whether differences

468 in ecophysiological traits vary among cereals, legumes and forbs. In addition, we
469 investigated whether the ecophysiological traits differ between the different types of wild
470 progenitors depending on the primary organ under selection. To do this, we included
471 organ under selection (categorical variable: flower/fruit, leaf/shoot, seed, root, and none)
472 and photosynthetic pathway as predictors in the PGLSs.
473   To perform the PGLSs, we first built a phylogenetic tree for the 1,103 wild annual
474 herbaceous species in our *global dataset*. This phylogenetic tree was derived from the
475 most updated and expanded mega-tree of angiosperms (GBOTB.extended.LCVP.tre [96]).
476 Of the 1,103 wild species in our *global dataset*, 961 (87 %) were included in the mega-
477 tree. The remaining 144 were added to our tree as polytomies at the middle point of the
478 corresponding genus branch, using the *phylo.maker* function with scenario three in the
479 'V.PhyloMaker2' R package [96], as recommended by [97]. To account for phylogenetic
480 uncertainty, all analyses were performed on 1000 randomly resolved trees by using the
481 *fix.poly* function of the 'RRphylo' R package [98]. PGLSs were implemented using the *gls*
482 function with corPagel phylogenetic correlation structure in the 'nlme' R package [99] . To
483 account for heteroscedasticity, the variance structure of the data was modelled using the
484 'varIdent' weights specification within the gls function. The significance of predictors was
485 estimated using the *anova* function with sequential (type II) sums of squares in the same
486 R package.
487
488 *Question 2*
489 The *experimental dataset* was used to assess the effects of domestication and subsequent
490 improvement on ecophysiological traits. We performed linear mixed-effect models
491 (LMMs), using the *lme* function in the 'nlme' R package [99]. Models included each
492 ecophysiological trait as a response variable and domestication status (wild, landrace,
493 improved) as fixed effects. Experimental design was taken into account in the statistical
494 model specification by considering accession nested within crop species as random
495 effects. Log_{10}-transformations were used when appropriate to meet assumptions of the
496 models. In the presence of heteroscedasticity (verified with the Levene's test), the
497 variance structure of the data was modelled using the weights option (VarInt comand)
498 within the *lme* function. Significance of the fixed factors of the models was estimated by
499 using the *anova.lme* function with sequential (type II) sums of squares in the 'nlme' R
500 package [99]. The amount of variance explained by the models was evaluated using the
501 *r.squaredGLMM* function from the 'MuMIn' R package [100]. Pairwise comparisons among

502   domestication statuses and species were performed using the *pairwise_t_test* function in

503   the 'rstatix' R package [101] with false discovery rate control.

504

505   *Question 3*

506   To measure the size, uniqueness and overlap of the phenotypic space of crops *vs*. that of

507   wild species, we used the hypervolume approach of Blonder *et al*. [102,103]. This approach

508   quantifies the n-dimensional phenotypic space using a set of observations and assuming

509   kernel density estimation, and estimates shared and unshared trait combinations between

510   two or more groups. Compared to previous mathematical approaches, it is not sensitive

511   to outliers, can detect gaps (or holes) and allows resampling to correct for sample size

512   effects [104].

513   First, we built a two-dimensional space for each bivariate trait combination and

514   each plant type (crop *vs*. wild), using the *global dataset*. In the wild-type subset, we

515   excluded crops' wild progenitors, as they are part of the primary gene pool of crops and

516   in most cases belong to the same species. The number of dimensions was set to n = 2 in

517   order to have enough number of data points for computing the hypervolumes (*i.e.* roughly

518   <10 times the number of dimensions [102]) and to increase interpretability by displaying

519   specific ecophysiological traits in the hypervolume axes. Traits were $\log_{10}$-transformed

520   and scaled (mean = 0 and SD = 1). Since all values of $\delta^{13}C$ were negative, we $\log_{10}$-

521   transformed and scaled its absolute values. For each trait combination, a principal

522   component analysis (PCA) was performed on the wild- and crop- type subsets together,

523   as hypervolume calculations can be sensitive to collinear variables [102]. Separate

524   hypervolumes were then calculated from the two PCA axes corresponding to each subset.

525   There were less crops than wild species and the proportion of C_4 species was higher in

526   the wild-type subsets. To account for these differences, the number of wild species and

527   the proportion of C_4 wild species was matched to that of crops to thus make the size of

528   phenotypic spaces comparable (see 'species sample' and 'percent of C_4' columns in

529   Extended Data Table 5). Therefore, the phenotypic spaces of wilds were generated from

530   1000 randomly sampled subsets by sampling with replacement the same number of points

531   and the same proportion of C_4 species in the wild-type than in the crop-type subset [105].

532   PCAs were performed using the *PCA* function of 'FactoMineR' R package [106] and

533   phenotypic spaces were calculated based on Gaussian kernel density estimation using the

534   *hypervolume_gaussian* function with default settings (Silverman bandwidth estimator

535 and 95% probability threshold) in the 'hypervolume' R package [107]. Finally, we calculated

536 the mean size and standard deviation of all phenotypic spaces.

537   Second, we calculated the phenotypic overlap between the two plant types. We

538 defined overlap as the ratio of the size of the intersection over union (Jaccard index:

539 $(A \cap B)/(A \cup B)$). Trait space overlap represents the similarity of the wild- and crop-

540 type phenotypic spaces, with values ranging from 0 (species are completely dissimilar) to

541 1 (species are completely similar). For each trait pair, we computed the intersection, union

542 and unique components of all pairwise phenotypic space combinations using the

543 *hypervolume_set* function in the 'hypervolume' R package [107]. To ensure that our results

544 were not biased by the species selected in the random sample, we repeated each pairwise

545 analysis on the 1000 random wild subsets. For each pairwise combination, we then

546 calculated the Jaccard index and the unique fraction of each plant type, and reported the

547 mean and standard deviation for each trait pair. Finally, to test the significance of

548 statistics, we built up hypervolumes based on null expectations. Specifically, we

549 generated a 100-sized randomized distribution for the Jaccard index and unique fractions

550 under the null hypothesis that the wild- and crop-type phenotypic spaces were drawn from

551 both plant types. We then calculated the *P*-value for each observed statistic with respect

552 to the generated null distribution using the *hypervolume_overlap_test* function in the

553 'hypervolume' R package [107], and reported the median *P*-value.

Data availability

Most of the data used to compile the *global dataset* are publicly available in plant trait databases (the TRY plant trait database (www.try-db.org), the Botanical Information and Ecology Network database (https://bien.nceas.ucsb.edu/bien/), the AusTraits database (www.austraits.org), the China plant trait database (https://doi.org/10.1038/s41597-022-01884-4), the LEDA Traitbase (www.leda-traitbase.org), and the Plants of the World Online database (www.plantsoftheworldonline.org)) and published literature (see Supplementary Table 1). The raw data of the *experimental dataset* and compiled species-level data on woodiness, growth form, life cycle and photosynthetic pathway are openly available at https://doi.org/10.6084/m9.figshare.24312577.v2 [108].

Code availability

The analyses carried out in this paper did not require the development of custom code. Functions were run as provided by the R packages mentioned in Methods.

Author contributions statement

Study conception and design: all authors; data compilation: AG-F; experimental data collection: all authors; analysis of data and interpretation of results: AG-F; draft manuscript preparation: AG-F; reviews and approval of the final version of the manuscript: all authors.

Competing interests statement

The authors declare no competing interests.

Figure legends

588 **Fig. 1 Conceptual framework**. (a) Previous work has shown that agricultural species
589 have a more acquisitive ecophysiological profile than wild species [7,8]. This observed
590 pattern can be attributed to two processes –early human selection of crops' wild
591 progenitors and/or further evolution under cultivation–. (b) Early selection might have
592 led to crops' progenitors having more acquisitive ecophysiological traits compared to
593 other wild annuals. (c) Natural and artificial selection during domestication (progenitor
594 *vs*. landrace) and improvement (landrace *vs*. improved) might have promoted acquisitive
595 and fast-growing crops. (d) The combined effect of both processes would reflect
596 differences in the range of trait variation among all plant types and (e) might have caused
597 domesticated plants to fall outside the phenotypic space of wild species. Drawings
598 represent *Anthoxanthum odoratum* (wild herb), *Triticum dicoccoides* (crop's wild
599 progenitor), *T. dicoccum* (landrace) and *T. durum* (improved cultivar).

600 **Fig. 2 Early human selection.** Ecophysiological traits of wild annuals compared to the
601 wild progenitors of crops. Crops' wild progenitors (P) are shown in purple and other wild
602 annual herbs (W) in green. Symbols indicate photosynthetic pathway: C_3 (circles) *vs*. C_4
603 (triangles). Dots are trait means of species grouped by botanical order. Statistical
604 differences were evaluated from phylogenetic generalized least squares (PGLS) models
605 across 1000 randomly resolved trees and asterisks denote the mean *P*-value based on
606 analysis of variance (ANOVA) tests (., $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$;
607 see Extended Data Table 2a for exact *P*-values). Total sample size is shown for each trait,
608 plant type (P *vs*. W) and photosynthetic pathway. Abbreviations: A_{area}, net photosynthetic
609 rate per unit area; g_{wv}, stomatal conductance to water vapour; $[N_{mass}]$, leaf N
610 concentration; SLA, specific leaf area; and $\delta^{13}C$, ^{13}C isotopic composition.

611 **Fig. 3 Evolution under cultivation.** Effects of domestication and improvement on the
612 ecophysiological traits of crops. Wild progenitor (P; purple), landrace (L; yellow) and
613 improved (I; coral) accessions for 11 annual herbaceous crops are plotted separately by
614 photosynthetic pathway: C_3 *vs*. C_4. Boxplots show the median and 25th and 75th
615 percentiles of the data, with whiskers extending to 1.5 times the interquartile range. Dots
616 are the measured ecophysiological traits of individual plants (n = 264) and dot colours
617 indicate accession identifier (n = 66). Statistical differences between domestication
618 statuses within each crop were analysed by two-sided Student's t-tests and false-
619 discovery rate correction (·, $P < 0.1$; *, $P < 0.05$). For each ecophysiological trait, a linear

620   mixed-effects model (LMM) was run with domestication (P, L) or improvement (L, I) as

621   fixed effects and accession nested within crop species as random effects. Significance of

622   analysis of variance (ANOVA) tests is indicated by asterisks at the bottom of each panel

623   (see Extended Data Table 4 for exact *P*-values). Abbreviations: A_{area}, net photosynthetic

624   rate per unit area ($\mu mol\ m^{-2}\ s^{-1}$); g_{wv}, stomatal conductance to water vapour ($mmol\ H_2O$

625     $m^{-2}\ s^{-1}$); [N_{mass}], mass-based leaf N concentration (%); SLA, specific leaf area ($cm^2\ g^{-1}$);

626   and $\delta^{13}C$, ^{13}C isotopic composition (‰).

627   **Fig. 4 Domesticates *vs*. wilds.** Bivariate relationships between five ecophysiological

628   traits, showing the phenotypic space overlap of domesticates (D; orange) and wild annual

629   herbs (W; green). The lower left triangle of the matrix shows two-dimensional probability

630   density distributions derived through Gaussian kernel density estimation. Traits were

631   log_{10}-transformed and scaled. Points are species means. Symbols indicate photosynthetic

632   pathway: C_3 (circles) *vs*. C_4 (triangles). The colour gradient indicates regions of highest

633   (dark) to lowest (pale) occurrence probability of trait combinations with contour lines

634   indicating 0.5 and 0.95 quantiles. The upper right portion shows comparative analyses on

635   pairwise phenotypic spaces, where the numbers at the extremes specify the percentage of

636   area unique to each plant type and the numbers in the middle indicate the overlapping

637   percentage (*i.e.* Jaccard index). Significant values ($P < 0.05$) are highlighted in bold and

638   mean significant differences from resampled null distributions. The diagonal displays the

639   total sample sizes for each trait, plant type (D *vs*. W) and photosynthetic pathway. For

640   trait abbreviations and units see legend to Fig. 3.

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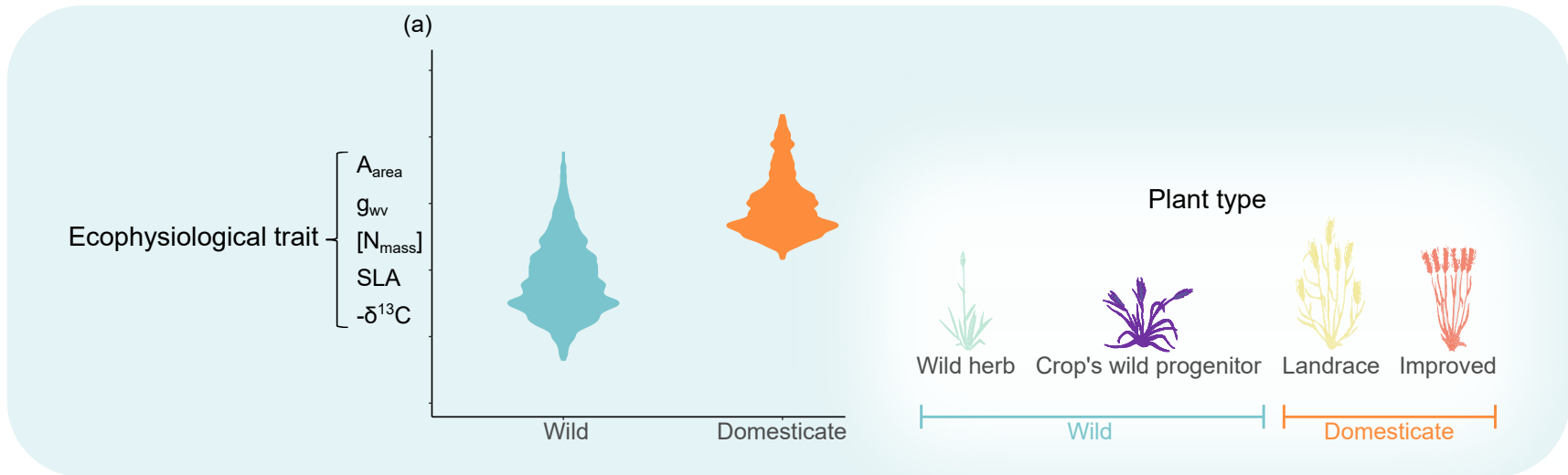
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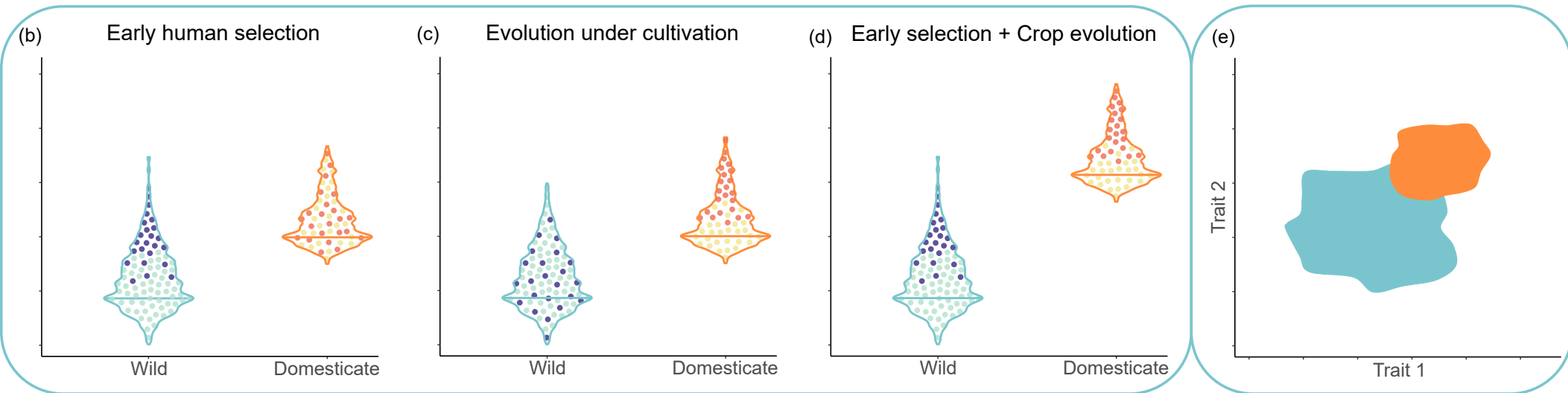868   phylogenetic structure of species assemblages? *Plant Divers* **43**, 255–263 (2021).

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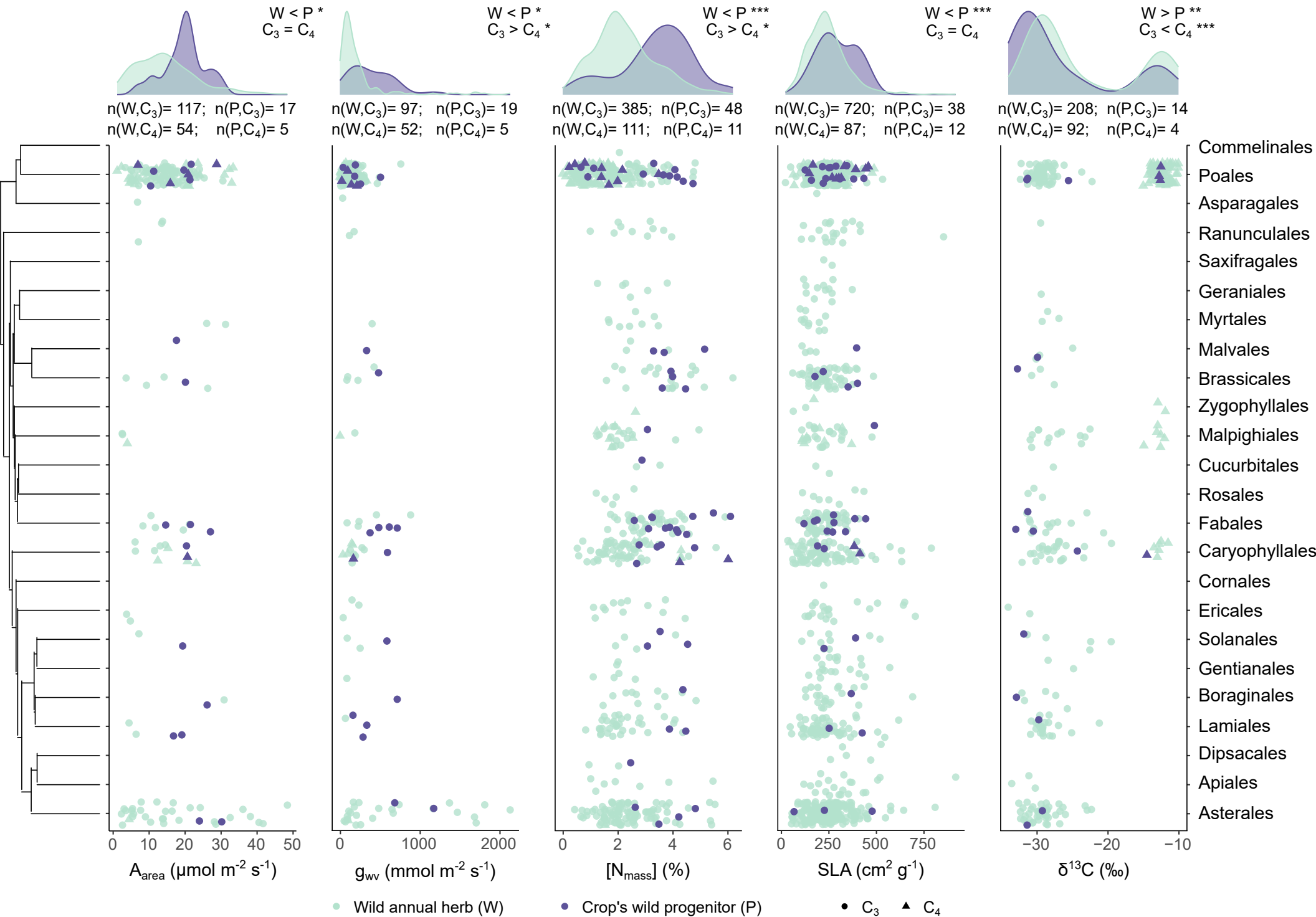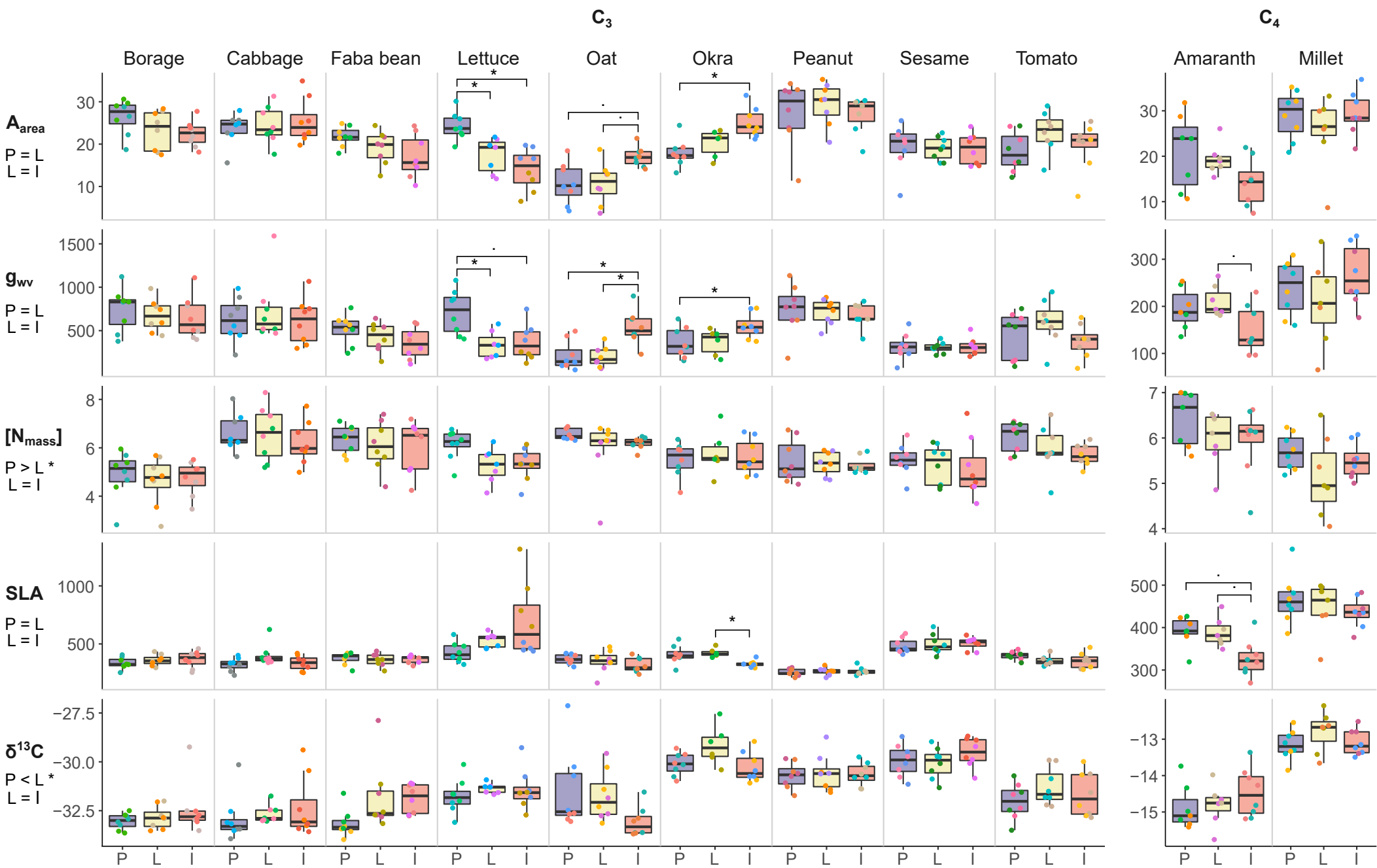890   https://doi.org/10.6084/m9.figshare.24312577.v2 (2023).

PREVIOUS WORK

(a)

Ecophysiological trait
- A_{area}
- g_{wv}
- $[N_{mass}]$
- SLA
- $-\delta^{13}C$

Wild   Domesticate

Plant type

Wild herb   Crop's wild progenitor   Landrace   Improved

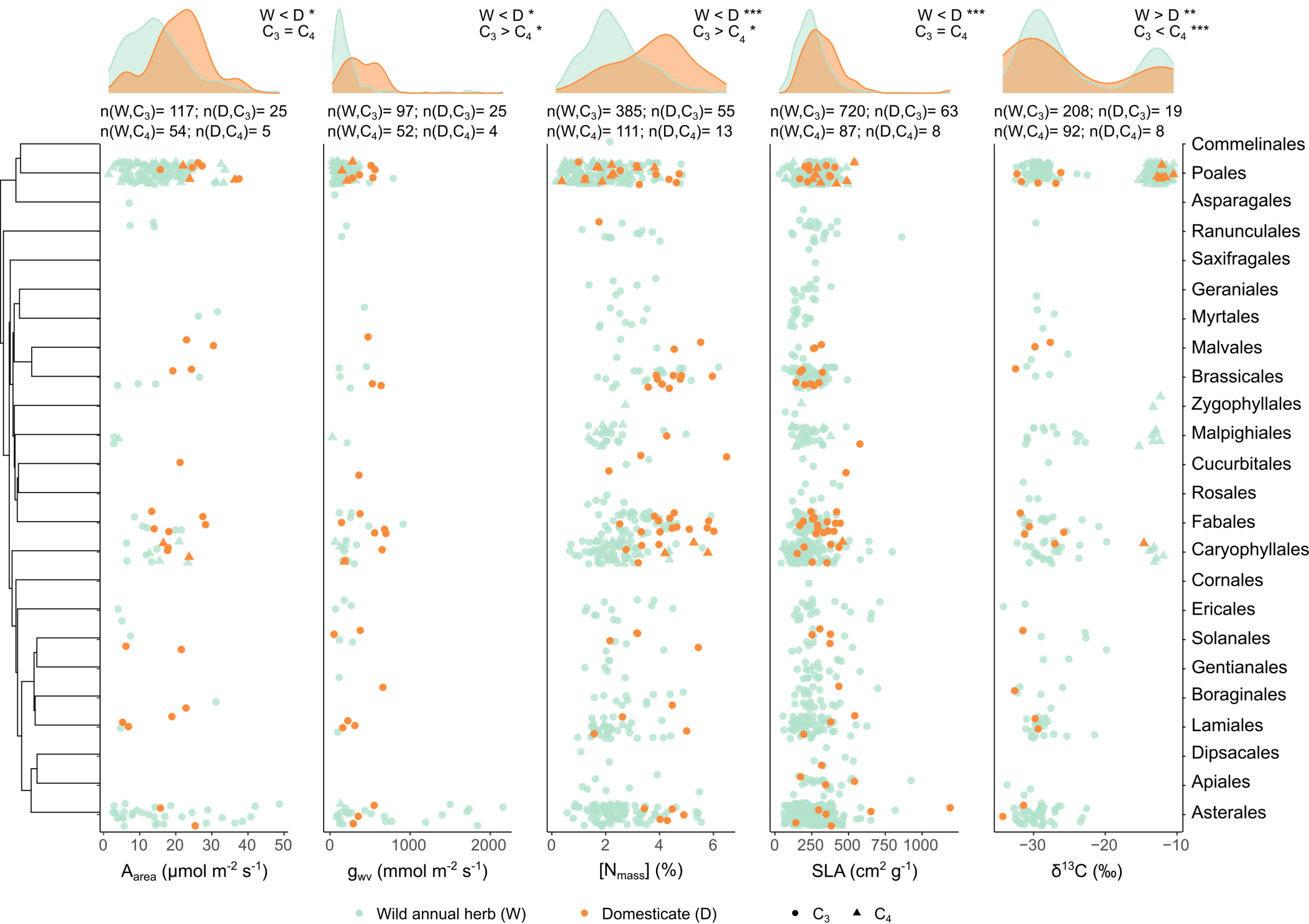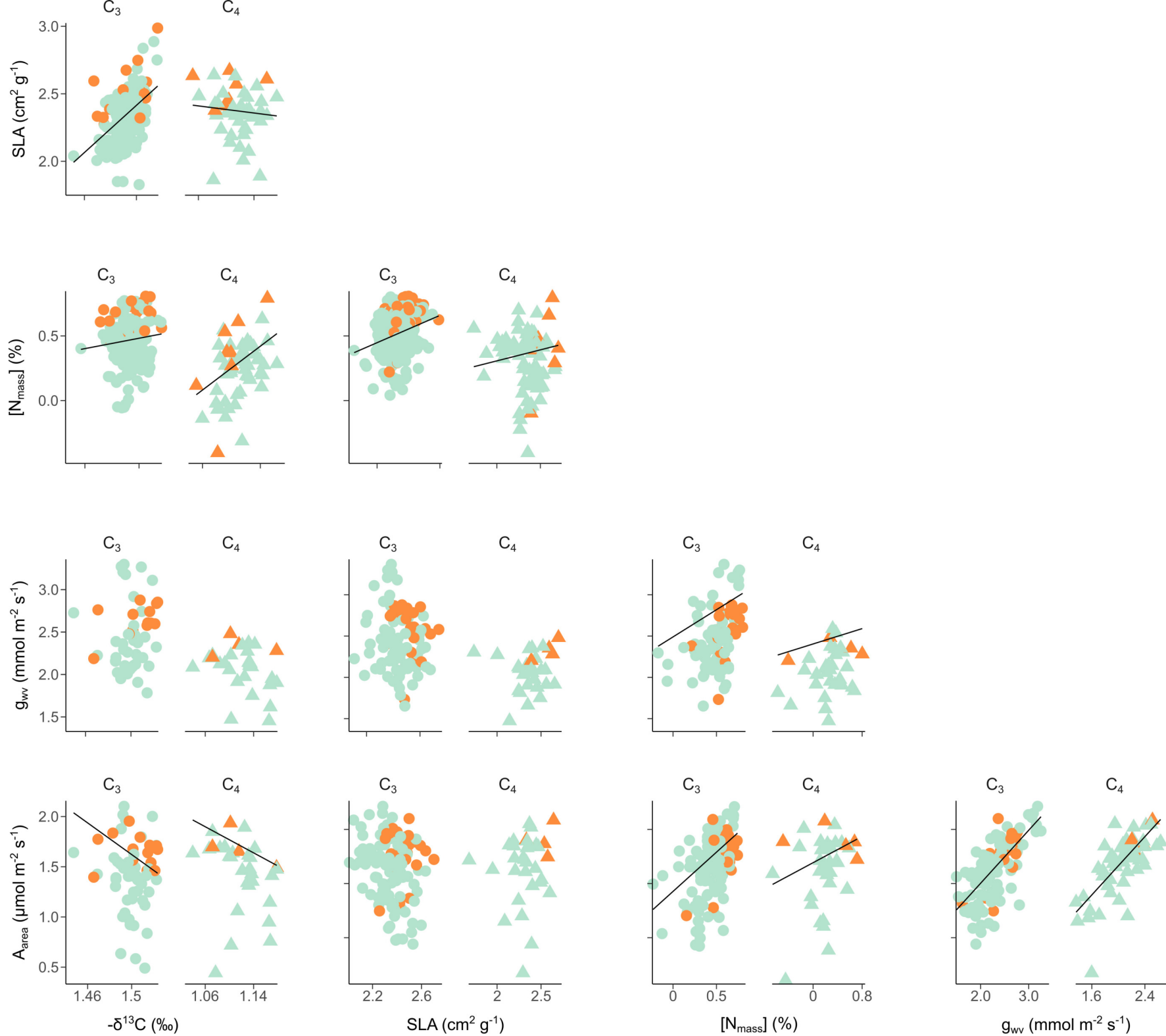Wild   Domesticate

CAUSES

(b) Early human selection

Wild   Domesticate

(c) Evolution under cultivation

Wild   Domesticate

(d) Early selection + Crop evolution

Wild   Domesticate

CONSEQUENCES

(e)

Trait 2

Trait 1

Early human selection

A_{area} ($\mu mol\ m^{-2}\ s^{-1}$) g_{wv} ($mmol\ m^{-2}\ s^{-1}$) [N_{mass}] (%) SLA ($cm^2\ g^{-1}$) $\delta^{13}C$ (‰)

W < P *   W < P *   W < P ***   W < P ***   W > P **
C$_3$ = C$_4$ C$_3$ > C$_4$ *   C$_3$ > C$_4$ *   C$_3$ = C$_4$ C$_3$ < C$_4$ ***

n(W,C$_3$)= 117; n(P,C$_3$)= 17   n(W,C$_3$)= 97; n(P,C$_3$)= 19   n(W,C$_3$)= 385; n(P,C$_3$)= 48   n(W,C$_3$)= 720; n(P,C$_3$)= 38   n(W,C$_3$)= 208; n(P,C$_3$)= 14
n(W,C$_4$)= 54; n(P,C$_4$)= 5   n(W,C$_4$)= 52; n(P,C$_4$)= 5   n(W,C$_4$)= 111; n(P,C$_4$)= 11   n(W,C$_4$)= 87; n(P,C$_4$)= 12   n(W,C$_4$)= 92; n(P,C$_4$)= 4

Commelinales
Poales
Asparagales
Ranunculales
Saxifragales
Geraniales
Myrtales
Malvales
Brassicales
Zygophyllales
Malpighiales
Cucurbitales
Rosales
Fabales
Caryophyllales
Cornales
Ericales
Solanales
Gentianales
Boraginales
Lamiales
Dipsacales
Apiales
Asterales

Wild annual herb (W)   Crop's wild progenitor (P)   C$_3$ C$_4$

Evolution under cultivation

Domesticates *vs.* wilds

δ¹³C

n(D,C₃) = 19
n(D,C₄) = 8
n(W,C₃) = 208
n(W,C₄) = 92

SLA on δ¹³C — 20.7% | 46.2% | 33.1%

[Nmass] on δ¹³C — 21.2% | 40% | 38.8%

gwv on δ¹³C — 54.2% | 39.0% | 6.8%

Aarea on δ¹³C — 52.4% | 41.0% | 6.6%

SLA

n(D,C₃) = 63
n(D,C₄) = 8
n(W,C₃) = 720
n(W,C₄) = 87

[Nmass] on SLA — 28.2% | 50.2% | 21.6%

gwv on SLA — 47.4% | 41.6% | 11.0%

Aarea on SLA — 47.4% | 38.2% | 14.4%

[Nmass]

n(D,C₃) = 55
n(D,C₄) = 13
n(W,C₃) = 385
n(W,C₄) = 111

gwv on [Nmass] — 38.9% | 43.9% | 17.2%

Aarea on [Nmass] — 38.3% | 42.5% | 19.2%

gwv

n(D,C₃) = 25
n(D,C₄) = 4
n(W,C₃) = 97
n(W,C₄) = 52

Aarea on gwv — 42.8% | 49.0% | 8.2%

Aarea

n(D,C₃) = 25
n(D,C₄) = 5
n(W,C₃) = 117
n(W,C₄) = 54

Legend: ● Domesticate (D) ● Wild annual herb (W) ● C₃ ▲ C₄

Wild annual herb (W)   Domesticate (D)   ● C_3 ▲ C_4

A_{area}

g_{wv}

SLA

$\delta^{13}C$

$[N_{mass}]$

Wild annual herb (W)   Crop's wild progenitor (P) C_3 C_4

(a) A_{area}

(b) g_{wv}

(c) $[N_{mass}]$

(d) SLA

(e) $\delta^{13}C$
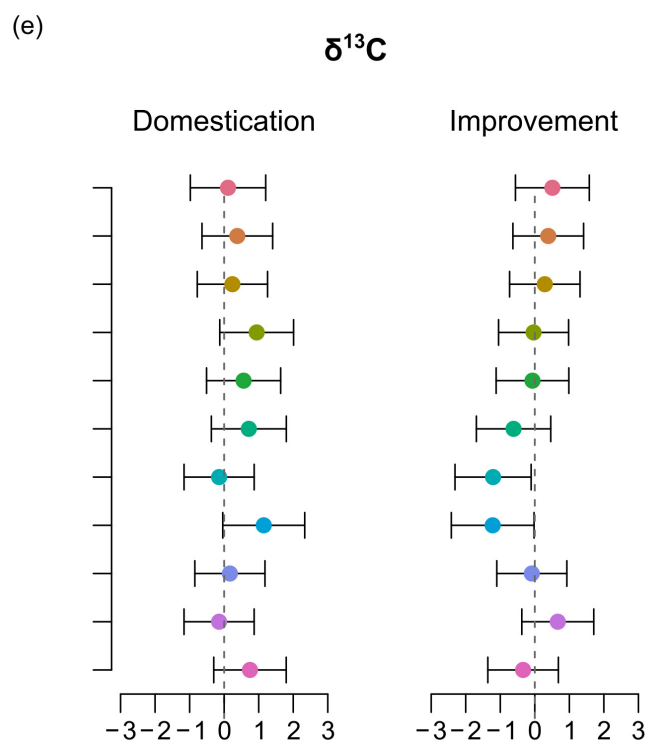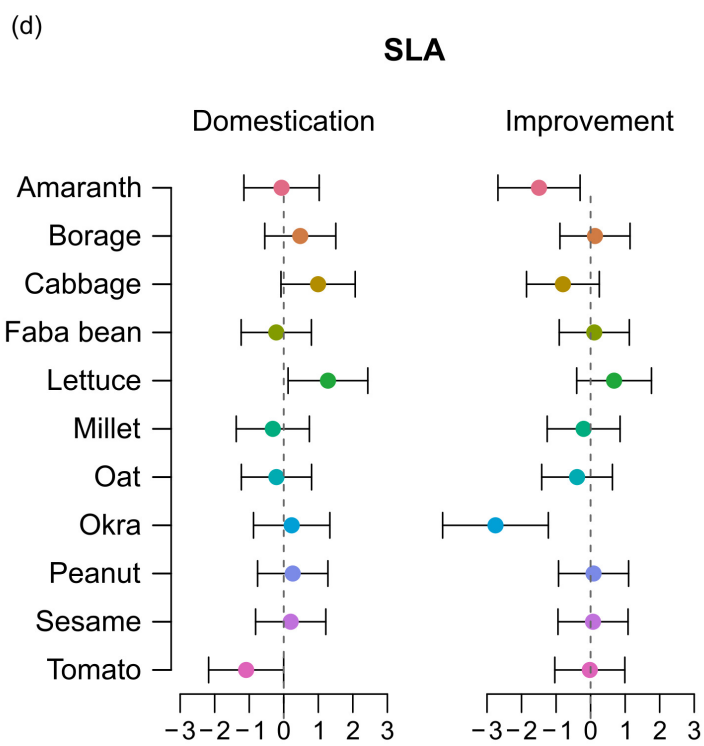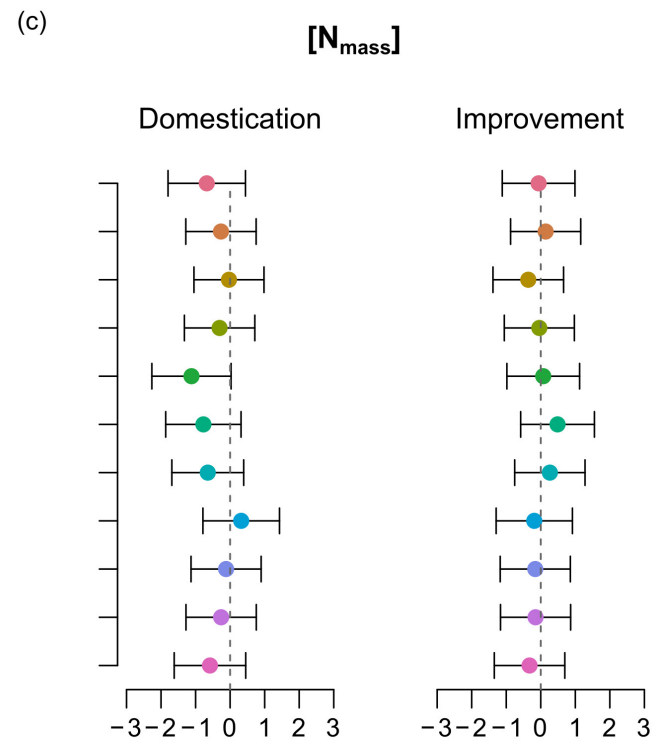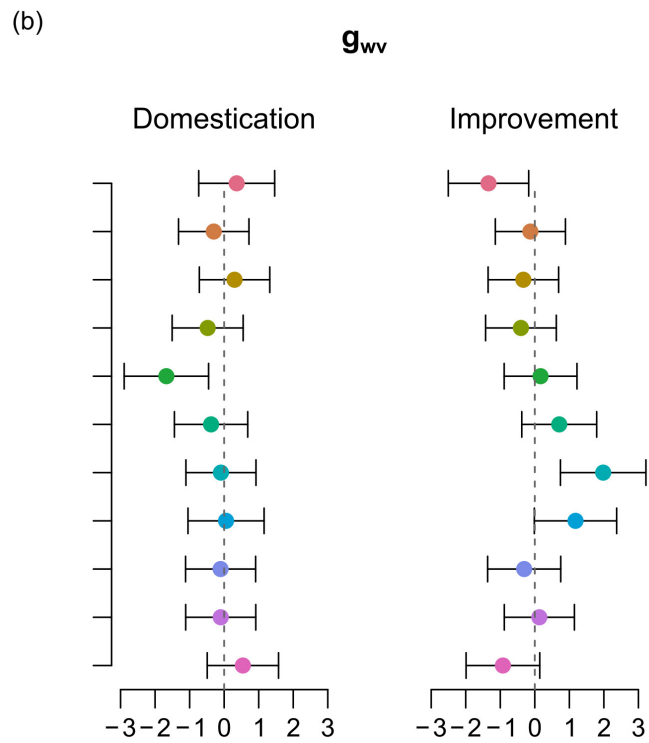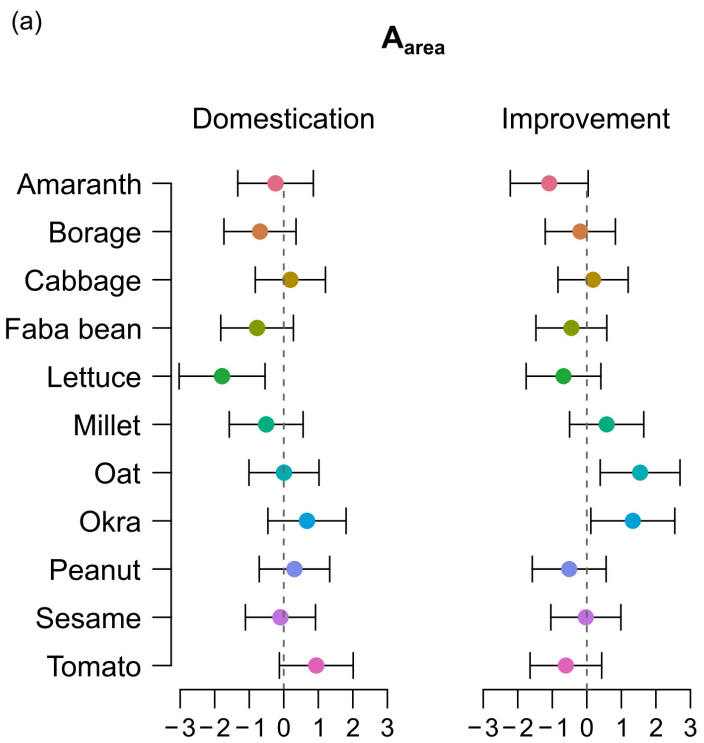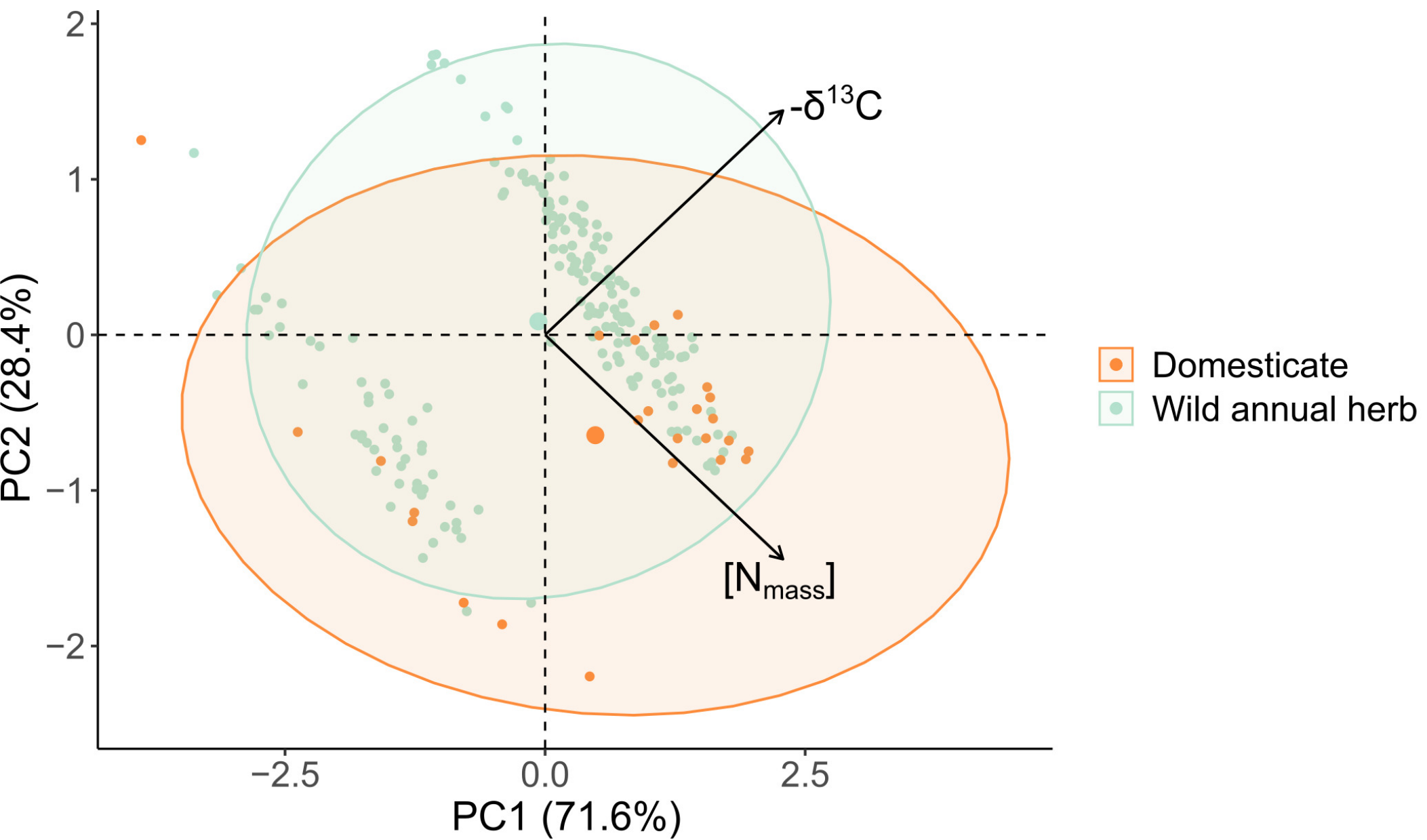
Trait	Abbr.	Unit	Range	No. of observations	No. of studies	No. of W	No. of P	No. of D
Net photosynthetic rate per unit area	A_{area}	$\mu mol\ m^{-2}\ s^{-1}$	1.41 to 48.7	3,756	62	171	22	30
Stomatal conductance to water vapour	g_{wv}	$mmol\ m^{-2}\ s^{-1}$	26.3 to 2,160	2,392	67	149	24	29
Mass-based leaf N concentration	$[N_{mass}]$	%	0.14 to 6.49	4,657	87	496	59	68
Specific leaf area	SLA	$cm^2\ g^{-1}$	29.3 to 1,190.5	14,676	101	807	50	71
^{13}C isotopic composition	$\delta^{13}C$	‰	-34.3 to -10.5	894	17	300	18	27

Total no. of observations = 26,375

Total no. of studies = 193

Total no. of species = 1,146

W = 1,034

P = 69

D = 86

	Plant type (Progenitor, Wild)					Photosynthetic pathway (C_3, C_4)				
	Estimate	SE	F	d.f.	P	Estimate	SE	F	d.f.	P
(a) Global (Outdoors + Indoors)										
A_{area}	-3.73 (±0.03)	1.79 (±0.00)	4.33 (±0.06)	1,190	0.04 (±0)	1.21 (±0.02)	2.32 (±0.00)	0.27 (±0.01)	1,190	0.60 (±0)
g_{wv}	-93.7 (±1.06)	46.8 (±0.12)	3.82 (±0.07)	1,170	0.05 (±0)	-135.3 (±1.5)	68.1 (±0.31)	3.95 (±0.05)	1,170	0.05 (±0)
[N_{mass}]	-0.85 (±0.00)	0.13 (±0.00)	42.2 (±0.04)	1,552	0.00 (±0)	-0.43 (±0.00)	0.19 (±0.00)	5.33 (±0.01)	1,552	0.02 (±0)
SLA	-58.7 (±0.08)	15.6 (±0.01)	14.2 (±0.05)	1,862	0.00 (±0)	-17.3 (±0.41)	22.5 (±0.06)	0.59 (±0.03)	1,854	0.44 (±0)
$\delta^{13}C$	1.39 (±0.01)	0.45 (±0.00)	6.94 (±0.12)	1,315	0.01 (±0)	14.3 (±0.02)	0.48 (±0.00)	881.2 (±3.7)	1,315	0.00 (±0)
(b) Indoors (*i.e.* under controlled experimental conditions)										
A_{area}	-4.45 (±0.05)	2.00 (±0.00)	4.93 (±0.09)	1,143	0.03 (±0)	0.72 (±0.04)	2.78 (±0.01)	0.07 (±0.01)	1,143	0.80 (±0)
g_{wv}	-111 (±1.49)	46.9 (±0.16)	5.66 (±0.12)	1,139	0.02 (±0)	-76.7 (±1.80)	73.6 (±0.57)	1.09 (±0.04)	1,139	0.30 (±0)
[N_{mass}]	-0.44 (±0.00)	0.27 (±0.00)	2.61 (±0.00)	1,116	0.11 (±0)	-0.89 (±0.00)	0.49 (±0.00)	3.29 (±0.00)	1, 116	0.07 (±0)
SLA	-32.7 (±0.12)	16.0 (±0.01)	4.18 (±0.03)	1,232	0.04 (±0)	-8.49 (±0.87)	31.3 (±0.08)	0.07 (±0.01)	1,232	0.79 (±0)
$\delta^{13}C$ *	2.14	0.44	15.1	1,19	0.00	17.3	1.00	302.2	1,1	0.00

		Plant type (Progenitor, Wild)					Photosynthetic pathway (C$_3$, C$_4$)				
		Estimate	SE	F	d.f.	P	Estimate	SE	F	d.f.	P
(a)	Cereal										
	A_{area}	-1.96 (±0.02)	2.34 (±0)	0.71 (±0.02)	1,109	0.40 (±0.01)	1.32 (±0.01)	2.12 (±0.02)	0.39 (±0.01)	1,109	0.53 (±0.01)
	g_{wv}	-54.9 (±0.09)	37.8 (±0.01)	2.62 (±0.04)	1,94	0.11 (±0.00)	-76.5 (±0.33)	13.2 (±0.90)	33.9 (±4.20)	1,94	**0.00 (±0.00)**
	[N_{mass}]	-0.51 (±0.00)	0.22 (±0)	7.72 (±0.03)	1,157	**0.01 (±0.00)**	-1.25 (±0.00)	0.19 (±0.00)	43.2 (±0.35)	1,157	**0.00 (±0.00)**
	SLA	-28.5 (±0.09)	19.2 (±0.01)	2.21 (±0.01)	1,174	0.14 (±0.00)	6.15 (±0.16)	33.9 (±0.43)	0.03 (±0.00)	1,174	0.86 (±0.01)
	$\delta^{13}C$	0.08 (±0.01)	0.51 (±0)	0.57 (±0.03)	1,137	0.45 (±0.01)	14.7 (±0.03)	0.49 (±0.00)	906.5 (±15.6)	1,137	**0.00 (±0.00)**
(b)	Legume										
	A_{area} *	-7.94	3.82	4.33	1,6	0.08	-	-	-	-	-
	g_{wv} *	-292.6	131.7	4.94	1,7	0.06	-	-	-	-	-
	[N_{mass}]	-0.80 (±0.00)	0.29 (±0.00)	7.46 (±0.00)	1,49	**0.01 (±0.00)**	-	-	-	-	-
	SLA	-44.3 (±0.07)	25.5 (±0.01)	3.01 (±0.01)	1,65	0.09 (±0.00)	-	-	-	-	-
	$\delta^{13}C$ *	3.55	1.94	3.34	1,13	0.09	-	-	-	-	-
(c)	Forb										
	A_{area} *	-7.72	3.12	6.11	1,70	**0.02**	-0.23	3.18	0.01	1,70	0.94
	g_{wv} *	-153.6	128.4	1.87	1,64	0.18	-277.2	134.5	4.25	1,64	**0.04**
	[N_{mass}]	-1.15 (±0.00)	0.19 (±0.00)	35.9 (±0.04)	1,341	**0.00 (±0.00)**	0.05 (±0.00)	0.23 (±0.00)	0.04 (±0.00)	1,341	0.84 (±0.00)
	SLA	-99.4 (±0.19)	27.4 (±0.02)	13.11 (±0.07)	1,618	**0.00 (±0.00)**	-26.5 (±0.47)	28.5 (±0.06)	0.86 (±0.03)	1,618	0.35 (±0.01)
	$\delta^{13}C$	1.98 (±0.01)	0.80 (±0.00)	4.83 (±0.06)	1,160	**0.03 (±0.00)**	14.6 (±0.02)	0.76 (±0.00)	365.6 (±0.62)	1,160	**0.00 (±0.00)**

	Domestication (Progenitor – Landrace)				Improvement (Landrace – Improved)			
	Dom				Imp			
	$F_{1,32}$	*P*	R^2m	R^2c	$F_{1,32}$	*P*	R^2m	R^2c
A_{area}	0.89	0.352	0.003	0.48	0.00	0.947	0.000	0.56
A_{mass}	0.04	0.852	0.000	0.50	1.32	0.259	0.005	0.54
g_{wv}	0.80	0.379	0.003	0.51	0.04	0.850	0.000	0.53
ETR	0.47	0.499	0.001	0.62	0.16	0.690	0.001	0.59
Fv'/Fm'	2.13	0.154	0.006	0.50	0.24	0.626	0.001	0.62
iWUE	0.04	0.853	0.000	0.54	0.88	0.356	0.003	0.63
SLA	1.10	0.301	0.005	0.61	0.84	0.366	0.004	0.69
$\delta^{13}C$	4.56	**0.041**	0.001	0.99	0.61	0.441	0.000	0.98
$\delta^{15}N$	1.16	0.289	0.004	0.46	0.54	0.467	0.002	0.46
[N_{area}]	5.05	**0.032**	0.023	0.60	0.85	0.363	0.003	0.62
[N_{mass}]	7.14	**0.012**	0.039	0.38	0.06	0.814	0.000	0.24
CN	3.78	0.061	0.014	0.36	0.74	0.395	0.003	0.34
PNUE	1.39	0.248	0.004	0.59	0.99	0.327	0.004	0.63

	Species sample	Percent of C$_4$	Size		Uniqueness of wild species		Uniqueness of domesticates		Overlap	
	n	pct (%)	W	C	Unique fraction	P	Unique fraction	P	Jaccard index	P
A$_{area}$ on g$_{wv}$	28	14	17 (±3)	10	0.43 (±0.09)	**0.010** (±0.06)	0.08 (±0.06)	0.862 (±0.21)	0.49 (±0.06)	**0.026** (±0.10)
A$_{area}$ on [N$_{mass}$]	29	14	18 (±5)	13	0.38 (±0.10)	0.093 (±0.09)	0.19 (±0.08)	0.273 (±0.18)	0.43 (±0.04)	**0.028** (±0.05)
A$_{area}$ on SLA	29	11	19 (±4)	11	0.47 (±0.07)	**0.004** (±0.02)	0.14 (±0.05)	0.331 (±0.17)	0.38 (±0.05)	**0.001** (±0.01)
A$_{area}$ on δ^{13}C	18	22	20 (±5)	10	0.52 (±0.10)	**0.029** (±0.06)	0.07 (±0.07)	0.736 (±0.25)	0.41 (±0.07)	**0.031** (±0.08)
g$_{wv}$ on [N$_{mass}$]	27	12	17 (±4)	12	0.39 (±0.09)	**0.028** (±0.06)	0.17 (±0.08)	0.460 (±0.19)	0.44 (±0.04)	**0.029** (±0.05)
g$_{wv}$ on SLA	28	11	21 (±4)	12	0.47 (±0.08)	**0.004** (±0.03)	0.11 (±0.06)	0.545 (±0.22)	0.42 (±0.05)	**0.002** (±0.03)
g$_{wv}$ on δ^{13}C	17	24	19 (±4)	9	0.54 (±0.08)	**0.000** (±0.01)	0.07 (±0.06)	0.750 (±0.24)	0.39 (±0.04)	**0.013** (±0.01)
[N$_{mass}$] on SLA	56	13	20 (±4)	18	0.28 (±0.07)	0.086 (±0.09)	0.22 (±0.07)	0.220 (±0.18)	0.50 (±0.04)	**0.039** (±0.04)
[N$_{mass}$] on δ^{13}C	25	30	16 (±3)	20	0.21 (±0.05)	0.193 (±0.11)	0.39 (±0.09)	**0.012** (±0.04)	0.40 (±0.06)	**0.009** (±0.02)
SLA on δ^{13}C	24	27	18 (±5)	20	0.21 (±0.07)	0.238 (±0.15)	0.33 (±0.12)	0.125 (±0.16)	0.46 (±0.08)	0.059 (±0.13)