1   **Crops and the seed mass-seed output trade-off in plants**

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8   **Abstract**

9   A trade-off between seed mass (SM) and seed output (SO) defines a central axis

10   of ecological variation among plants, with implications for understanding both plant trait

11   evolution and plant responses to environmental change. While an observed negative SM-

12   SO relationship is hypothesized to reflect universal constraints on resource allocation in

13   all plants, domestication has likely fundamentally altered this relationship. Using a

14   dataset of SM and SO for 41 of the world most widespread crops and 1,190 wild plant

15   species, coupled with observational data on these traits in soy (*Glycine max*) and maize

16   (*Zea mays*), I show that domestication has systematically rewired SM-SO relationships in

17   crops. Compared to wild plants, virtually all crops express a higher SM for a given SO;

18   this domestication signature is especially prominent in seed crops, and also influences the

19   phylogenetic signal in SM and SO. In maize these traits have become positively related

20   likely due to simultaneous selection for greater SM and SO, while in soy these traits have

21   become decoupled likely due to primary selection for SM only. Evolved relationships

22   between SM and SO in plants have been disrupted by both conscious and unconscious

23   artificial selection, which represents a key aspect of how the functional biology of crops

24   differ fundamentally from wild plants along "universal" plant trait spectra.

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26

27 **Introduction**

28 *Seed mass and seed output as a critical dimension of plant functional ecology*

29   Differences in seed traits including mass, output, shape, dispersal, biochemical

30 constitution, and dormancy have come to represent critical axes of life-history variation

31 among plant species worldwide (Westoby et al. 1996, Moles et al. 2005, Diaz et al.

32 2016). Understanding and quantifying variation in these seed traits among terrestrial plant

33 species has been central in better understanding a range of large-scale processes including

34 the evolution of angiosperms and plant biogeography (e.g. Westoby et al. 1992,

35 Thompson et al. 1993, Westoby et al. 1996, Moles and Westoby 2004, Moles et al. 2005),

36 as well as multiple aspects of plant life history strategy including dispersal ability, stature,

37 seedling competitiveness and survivorship, plant- and species responses to disturbance,

38 colonization ability, and persistence of seeds in soils (Thompson et al. 1993, Westoby et

39 al. 1996, Leishman et al. 2000, Moles and Westoby 2003, 2004). Of the seed traits

40 explored in the comparative plant sciences, seed mass (SM) has received the most

41 research attention (cf. Kattge et al. 2011), with comparative analyses including thousands

42 of plant species indicating that SM varies by up to 6 orders of magnitude across species

43 (Westoby et al. 2002, Moles and Westoby 2003). When considered independently or

44 alongside other leaf-, stem- and whole-plant traits, variation in SM across species

45 represents a key trait defining the functional ecology of plants worldwide (e.g. Westoby

46 1998, Cornelissen 1999, Westoby et al. 2002, Diaz et al. 2016).

47   In plant ecology, a long-recognized trade-off between SM and seed output (SO)

48 remains central to plant resource allocation and life-history theories, particularly as it

49 pertains to plant reproduction strategies (Harper et al. 1970, Smith and Fretwell 1974,

50 Lloyd 1987, Westoby et al. 2002, Moles et al. 2004). Under conditions of finite

51 resources, theory and observation suggest plant species differentiate from one another

52 along a SM-SO axis that is hypothesized to optimize reproductive fitness and success,

53 given a certain set of environmental conditions (Sadras 2007). In the simplest conceptual

54 terms, the endpoints of the SM-SO trade-off are defined by plants allocating resources to

55 a small number of large seeds, vs. plants that allocate resources to a large number of very

56 small seeds; the wide variation that exists in between these conceptual points reflects

57 "optimized" solutions to resource allocation (Sadras 2007). Similar to the evidence that

58   supports the existence of universal trade-offs (or correlations) among other plant

59   functional traits (e.g. Wright et al. 2004), global databases including trait values from

60   thousands of species can be used to define a "universal SM-SO" trade-off that exists

61   among plants globally. The shape of this trade-off reflects evolutionarily defined

62   constraints on possible combinations of SM and SO that can (or are most likely to) occur

63   across non-domesticated plant species (hereafter referred to as "wild plants").

64

65   *Seed mass and seed output trade-offs and crops*

66   Historical analyses(Meyer et al. 2012) coupled with recent observational and

67   experimental studies, have refined our understanding of how plant trait variation and

68   correlations have been fundamentally altered by crop domestication (Meyer et al. 2012,

69   Milla et al. 2014, Martin et al. 2017). While the suites of traits that are under intentional

70   and unintentional artificial selection is wide – including whole-plant, leaf-, and root traits

71   (e.g. Milla et al. 2014) – plant yield components including SM and/ or SO have been

72   under the most intensive selection (Sadras 2007).

73   Assuming that crops have been selected for increased SM and SO leads to the

74   hypothesis ("Hypothesis 1) that, as compared to a "global SM-SO trade-off", artificial

75   selection results in all crops expressing a higher SM for a given SO (or vice versa) as

76   compared to wild plants. Additionally though, artificial selection directly targets SM and

77   SO only for a certain group of crops such as cereals (e.g. wheat, rice, and maize), oil seed

78   crops, or legumes including soy and other pulses. Therefore, one may also hypothesize

79   ("Hypothesis 2") that for a given crop species, the degree of divergence away from a

80   global SM-SO trade-off differs according to the plant organ under selection, with seed

81   crops showing the strongest divergences on average.

82   Yet even for crops under selection for seeds, within-species SM-SO trade-offs

83   may differ considerably according to plant growth form and reproductive strategy. In

84   certain crops including maize – one of the crops employed in my analysis here – both

85   increased SM (i.e. mean kernel mass) (Hufford et al. 2012) and SO (i.e. mean kernels per

86   plant)(Brown et al. 2011) have been simultaneously targeted by artificial selection. This

87   leads to the hypothesis (Hypothesis 3) that, counter to a global SM-SO trade-off, crops

88   such as maize express a positive SM-SO correlation. Alternatively, genome sequencing

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89 indicates that increased SM in soybean – also employed in my analysis here – has been

90 targeted during artificial selection (Liu et al. 2007, Zhou et al. 2015), while the number of

91 inflorescences and ultimately SO remains plastic, and largely determined by local

92 resource availability and concomitant plant growth rates (Andrade et al. 2005). This leads

93 to the hypothesis (Hypothesis 4) that in soy, covariation along an intraspecific SM-SO

94 trade-off would be weak or potentially non-existent. Here, I used a large dataset of SM

95 and SO from 1,190 wild plant species and 41 of the world's most widespread crops,

96 derived from both functional trait databases and field studies on maize and soy, in order

97 to test these four complementary hypotheses.

98

99 **Methods**

100 *Generating a global SM-SO trade-off with functional trait data*

101 Data for both SM and SO were acquired from a structured enquiry submitted to

102 the TRY Functional Trait Database (Kattge et al. 2011). We specifically requested

103 information on trait ID 26 ("seed dry mass", corresponding to SM) and trait ID 131

104 ("seed number per plant", corresponding to SO). This request returned n=117,882 and

105 n=9,292 observations for SM and SO respectively. All statistical analyses were then

106 performed using R version 3.4.0 (R Foundation for Statistical Computing, Vienna,

107 Austria). First, for each observation I used the 'TPL' function in the "'Taxonstand' R

108 package (Cayuela et al. 2017) in order to cross-reference all species, genus, and family

109 identities with The Plant List and resolve all synonyms or errors. Once taxonomy checks

110 were complete, species-level mean values for both SM and SO were then calculated.

111 This list of species was then cross-referenced with a list of the world's crop

112 species reported by the Food and Agricultural Organization of the United Nations (FAO)

113 (FAO 2018), which was refined to species-level taxonomy by Martin and Isaac (2015).

114 This procedure led to identification of n=38 crop species which had both paired SM-SO

115 data in TRY, and have been identified by the FAO as a commodity species. I therefore

116 supplemented the TRY dataset with species mean SM and SO values extracted from the

117 literature for a number of additional common crops including soy (*Glycine max(Hayes et*

118 *al. 2018)*), sunflower (*Helianthus annuus*(Libenson et al. 2002), rice (*Oryza sativa*(Wang

119 et al. 2008)), and maize (*Zea mays*(Maddonni and Otegui 2006)); data for SM and SO

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120   was also sought for all additional crops listed by Martin and Isaac (2015) which were not

121   in TRY, but this data was not available in peer-reviewed literature. Therefore in sum, this

122   data consolidation process resulted in paired SM-SO data for n=1231 species in total.

123   Each of the 41 crop species were then classified broadly according to the main

124   commercial portion of the plant as one of: i) "seed plants" which are harvested for seeds

125   (n=17 crop species); ii) "tree crops" which are harvested for timber or as ornamental

126   species (n=3 crop species); iii) "other crops" which are harvested for other plant parts

127   including leaves, roots, or large inflorescences (n=21 crop species); or iv) "wild species"

128   which are non-domesticated plants (n=1190 species).

129

130   *Crops along an SM and SO trade-off*

131   Analyses using the 'fitdist' function in the 'fitdistrplus' R package (Delignette-

132   Muller and Dutang 2015) indicating that both the SM and SO datasets were better

133   described by normal or log-normal distributions (as per lower log-likelihood scores;

134   Table 1), so log-transformed data was used in all subsequent analyses. I first fit a

135   standardized major axis regression (SMA) model to the entire log-SM and log-SO, in

136   order to test for the presence of a "global SM-SO trade-off". This SMA was implemented

137   in using the 'sma' function in the 'smatr' R package(Warton et al. 2012), with 95%

138   confidence limits surrounding the overall model generated through bootstrapping.

139   All SMA model residuals associated with each species were then extracted, and

140   significant differences in residuals among the four different plant types were evaluated.

141   Due to unequal sample sizes and non-independence of data points owing to phylogenetic

142   structure in the data (see below), this test was performed as a linear mixed effects model

143   using the 'lme' function in the 'nlme' R package(Pinheiro et al. 2016). Specifically, in

144   this model SMA residuals were predicted as a function of plant type (as a fixed effect),

145   while accounting for genus identity nested within family identity (as random effects). In

146   addition to assessing overall significance of the plant type term (i.e. the fixed effect), I

147   calculated mean (± S.E.) SMA residuals for each plant type using the 'lsmeans' function

148   in the 'lsmeans' R package (Lenth 2016), and assessed the pairwise differences in mean

149   SMA model residuals among all four plant types using a Tukey post-hoc tests (also

150   implemented with the 'lsmeans' function). Post-hoc tests based on this linear mixed-

151   effect model were considered significant when assessed against a Bonferonni-corrected

152   *p*-value of 0.008.

153

154   *Phylogenetic signal in SM and SO*

155   A phylogenetic tree was constructed for the entire *n*=1,231 species using

156   Phylomatic (Webb and Donoghue 2005) to generate a phylogenetic tree, based on the

157   Angiosperm Phylogeny Group megatree ("R20120829.new"). The BLADJ algorithm in

158   Phylocom(Webb et al. 2008) was used to estimate phylogenetic branch lengths according

159   to clade ages based on fossil records (Wikstrom et al. 2001) which were updated by

160   Gastauer and Meira-Neto (2016). Unresolved evolutionary relationships were treated as

161   polytomies.

162   Phylogenetic signal in log-SM and log-SO across the entire phylogeny was then

163   quantified as Pagel's λ *(Pagel 1999)*. For this analysis, a Pagel's λ value equal to 0

164   represents instances of no phylogenetic signal (i.e. where evolution of SM and/or SO is

165   entirely independent of phylogeny), and Pagel's λ values of 1 represent instances where a

166   phylogeny perfectly predicts trait data (i.e. where evolution of SM and/or SO perfectly

167   matches a Brownian model of trait evolution) (Pagel 1999). Values of Pagel's λ were

168   calculated using the 'phylosig' function in the 'phytools' R package (Revell 2012).

169   Significance tests for were performed as randomization tests (with n=1000

170   randomizations used), where SM and SO data were randomly shuffled across the

171   phylogeny, and Pagel's λ was recalculated on each randomized dataset; phylogenetic

172   signal was considered statistically significant if the observed Pagel's λ fell within the

173   upper 95% of this randomized distribution.

174   In order to assess if the presence of crops influenced phylogenetic signal in SM

175   and SO, I then recalculated Pagel's λ with crop species removed from the dataset (where

176   *n*=1,190 in this reduced phylogeny and trait dataset). Specifically, if Pagel's λ was to

177   increase when crops were removed from the phylogeny, this could be interpreted as crops

178   reducing the strength of the phylogeny signal in SM or SO. All trait-phylogeny

179   relationships were also graphed visually using the 'plotTree.wBars' function in the

180   'phytools' R package (Revell 2012).

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182   *Soy and maize along an SM-SO trade-off*

183   I employed two crop species-specific datasets, both derived from field studies, to

184   evaluate if soy and maize expressed an SM-SO trade-off that was consistent with a global

185   pattern (i.e. based on the n=1,231 species dataset). Soy data was taken from a published

186   field study focused on soy leaf economics traits that was conducted on a 30-year old

187   experimental farm in Guelph, Canada (43° 32′ N, 80° 12′ W) (Hayes et al. 2018). This

188   study provided paired plant-level SM and SO data for n=45 soy plants (detailed in (Hayes

189   et al. 2018)). Maize data was taken from two different field studies conducted at the same

190   site, where paired SM and SO data was directly available (Maddonni and Otegui 2006,

191   Mayer et al. 2012). Specifically, n=26 paired maize SM-SO observations were available

192   in Table 1 of (Maddonni and Otegui 2006), while n=8 paired maize SM-SO data were

193   taken from Table 1 of (Mayer et al. 2012). Data from both maize studies were derived

194   from field experiments at the same site (the Experimental Station of the National Institute

195   of Agricultural Technology) in Pergamino, Argentina (33° 56′ S, 60° 34′ W). I then used

196   fit a SMA model (as described above) to both soy and maize datasets separately to

197   describe intraspecific SM and SO patterns, and where SMA models were significant,

198   95% confidence limits were generated through bootstrapping with replacement (with

199   1000 replicates used) implemented with the 'bootstrap' function in the 'modelr' R

200   package (Wickham 2017).

201

202   *Data availability*

203   The compiled database of n=1,231 plant species used in my analyses here

204   (presented in Figs. 1 and 4) are available as individual datasets in the TRY Functional

205   Trait Database. Compiled data on soy and maize (presented in Fig. 3) are available upon

206   request from the author, or in the original publications as cited in the methods.

207

208   **Results**

209   *Crops along a global seed mass seed output trade-off*

210   Data from n=1231 species across 517 genera and 92 families demonstrate the

211   presence of a SM-SO trade-off in plants globally, with a standardized major axis (SMA)

212   regression slope of -0.86 (95% C.I. = -0.91, -0.82, SMA r^2=0.06, p<0.0001; Fig. 1). Of

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213   the 41 crop species represented in the SM-SO dataset, 90.2% (37 crop species) feel above

214   the global SM-SO axis (where SMA model residuals ≥ 0) while only four fell below the

215   primary SM-SO axis (Fig. 1). In comparison, 46.1% and 53.9% of the n=1190 wild plant

216   species were approximately evenly distributed above and below the primary SM-SO

217   model, respectively (Figs. 1 and 2).

218   Across all 1231 species, SMA model residuals ranged from -8.4 to 11.7 (average

219   residual=1.14e-11±2.5 (S.D.)). While accounting for the phylogenetic non-independence

220   of data (Figs. S1 and S2) and uneven sample sizes, the extent of divergence from the SM-

221   SO axis differed significantly across crop types (mixed-effects model $F_{4, 711}$=13.1,

222   p<0.001, Fig. 2). Specifically, SMA residuals for seed- and tree crops were significantly

223   greater than zero ($p \leq 0.001$), while residuals for non-seed/ tree crops and wild plant

224   species did not differ from zero ($p \geq 0.067$, Table S1).

225   There was a gradation of divergence from a central SM-SO trade-off (Fig. 2).

226   Tree crops and seed crops expressed the highest SM for a given SO, and in comparison

227   non-seed crops and wild plant expressed lower SM for a given SO; these groups broadly

228   differed significantly from one another in terms of average divergence from a central SM-

229   SO axis (Table S1). Crops harvested for seeds diverged significantly more strongly from

230   a central SM-SO trade-off as compared to wild plants (post-hoc contrast $p \leq 0.0001$; Table

231   S2). Furthermore, 17 seed crops expressed higher average SMA residuals (3.4±1.6 (S.D.),

232   in comparison to the average SMA residuals observed in 21 non-seed crops (1.6±1.8

233   (S.D.) (Fig. 2, Table S2) The three tree crops in the dataset differed most strongly from a

234   central SM-SO trade-off, showing SMA residuals which were significantly higher than

235   all other crops and wild plants (8.4±1.8 (S.D.); post-hoc $p \leq 0.04$ for all three contrasts;

236   Fig. 2). Among seed crops, notable divergences from the global SM-SO model included

237   hazelnut (*Corylus avellana*, SMA residual=7.3), maize (*Zea maize*, SMA residual=5.1),

238   and sunflower (*Helianthus annuus*, SMA residual=4.8).

239

240   *Within-crop seed mass seed output trade-offs*

241   Data from soy (n=45) and maize (n=35) indicated that SM-SO patterns differed

242   both between these crops, as well as in comparison to a global SM-SO pattern. In maize

243   SM and SO covaried significantly among individual plants (SMA r^2=0.334, p<0.0001;

244   Fig. 3), however artificial selection has resulted in this relationship being positive and

245   therefore opposite that of a global SM-SO pattern (maize SMA slope=0.27, 95% C.I. =

246   0.20, 0.37, Fig. 3). Alternatively, soy data indicate that targeted selection for higher SM

247   alone has resulted in a decoupling of SM and SO (Fig. 3). These two seed traits were not

248   significantly related in soy, expressing only a weak negative relationship (SMA slope=-

249   0.14, 95% C.I.=-0.2, -0.11, SMA r^2=0.002, p=0.757; Fig. 3). Consistent with

250   reproductive allocation theory and targeted selection for SM(Sadras 2007), the lack of a

251   significant SM-SO relationship in soy was qualitatively associated with variation in SM

252   which was nearly an order of magnitude lower than variation in SO (where CV=9.5 and

253   76.3, respectively; Table S1).

254

255   *Phylogenetic signal along the seed mass-seed output trade-off*

256   Across the entire dataset (n=1231) both SM and SO expressed significant

257   phylogenetic signal, with Pagel's λ of 0.995 and 0.853, respectively (p<0.001 in both

258   cases, Fig. 4). When crops are removed from the dataset, SM and SO are better predicted

259   by phylogenetic relatedness than when artificially crops are present. Specifically,

260   excluding crops from the datasets resulted in a small, albeit detectable, increase in Pagel's

261   λ for both SM (0.996 with crops) and SO (0.859 with crops).

262

263   **Discussion**

264   *The functional profile of crops vs. wild plants*

265   Research documenting the traits that have been targeted by crop domestication

266   suggests that SM and/or SO are among those under the most intensive artificial selection

267   (Meyer et al. 2012). While much of this research has taken archaeological and/or genetic

268   approaches the analysis presented here refines a functional trait-based signature of crop

269   domestication and artificial selection. Specifically, consistent with my hypotheses i)

270   artificial selection has led to most crops significantly deviating from a global SM-SO

271   trade-off (Fig. 1), such that ii) crops under selection for seeds deviate most strongly as

272   compared to non-seed crops (Fig. 2). Yet within seed crops the degree to which artificial

273   selection has reshaped the evolved biomechanical and/ or physiological constraints on

274   trait syndromes (or trait trade-offs), depends on the specific reproductive traits/ yield

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275 components being targeted (Fig. 3). In certain crops such as maize, artificial selection has

276 fundamentally altered the direction of trait trade-offs imposed by natural selection, while

277 in others such as soy artificial selection may only act to decouple the covariation among

278 reproductive traits (Fig. 3)

279 When taken with studies examining other suites of crop functional traits and trait

280 spectra (Milla et al. 2014, Martin et al. 2017), the shifts in SM-SO trade-offs in crops vs.

281 wild plants observed here (Figs. 1-3) represent components of a broader "disruption" in

282 plant resource-use syndromes incurred by artificial selection (Milla et al. 2014). Other

283 and observational data indicate that crops generally express greater values of resource

284 capture traits as compared to their wild progenitors. Indeed, detailed analyses of leaf traits

285 indicate that certain crops express among the most extreme "resource-acquiring" trait

286 syndromes in plants globally (Martin et al. 2018), while at the same time artificial

287 selection has resulted in trait relationships, or "phenotypic integration"(Milla et al. 2014),

288 that are considerably weaker in crops vs. wild plants (Milla et al. 2014, Martin et al.

289 2017).

290 While neither SM nor SO values in crops have been shifted to extreme ends of a

291 reproduction trait spectrum (Fig. 4), the analysis here indicates that relationships between

292 SM and SO within individual species may be fundamentally rewired through

293 domestication (Fig. 3). Our results and other studies exploring trait syndrome disruption

294 (e.g. Milla et al. 2014) provide compelling evidence to indicate crops fundamentally

295 differ from wild plants along a global spectrum of plant form and function(Diaz et al.

296 2016). Quantifying the position of crops and how their traits trade-off along a global trait

297 spectra (Wright et al. 2004, Diaz et al. 2016) represents a means of synthetically defining

298 the functional ecology of crops, which in turn would support a range of hypotheses on the

299 unintended impacts of artificial selection.

300

301 *Conscious and unconscious selection and trait trade-offs in crops*

302 Studies employing quantitative trait locus (QTL) mapping would suggest that the

303 results here deviations of crops away from a central SM-SO trade-off (Fig. 1), have likely

304 occurred largely in response to "conscious selection" for these individual traits (e.g. Tao

305 et al. 2017). Major shifts in the shape of the SM-SO relationship in the two crops

306   explored here is also consistent with strong conscious selection for these particular traits

307   (Fig. 3). Furthermore, analyses of phylogenetic patterns in seed traits here demonstrated a

308   small albeit detectable reduction in phylogenetic signal when crops are removed from

309   analyses (Fig. 4). Major deviations in SM and SO among crops vs. wild relatives, both

310   here and in experimental studies, are most likely consistent with long-term conscious

311   selection of seed traits.

312   At the same time though, theories from functional trait-based ecology do

313   hypothesize that unconscious selection has also played a role in reshaping SM-SO

314   relationships in crops. Specifically, from a plant resource allocation/ natural selection

315   perspective, higher SM at a given SO in open cultivated agricultural environments would

316   be expected to competitive benefits to crop plants, including greater seedling growth rates

317   and survival at greater burial depths. Yet while this theory derived from plant resource

318   allocation theory suggests that unconscious selection may also have contributed to the

319   patterns observed here, experimental evidence in support of this hypothesis is currently

320   lacking (reviewed by Milla et al. 2015). Detailed partitioning of the relative importance

321   of conscious vs. unconscious selection remains a leading avenue for better understanding

322   the genetic vs. phenotypic controls on SM, SO, and their relationships in crops.

323

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488   **Figures**
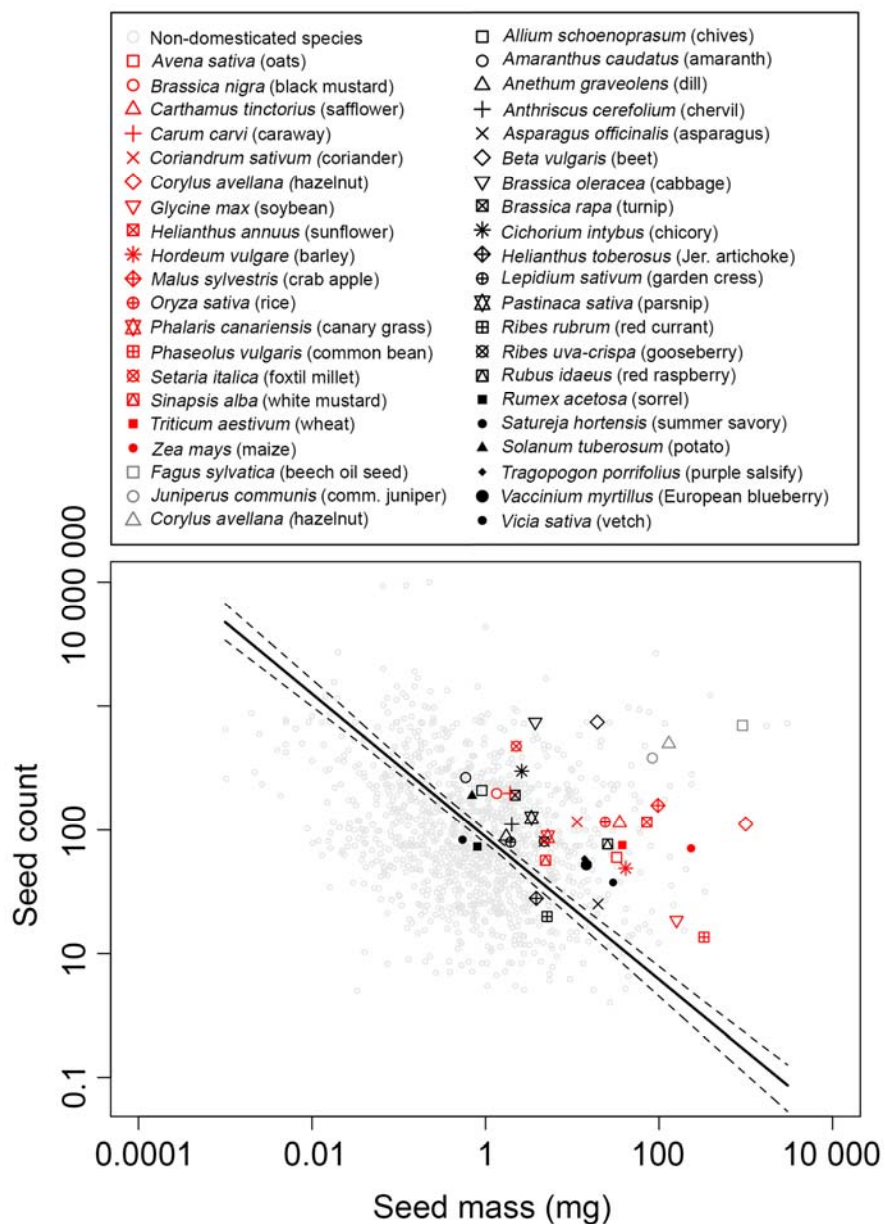
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491   **Fig. 1.** Relationship between seed mass and seed output across n=1190 non-domesticated

492   species and n=41 of the world's most widespread crops. Solid black trend line represents

493   a standardized major axis regression fit across the entire dataset (n=1231) and dashed

494   lines represent 95% confidence limits.

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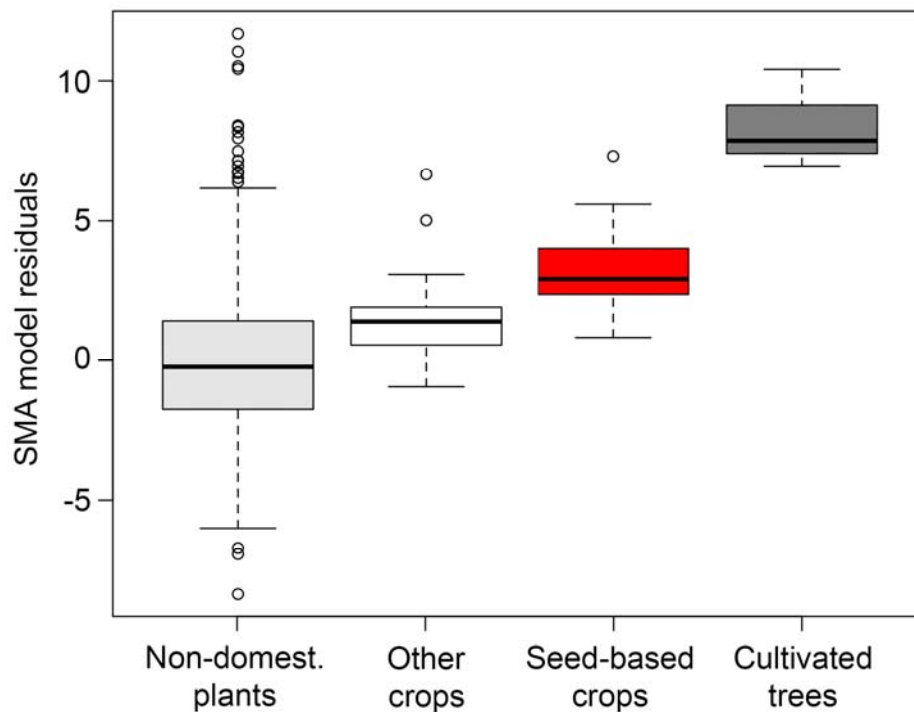
Fig. 2. Deviations from a global seed mass-seed output trade-off in three types of crops and non-domesticated plants. Deviations from a global SM-SO relationship are calculated as residuals from a standardized major axis regression fit to n=1231 plant species (see Fig. 1). "Other crops" (n=21) correspond to plant species cultivated for vegetative- or belowground structures. Sample sizes for seed-based crops, cultivated trees, and non-domesticated plants are n=17, n=3, and n=1190, respectively.
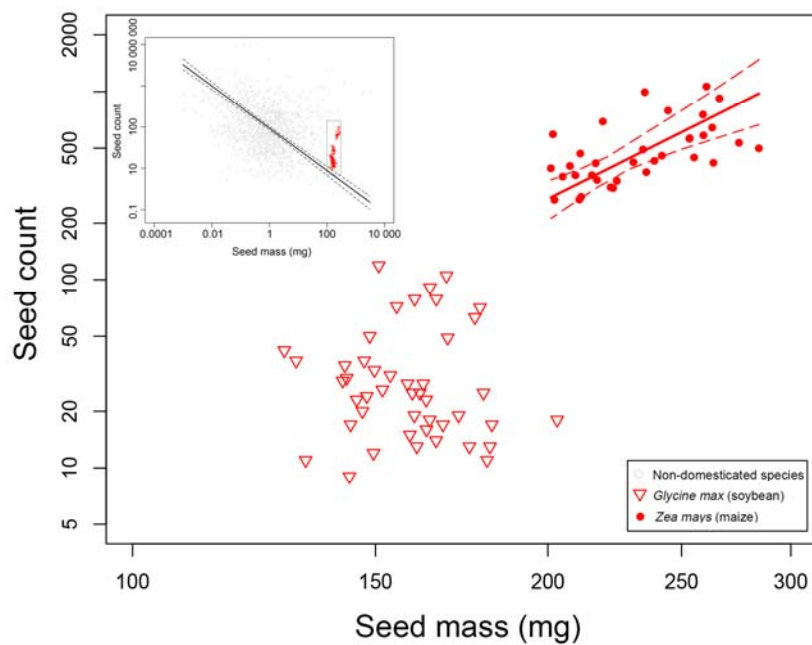
Fig. 3. Seed mass and seed output in soybean (*Glycine max*, *n*=45) and maize (*Zea maize*, *n*=37). Data are presented in relation to a SM-SO trade-off observed across 1231 plant species (gray rectangle, inset graph). Solid red trend line represents a standardized major axis (SMA) regression fit to the maize data with red dashed lines representing 95% confidence limits. The SMA model fit to soy data was not significant, so is not presented here.

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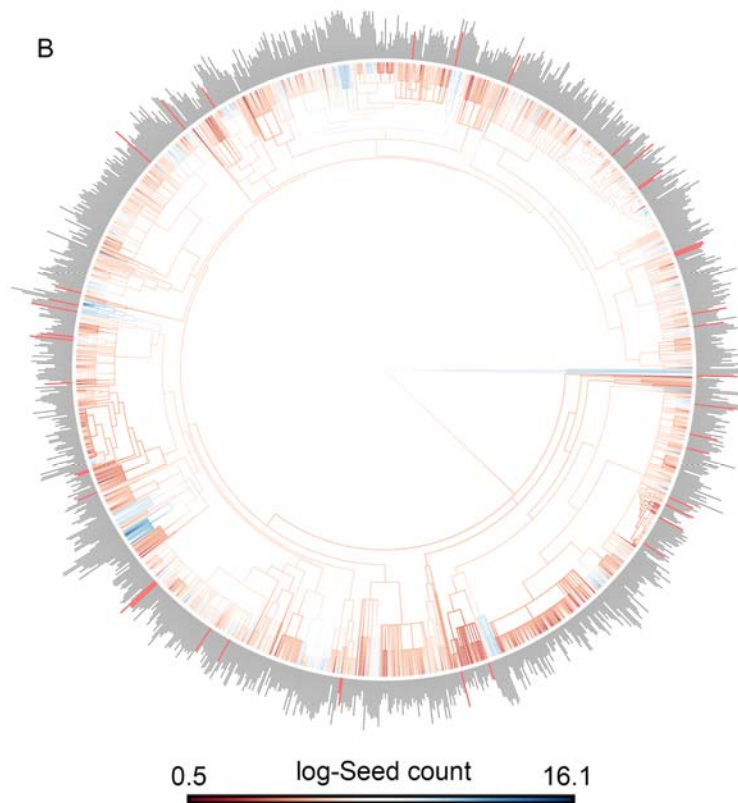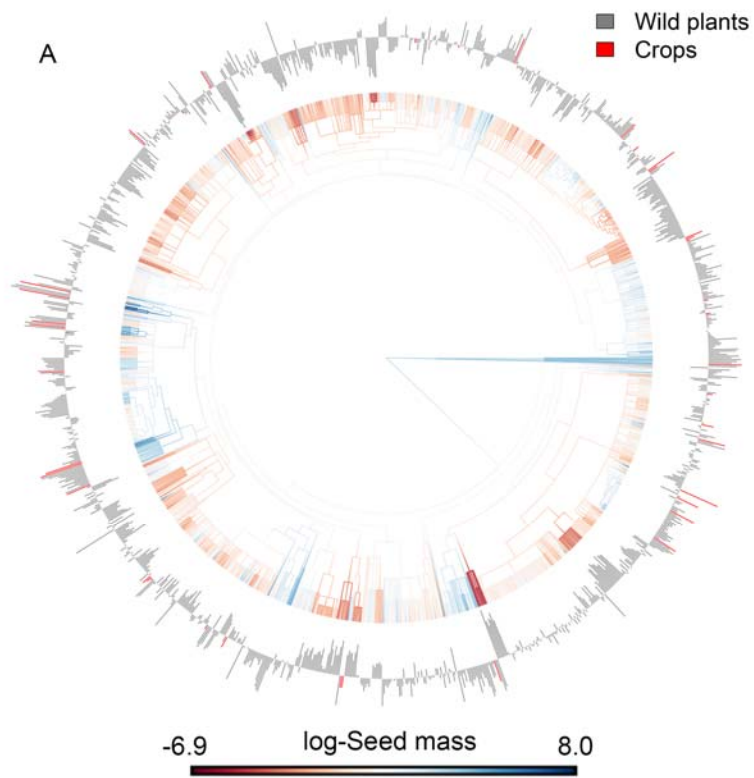
512   **Fig. 4.** Variation in seed mass (A) and seed output (B) across a phylogeny of 1,231 crop-

513   and wild plant species**.** Bars across the tips of the phylogeny represent mean seed mass

514   and seed count (plant^{-1}) values, with crop species highlighted in red and wild plants in

515   gray.