

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

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7

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.

25

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

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

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 (\pm 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).

181

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 ($43^{\circ} 32' N$, $80^{\circ} 12' W$) (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 ($33^{\circ} 56' S$, $60^{\circ} 34' W$). 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

213 the 41 crop species represented in the SM-SO dataset, 90.2% (37 crop species) fell 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= $1.14e-11 \pm 2.5$ (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 mays*, 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

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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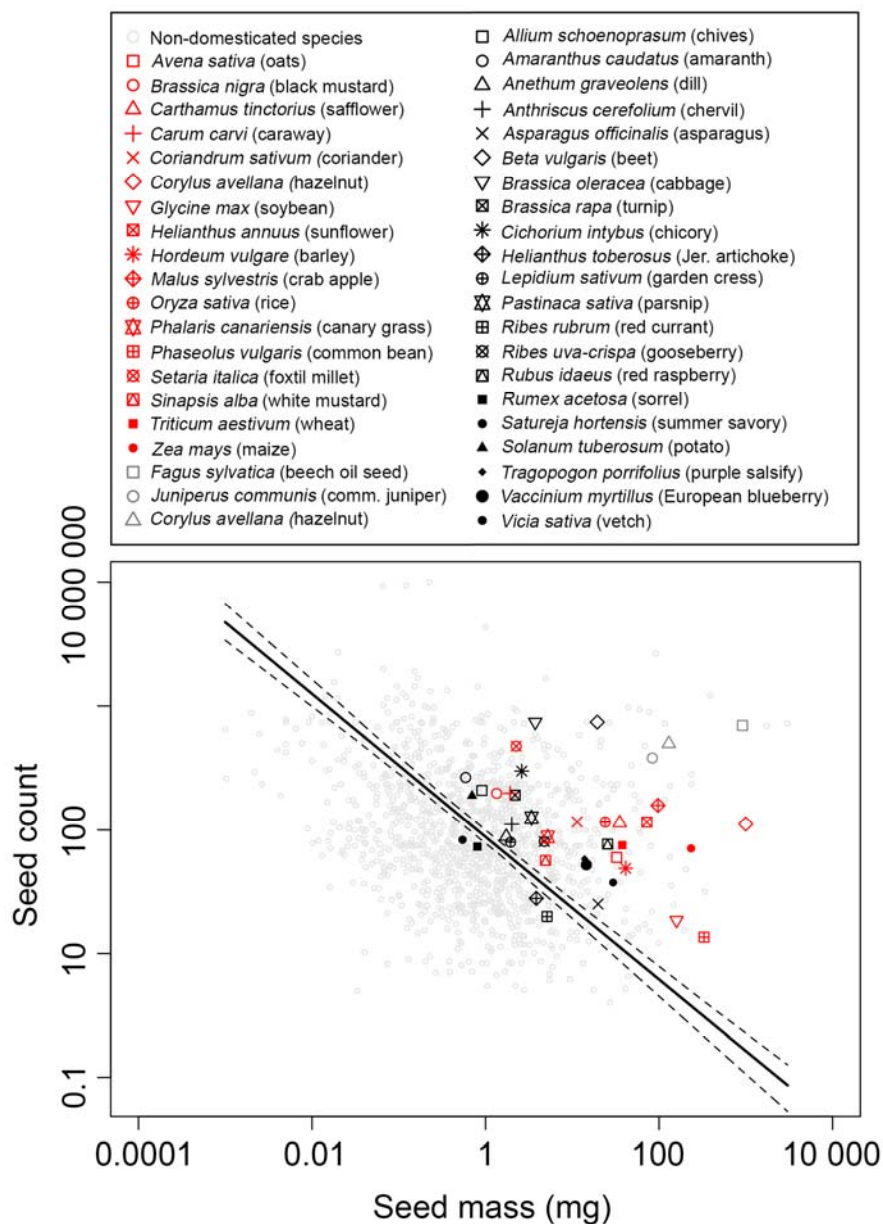
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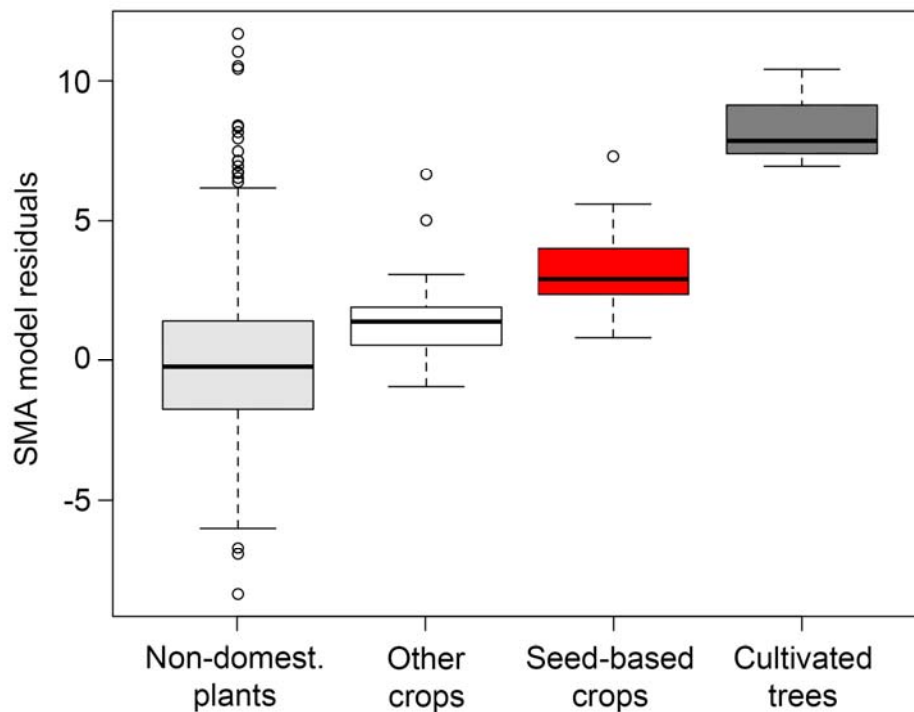
488 **Figures**



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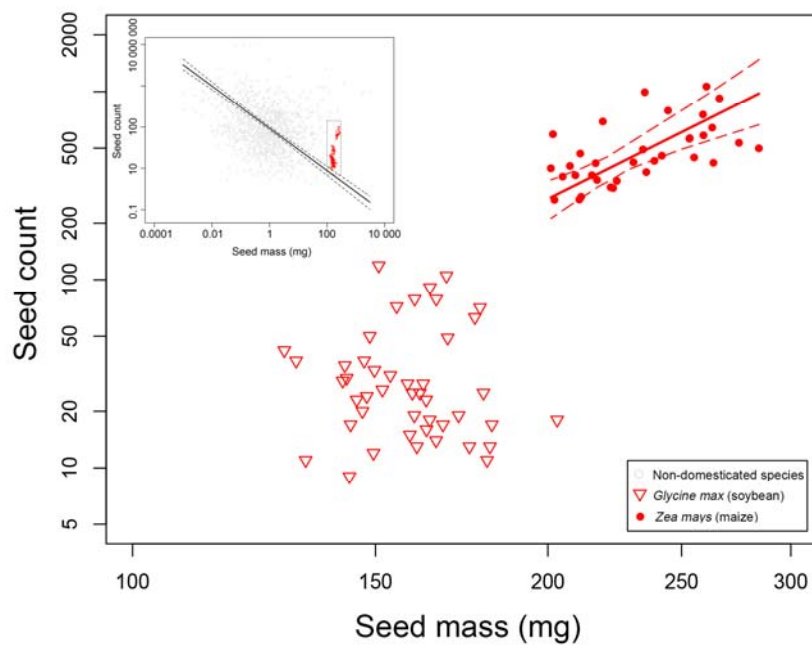
491 **Fig. 1.** Relationship between seed mass and seed output across $n=1190$ non-domesticated
 492 species and $n=41$ of the world's most widespread crops. Solid black trend line represents
 493 a standardized major axis regression fit across the entire dataset ($n=1231$) and dashed
 494 lines represent 95% confidence limits.



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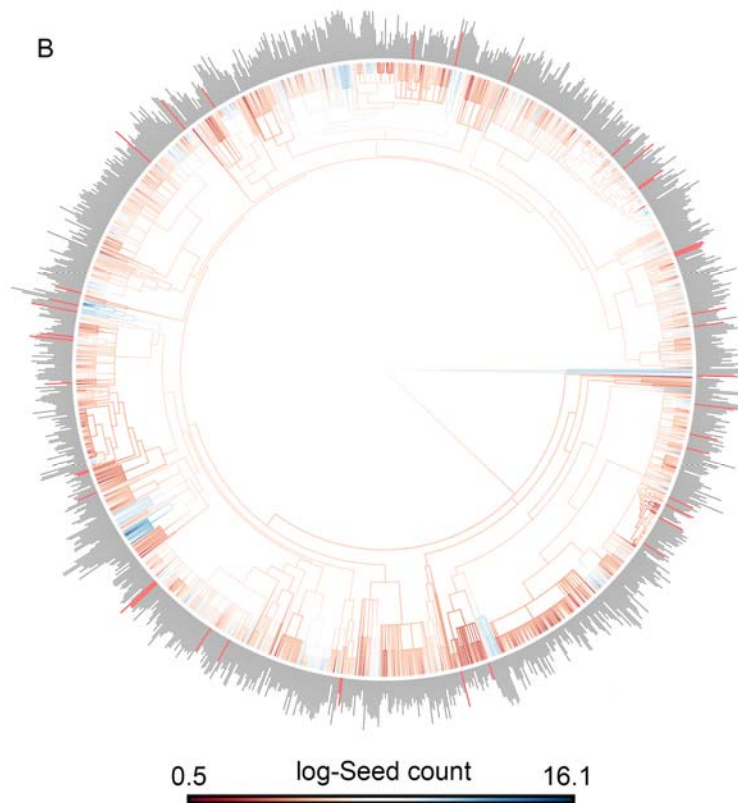
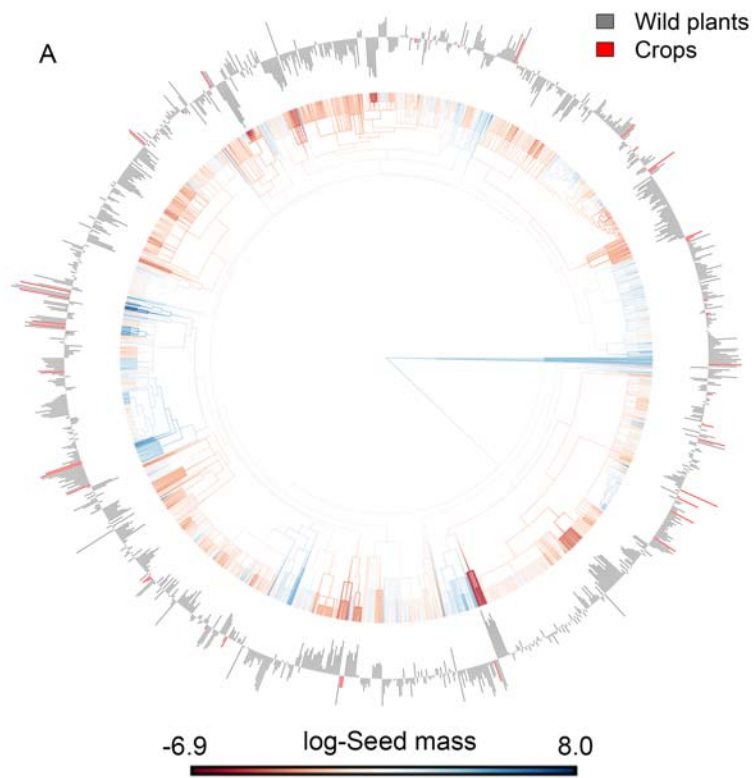
497 **Fig. 2.** Deviations from a global seed mass-seed output trade-off in three types of crops
498 and non-domesticated plants. Deviations from a global SM-SO relationship are calculated
499 as residuals from a standardized major axis regression fit to $n=1231$ plant species (see
500 Fig. 1). “Other crops” ($n=21$) correspond to plant species cultivated for vegetative- or
501 belowground structures. Sample sizes for seed-based crops, cultivated trees, and non-
502 domesticated plants are $n=17$, $n=3$, and $n=1190$, respectively.



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505 **Fig. 3.** Seed mass and seed output in soybean (*Glycine max*, $n=45$) and maize (*Zea mays*,
506 $n=37$). Data are presented in relation to a SM-SO trade-off observed across 1231 plant
507 species (gray rectangle, inset graph). Solid red trend line represents a standardized major
508 axis (SMA) regression fit to the maize data with red dashed lines representing 95%
509 confidence limits. The SMA model fit to soy data was not significant, so is not presented
510 here.



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.