

The influences of progenitor filtering, domestication selection and the boundaries of nature on the domestication of grain crops

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Funding information

Universidad Nacional del Comahue, Grant/Award Number: B152/04; Fondo para la Investigación Científica y Tecnológica, Grant/Award Number: PICT 2013-1079 and PICT 2015-2333; Consejo Nacional de Investigaciones Científicas y Técnicas, Grant/Award Number: PIP 114-201101-00201; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: RGPIN/107375-2012

Handling Editor: Adam Martin

Abstract

1. Domestication generally involves two sequential processes: initial identification of wild species with desirable characteristics ('progenitor filtering') and subsequent artificial and natural selection that, respectively, improve features preferred by humans and adapt species to cultivation/captivity ('domestication selection'). Consequently, domesticated species can differ from wild species and may share characteristics owing to convergent evolution ('domestication syndrome'). Baring evolutionary constraints, domestication selection may generate extreme phenotypes that transcend the 'boundaries of nature' evident for wild species. Despite evidence of domestication syndromes in some clades, broader contributions of progenitor filtering and domestication selection to characteristics of contemporary domesticated species have received limited attention.
2. Using comparative analysis of 49 grain-crop and 87 wild annual plant species from 15 families, we (1) addressed whether plants of crop and wild species differ for mean seed number, per-seed mass and total seed-mass investment; (2) assessed contributions of (a) progenitor filtering and (b) domestication selection to these differences; (3) evaluated whether crop characteristics exceed the boundaries of nature and (4) assessed whether seed-production characteristics of grain crops constitute components of a generic domestication syndrome.
3. On average, grain-crop plants produce heavier seeds and greater total seed mass than wild species, but seed number per plant does not differ. Comparison of wild species between genera with or without crop species found no evidence of progenitor filtering. In contrast, crop species differed from congeneric wild species for the mass traits, but not for seed number. Greater seed investment by crops is consistent with artificial selection for enhanced seed yield (mass per harvested area), whereas heavier individual seeds suggest selection for improved nutritional quality and (or) adaptation to cultivation environments.
4. Seed number–size characteristics of grain-crop species lie within the bivariate variation among wild species and so do not exceed the boundaries of nature. Seed number and size varied similarly between species types and generally aligned with seed-investment isoclines, suggesting an upper investment limit.

5. Despite greater average investment in seed production and individual seeds by grain-crop species, seed-production characteristics did not vary less among crop species than among wild species, which is inconsistent with a common domestication syndrome.

KEYWORDS

domestication, grain crops, life histories, plant breeding, seed investment, seed mass, seed number, trade-off

1 | INTRODUCTION

The seeds of a small number of annual grain-crop species have increasingly become key elements of human diets during the past ~12,000 years (Harlan, 1992; Khoury et al., 2014). Characteristics of these species commonly differ from those of their wild relatives. In particular, individuals of grain crops often produce larger and (or) more seeds with limited dormancy that they retain longer before dispersal (Brown et al., 2009; Fuller, 2007; Meyer et al., 2012; Preece et al., 2017; Purugganan & Fuller, 2009). These differences could reflect two goal-directed aspects of domestication (Abbo & Gopher, 2017; Kluyver et al., 2017; Milla et al., 2015). The first involves 'progenitor filtering', whereby humans identify wild species with particularly desirable traits (e.g. high productivity, ease of harvest, rich nutritional quality, non-toxic) as targets for domestication (Cunniff et al., 2014; Milla et al., 2018; Preece et al., 2015). These species should be a non-random subset of all wild plant species for the relevant traits. Second, potential crops are subject to trait 'improvement' (Abbo & Gopher, 2017; Kluyver et al., 2017; Milla et al., 2015, 2018). Associated natural selection in response to agricultural environments and artificial selection imposed by farmers and plant breeders (collectively 'domestication selection'), and more recent genetic engineering have generated crop varieties that differ phenotypically and genetically from each other and their wild relatives (Abbo & Gopher, 2017; Milla et al., 2015; Olsen & Wendel, 2013; Purugganan & Fuller, 2009). As domestication is expected to begin with distinctive species (progenitor filtering) and accentuate their distinctiveness (domestication selection), phenotypic comparison of related domesticated and wild species should expose the influences of these processes. This evidence might also usefully inform the design of breeding programs, especially intentional progenitor filtering, needed to meet the dietary demands of the growing, and increasingly affluent, human population (Roberts, 2011).

The domestication selection responsible for trait adaptation in crops differs from that experienced by wild individuals in two important ways. First, agricultural environments typically impose more intense intraspecific competition, but less intense interspecific competition, fewer pests, and greater nutrient, light and water availability (Anten & Vermeulen, 2016; Harlan et al., 1973). Second, plant breeding and natural selection involve different performance measures: crops are selected to maximize collective annual reproductive output per harvested area (yield), rather than age-weighted genetic

contributions to the next generation by individuals (fitness; Anten & Vermeulen, 2016; Harlan et al., 1973). Together, the characteristic features of natural and artificial selection during crop domestication should favour altered resource allocation patterns and life histories (Milla et al., 2015, 2018). Indeed, owing to the uniqueness of both agricultural environments and the performance measures that accompany domestication, crop evolution may be able to transgress the 'boundaries of nature' that restrict feasible trait combinations for wild plants (Van Tassel et al., 2010).

Particularly relevant is the influence of trade-offs imposed by limited resource availability or investment that often constrain allocation options for individual plants (Lloyd, 1987, 1988). In the context of seed production, the relations of a plant's mean seed size (S ; mass), its total seed number (N) and its resource investment in seed production (I ; mass) govern these options. For an individual plant that fully expends its seed investment (i.e. $I = S \cdot N$), the physical conservation of matter imposes a strict trade-off on feasible combinations of seed number and mean seed size,

$$N = \frac{I}{S} = IS^{-1}. \quad (1)$$

(Figure 1, grey lines: Lloyd, 1987; Smith & Fretwell, 1974). This relation will also hold for a collection of plants that invest similarly in seed production but differ in the number–size combinations that they have implemented. If instead investment differs among individuals, populations or species, seed number and mean size need not vary strictly inversely among them (i.e. exponent $\neq -1$; e.g. Moles et al., 2004), even though each individual is necessarily subject to its own strict trade-off (van Noordwijk & de Jong, 1986; Venable, 1992). Consistent deviations from an inverse relation among individuals (or species) identify particular associations of seed investment and its allocation among seeds. An exponent > -1 indicates that individuals with large seed investments produce proportionally larger seeds (Figure 1, gold line), whereas an exponent < -1 indicates that they produce proportionally more seeds (Figure 1, purple line). In such cases, the underlying inverse relation associated with within-individual trade-offs will be evident only after accounting for variation in total seed investment (e.g. Aarssen & Jordan, 2001; Henery & Westoby, 2001).

The characteristics of natural and artificial selection suggest different expectations for the evolution of seed investment and number–size relations. Natural selection of the optimal number–size combination ($N^* = S^{*-1}$) given seed investment per plant I balances

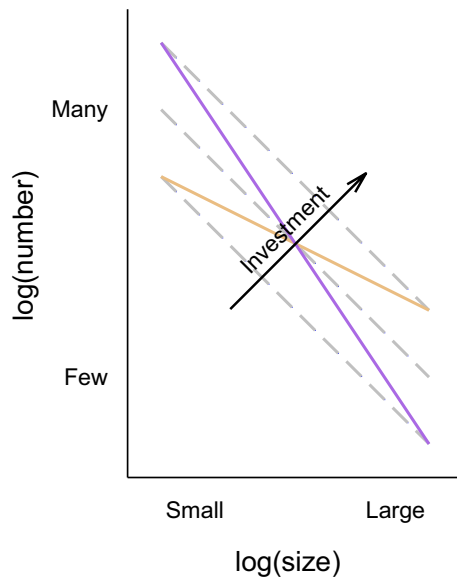


FIGURE 1 Consequences of changes in seed investment for number–size relations among individuals or species. Each dashed grey line depicts the feasible combinations of seed number, N , and size, S , for a specific investment, I , in seed production (i.e. $N = IS^{-1}$, or $\log N = \log I - [1]\log S$). The different grey lines indicate the effect of differing seed investment on these relations. The coloured lines represent cases in which individuals/species with more seed investment allocate disproportionately to larger seeds (gold, \log - \log slope > -1) or to more seeds (purple, \log - \log slope < -1) compared to those with less seed investment

the incremental (marginal) maternal fitness benefit of increased seed size and the incremental cost of decreased seed number (and vice versa: Lloyd, 1987). When seed investment is also subject to selection (e.g. optimization of overall reproductive investment and (or) of resource allocation to seed production vs. seed siring), the course of evolution depends additionally on the marginal benefits of increased seed investment (Venable, 1992) and the relative additive genetic variances of seed investment, seed number and size (Worley et al., 2003). In contrast, in the simplest agricultural context (i.e. yield maximization), yield,

$$Y = ID, \quad (2)$$

varies with seed investment, $I (= S \cdot N)$, but not among the feasible seed number–size combinations for a given seed investment and plant density (D ; plants per harvested area). Thus, successful artificial selection for greater yield necessarily increases seed investment, I , which should therefore be a pervasive feature of grain crops. Whether this evolution also entails increased seed number, size or both depends on their specific additional benefits. Minimally, increased seed mass seems likely, given its positive influences on sowing success, seedling survival and harvest quality (Cunniff et al., 2014; Leishman et al., 2000; Preece et al., 2017; Purugganan & Fuller, 2009; Sadras, 2007).

To the extent that crop species in different clades experienced similar initial progenitor filtering and subsequent domestication

selection, a suite of analogous traits could evolve that are more similar among crops than among their wild ancestors, or a ‘domestication syndrome’ (Fuller, 2007; Hammer, 1984; Harlan et al., 1973; Meyer et al., 2012; Preece et al., 2017). The details of this syndrome would depend on the consistency of domestication regimes (cultivation conditions, progenitor filtering, artificial selection) among species. Similar environments and qualitative farmer preferences (e.g. for more investment in larger seeds) should cause parallel evolution of a general domestication syndrome. If agricultural environments and practices specifically target a common phenotype, convergent evolution should generate a specific domestication syndrome. A general domestication syndrome is evident for crops in the Poaceae and Fabaceae (e.g. delayed dispersal of weakly defended seeds with limited dormancy: Fuller, 2007; Meyer et al., 2012), but seems less apparent among crops from other clades (Meyer et al., 2012).

Despite extensive archaeological and genetic research concerning domestication of major grain crops (Abbo & Gopher, 2017; Purugganan & Fuller, 2009), few comparative ecological studies (e.g. phenotypic space analyses) have assessed similarities and differences of components of seed production between grain-crop and wild species (although see Martin, 2021; Milla et al., 2015, 2018; Preece et al., 2015, 2017). Particularly lacking are comparisons of wild and grain-crop species concerning the association of seed investment and seed number–size relations (e.g. Gambín & Borrás, 2010; Sadras, 2007), despite its central role in domestication selection of seed production. To examine these features of domestication, we address four related objectives based on published records for wild and grain-crop species with annual life cycles. First, we (1) characterize the overall differences between wild and grain-crop species with respect to total seed number per plant (N), the mean mass of individual seeds (S) and the total mass investment in seed production (I). We then assess the contributions of (2a) progenitor filtering and (2b) domestication selection (improvement) to the observed differences. In addition, we (3) consider the extent to which the seed-production characteristics of contemporary grain crops transcend the boundaries of nature, as represented by the range of variation evident among wild species. Based on this evidence, we finally consider (4) the extent to which grain-crop characteristics constitute a domestication syndrome, and if so whether the syndrome is general or specific.

2 | MATERIALS AND METHODS

2.1 | Data collection

We surveyed published studies of annual wild and grain-crop species that reported mean per-seed mass (mg) and seed number per individual plant. The focus on annual species reflects three desirable characteristics. For annuals, the time-scales of performance relevant for artificial selection of crops (annual yield) and natural selection of wild and crop species (lifetime genetic contributions) are equivalent. In addition, total seed investment by annuals involves only resource

acquisition during the current growing season, rather than possible input from stored resources (Aarssen & Jordan, 2001). Finally, annuals are the progenitors of most staple grain crops, which have been subject to most concerted domestication (Harlan, 1992).

During 2012, we searched for data sources using Google Scholar. General search terms included 'seed number', 'seed weight', 'seed mass' and 'annual plant'. We also included terms such as 'wild soybean', 'cultivated soybean', etc. to enhance the representation of grain crops and their relatives. Publications identified during these searches were scanned for relevant measurements of at least two of the following variables: seed number per plant (N), per-seed mass (S) and total seed mass per plant (I). If the value for one variable was missing, it was calculated from the other two, based on $I = N \cdot S$. Data were gathered from tables, extracted from figures using imageJ software (<http://rsbweb.nih.gov/ij/index.html>), or obtained from authors when only summary statistics were published. In addition to the data located by these searches, we included more recent measurements reported by Preece et al. (2017). In total, 11 crop species are also represented by observations of conspecific wild varieties or subspecies, which we consider as separate 'species' in the analyses. Measurements for wild representatives of these grain crops were included only if the article stated that the specimens were the wild ancestor of the crop, a wild variety or a wild population. Many surveyed studies provided data for multiple years, populations, varieties or trials (collectively referred to as 'trials'), which we recorded separately. The final database includes 1,461 records from 139 studies (see Data sources section, Garibaldi et al., 2021) for 136 species from 15 families, comprising 49 grain-crop and 87 wild species (Figure S1). In all, 64 species belong to the Fabaceae (32) or Poaceae (32). Of the 136 species, 89 were examined by one study and only eight of the remaining 47 species were examined by >3 studies. Of the 139 studies, 114 examined a single species, and 10 of the 25 studies of multiple species involved multiple trials per species.

2.2 | Statistical analyses

2.2.1 | Phylogenetic relatedness

Analyses of objectives 1–3 fit general linear models that quantified the effects of relevant independent variables on interspecific variation of the three measured seed-production traits (seed number per plant, mean per-seed mass, total seed investment; all \log_{10} transformed). To account for possible lack of independence among species in these analyses associated with phylogenetic relatedness, the parameters of most models were estimated using generalized least squares after accounting for phylogenetic covariance among species (Paradis, 2012). These analyses were conducted with the `gls` function of the `nlme` package (version 3.1–150; Pinheiro et al., 2014) of R (version 4.0.2; R Core Team, 2020). As this program does not allow simultaneous consideration of phylogenetic covariance and intraspecific variation, these analyses involved the 136 species means.

Phylogenetic relatedness of the sampled species was represented by a tree with 136 tips (species) and 123 internal nodes based on Zanne et al.'s (2014) dated megatree for angiosperms (Figure S1). The accepted names for all species were identified using The Plant List (<http://www.theplantlist.org/>), which were then compared with the species included in Zanne et al.'s (2014) megatree. We represented the phylogenetic position of species missing from the megatree by that of their phylogenetically closest included relative. The megatree was then pruned to extract a dated phylogeny for just the species represented in the dataset (see Scholl et al., 2020 for a similar procedure). Finally, we included two refinements concerning *Amaranthus* and *Sesamum* species, which were not represented fully by Zanne et al. (2014). The topology and branch lengths for the 18 *Amaranthus* species were incorporated based on Waselkov et al. (2018). For *Sesamum*, we included *S. alatum* and *S. radiatum* in a polytomy with *S. indicum*, with branch lengths equal to half the 20.1 mya divergence age of *Uncarina* and *Sesamum* (Stevens, 2001).

Using this tree or subtrees appropriate for a particular objective, we analysed three evolutionary models of interspecific covariance, phylogenetic independence, Brownian motion and Grafen's model. The independence model specified no phylogenetic covariance among species. The Brownian motion model depicted the covariance between species i and j , $V_{ij} = \sigma^2 \cdot \delta_{ij}$, as increasing proportionally with the variance of a Brownian process, σ^2 , and the phylogenetic distance between the root and the species' most recent common ancestor, δ_{ij} (Paradis, 2012). In contrast, Grafen's model represented branch length as the scaled number of descendant species subtended by a node minus one. This count was scaled so that the root has height one and the heights of other nodes were raised to power $\rho > 0$, which was estimated from the data (Paradis, 2012). Phylogenetic covariance based on the Brownian and Grafen models was estimated using the `corBrownian` and `corGrafen` functions of the `R APE` package (version 5.4-1; Paradis et al., 2004). As AIC comparisons indicated that Brownian motion did not adequately represent phylogenetic covariance for any analysis, we do not mention those analyses further. Two variants of the analyses for phylogenetic independence and Grafen's model were considered that allowed either homogeneous or heterogeneous variances for different levels of categorical independent variables. We present the results for only the variance-covariance model with lowest AIC.

2.2.2 | Objective-specific methods

Objective 1: Characterize the overall seed-production differences between wild and grain-crop species—The complete sample of species means was used to compare wild and crop species with respect to both trait means and the covariation of seed number per plant and mean per-seed mass. All analyses included species type (wild or crop) as a categorical factor. The analysis of covariation considered \log_{10} (seed number per plant) as the dependent variable and \log_{10} (per-seed mass) as a continuous independent variable, in addition to species type and the species type \times \log_{10} (per-seed mass) interaction.

Back-transformation of the regression relation for a specific species type, $\log_{10}N = a + b \cdot \log_{10}S$, yields $N = 10^a S^b$, which is a general version of Equation 1, with 10^a estimating mean l and b estimating the scaling exponent of the number–size relation. Analysis of this relation did not include measurements of total seed investment, as it was not estimated independently of seed number and size for some species.

To illustrate the relation between seed number and mass, which are both random variables, we depict the first principal component of their correlation matrix, estimated separately for wild and crop species. The first principal component is equivalent to a major axis model II regression (Legendre & Legendre, 2012). Principal component analysis involved the `phyl.pca` function of the R `PHYTOOLS` package (version 0.7-70: Revell, 2012), which accounts for phylogenetic relatedness.

Objective 2a: Evidence of progenitor filtering of seed-production traits—Ideally, the extent to which domestication began with a non-random subset of wild species would be assessed by comparing traits between crop progenitors and species not subsequently subject to domestication when domestication began. In the absence of relevant historical measurements, we compared the trait means of wild species between genera with sampled grain-crop species (18 genera, 44 species) and those without grain-crop species (33 genera, 43 species). This comparison between genus types involved the generalized least squares methods described above and a phylogeny for only the 87 relevant species.

Objective 2b: Evidence of domestication selection on seed-production traits—In this case, the ideal comparison would contrast the contemporary trait means of grain crops with the historical means of their progenitors. As the historical traits of many crop progenitors are unknown, contemporary wild congeners of crop species provide conservative proxies. Using this approach, we compared seed-production characteristics between congeneric wild ($n = 44$) and grain-crop species ($n = 28$) for 18 genera. These analyses involved a general linear model with genus as a fixed blocking factor to impose within-genus comparison of species type (wild, crop). The phylogenetically independent observation model (with heterogeneous variances) was used for these analyses, as it fit better than the

Grafen model, indicating that the explicit inclusion of genus largely accounted for phylogenetic relatedness.

Objective 3: Boundaries of nature—We characterized the boundaries of nature as the 95% inclusion ellipse for mean of seed number per plant and per-seed mass (\log_{10} -transformed) for the sampled wild species, given a bivariate normal distribution. This ellipse was identified using the ellipse function of the R `MIXTOOLS` package (version 1.2.0). If crop species disproportionately transcend this range of variation, more than 5% of their means should lie outside the ellipse.

Objective 4: Domestication syndrome—Parallel or convergent evolution could generate different domestication syndromes. Parallel evolution would create a general domestication syndrome whereby grain-crop species differ in a qualitatively similar manner (e.g. larger seeds) from wild species. Results from the analyses for Objectives 1 and 2 are all relevant in this context. In contrast, a specific syndrome requires convergence among crop species to a similar phenotype. In this case, the among-species component of overall trait variation should additionally be smaller for crop species than for wild species. We tested the latter expectation for the complete sample of 1,461 trials with the `glimmix` procedure of SAS/STAT 15.1 (SAS Institute Inc., 2018), which allows between-group comparison of variance components with likelihood-ratio tests. For each of the three seed traits, the analysis included species type (crop or wild) as the fixed factor, and species within species type, studies nested within species, and trials for individual species within studies as random factors, with separate estimates of the associated variance components for each species type. Because these variance components were estimated for log trait values, their magnitudes are unaffected by differences in trait means (Lewontin, 1966) and can be compared directly.

3 | RESULTS

Based on 136 annual species, individual plants of grain crops invest more mass in seed production than those of wild species, on average (Objective 1: Table 1; Figure 2a, compare means in relation to grey

TABLE 1 Overall test statistics for comparisons of species mean seed number per plant (N), per-seed mass (S) and total seed investment ($I = N \cdot S$) relevant to Objectives 1 (characterize mean wild-crop differences), 2a (progenitor filtering) and 2b (domestication selection), and of the among-species variance component relevant to Objective 4 (domestication syndrome). Effects considered include species type (wild or grain-crop), genus type (with or without sampled grain-crops) and the genus to which species belong. Analyses of mean differences accounted for phylogenetic relatedness by either estimating the interspecific phylogenetic correlation (Grafen model: Obj. 1, 2a) or by including genus as an independent variable (Obj. 2b)

Objective and sample group	Effect	Dependent variable		
		$\log_{10}(N)$	$\log_{10}(M)$	$\log_{10}(I)$
Obj. 1: all species	Species type	$F_{1,134} = 0.70$	$F_{1,134} = 15.10^{***}$	$F_{1,134} = 12.87^{***}$
Obj. 2a: wild species	Genus type	$F_{1,85} = 2.40$	$F_{1,85} = 0.05$	$F_{1,85} = 2.03$
Obj. 2b: genera with crops	Species type	$F_{1,36} = 0.68$	$F_{1,36} = 22.22^{***}$	$F_{1,36} = 4.31^*$
	Genus	$F_{17,36} = 9.52^{***}$	$F_{17,36} = 23.74^{***}$	$F_{17,36} = 1.43$
	Genus \times species type	$F_{17,36} = 1.68$	$F_{17,36} = 2.61^{**}$	$F_{17,36} = 1.72$
Obj. 4: all species	Species type	$X_1^2 = 2.50$	$X_1^2 = 0.24$	$X_1^2 = 0.93$

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

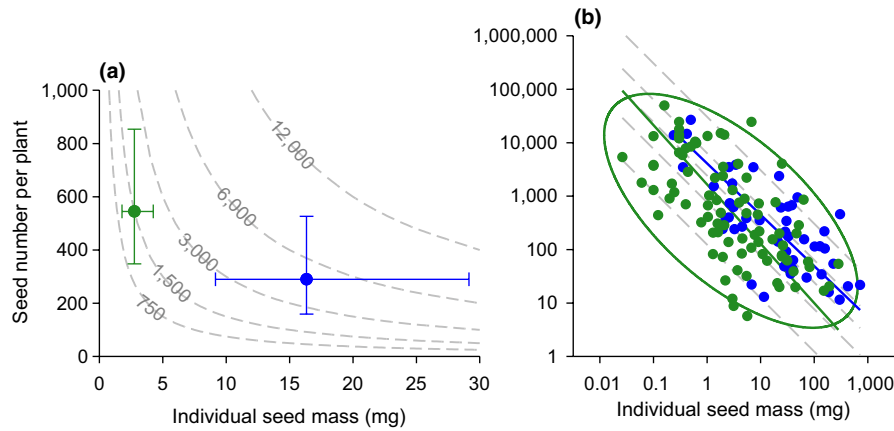


FIGURE 2 Relations of (a) overall mean ($\pm 95\%$ confidence interval) and (b) individual species mean seed number per plant and per-seed mass for 87 wild species (green) and 49 grain-crop species (blue). In panel (a), mean seed investment for wild and crop species can be compared with reference to the dashed grey lines, which indicate isoclines of indicated investments (the number–size product: mg). Panel (b) includes major axis regression lines for each species type and the green ellipse encloses 95% of the observations for the wild species (note the \log_{10} scaling). The dashed grey isoclines represent the 5, 25, 50, 75 and 95% quantiles (from left to right) of interspecific variation in seed investment for all species, for which the slope is -1

investment isoclines). This difference largely reflects the production of heavier individual seeds by grain crops, as total seed number per plant did not differ statistically between crop and wild species (Table 1; Figure 2a). Seed number varied strongly and negatively with per-seed mass ($F_{1,133} = 67.21$, $p < 0.001$). Overall, seed number per plant varied inversely among species with mean per-seed mass (major axis slope = -1.046), so interspecific variation aligned largely along seed investment isoclines for all species (Figure 2b). This relation did not differ statistically between wild and grain-crop species (interaction, $F_{1,132} = 0.29$, $p > 0.5$: generalized least-squares partial regression coefficients [95% confidence intervals], wild species, -0.597 [-0.793 , -0.402]; crops, -0.666 [-0.868 , -0.463]; major axis slopes, wild species, -1.109 ; crops, -0.961 : Objective 1).

The 87 wild species did not exhibit evidence of progenitor filtering (Objective 2a). Specifically, mean total seed number, per-seed mass and total seed investment did not differ statistically for wild species between genera that also include sampled grain-crop species and those that do not (Table 1).

In contrast, differences between wild and grain-crop species in genera with both species types indicated considerable domestication selection (Objective 2b). Overall, seed number per plant and per-seed mass varied extensively among genera, unlike total seed investment (Table 1, Obj. 2b, Genus; Figure 3). Comparisons between wild and crop species detected heavier seeds and somewhat greater total seed investment for crop species, but no general difference in total seed number per plant (Table 1, Obj. 2b, Species type). Contrasts of wild and crop species also differed among genera for per-seed mass, but not for seed number or investment (Table 1, Obj. 2b, Genus \times Species type interactions; Figure 3). Seeds of grain-crop species were numerically heavier than those of wild species, on average, in 16 of the 18 genera, with >18 -fold differences in *Helianthus*, *Hordeum* and *Vicia*. In contrast, individuals of grain-crop species produced numerically more seeds than wild species in eight

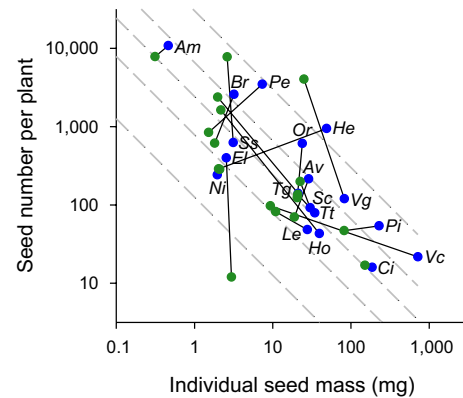


FIGURE 3 Contrasts of mean seed number per plant and per-seed mass between wild and grain-crop species within 18 genera. Linked green and blue symbols, respectively, represent the means of wild and crop species sampled for a genus. Letters beside blue symbols identify the associated genus: Am, *Amaranthus*; Av, *Avena*; Br, *Brassica*; Ci, *Cicer*; El, *Eleusine*; He, *Helianthus*; Ho, *Hordeum*; Le, *Lens*; Ni, *Nigella*; Or, *Oryza*; Pe, *Pennisetum*; Pi, *Pisum*; Sc, *Secale*; Ss, *Sesamum*; Tg, *Trigonella*; Tt, *Triticum*; Vc, *Vicia*; Vg, *Vigna*. The dashed grey isoclines represent the 5, 25, 50, 75 and 95% quantiles (from left to right) of interspecific variation in seed investment, for which the \log - \log slope is -1 . Note the \log_{10} scaling

genera, but fewer seeds in 10 genera, indicating more heterogeneous changes than for per-seed mass. Despite evidence of domestication selection, number-mass means for grain-crop species do not lie disproportionately outside the 95% inclusion ellipse for wild species (Figure 2b), and so do not transcend the boundaries of nature (Objective 3).

Seed characteristics of the 136 sampled species support general, but not specific, features of a domestication syndrome (Objective 4). As described above, grain-crop species commonly produce heavier

individual seeds and a greater total seed mass than wild species (Figures 2a and 3). However, contrary to expectations for convergent evolution, differences among grain-crop species do not account for less of the overall variances in seed number, mass or investment than for wild species (Table 1; Figure 4). Furthermore, differences among grain-crop species account for more of the total trait variance than intraspecific variation for both seed number per plant and per-seed mass (Figure 4). Thus, domestication selection of per-seed mass and seed investment maintained heterogeneity among grain-crop species, rather than promoting convergence towards a common crop phenotype.

4 | DISCUSSION

Comparative analysis of 87 wild species and 49 grain-crop species revealed mixed influences of domestication on seed-production characteristics. On average, grain-crop species invest greater mass in seed production per plant in association with production of larger, but not more, seeds (Figure 2a). This difference largely reflects responses by grain-crop species to domestication selection (Figure 3), as no effects of initial progenitor filtering were evident (Table 1). The resulting crop evolution did not alter the interspecific seed number-size relation compared to that among wild species (Figure 2b). Correspondingly, seed number-size phenotypes of grain-crop species lie within the boundaries of nature represented by the range of variation among wild species (Figure 2a). Greater total seed investment and heavier seeds (Figure 2) are features of a general domestication syndrome, but similar interspecific variation between grain-crop and wild species indicates that crop evolution has not targeted a specific syndrome.

4.1 | Progenitor filtering

The lack of evidence of progenitor filtering (Table 1, Obj. 2a) could reflect either of two aspects of the data. Progenitor filtering could have been involved early during the domestication of the grain-crop

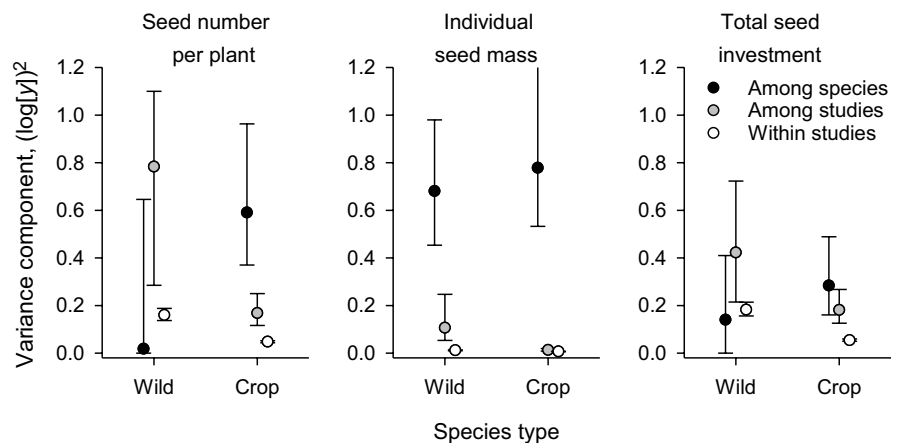
species included in our sample, but it involved traits other than seeds per plant, per-seed mass and seed investment (see Preece et al., 2018). For example, preliminary analyses of toxicity for the sampled species suggest less toxicity among wild species in genera with grain-crop species than in genera without crop species (M. Strelin, unpubl. data). Alternatively, the traits of contemporary wild species belonging to genera that also include crop species may be poor surrogates of the phenotypes of crop progenitors. Importantly, when grain-crop progenitors were first identified as worthy of cultivation they may have differed in desirable characteristics from both congeners and species in other genera. In addition, traits of non-progenitor congeners may have evolved since domestication of related grain-crop species was initiated, obscuring differences that may have existed when domestication began.

Despite the preceding qualification, our results may be representative of a generally limited contribution of progenitor filtering to differences in seed-production traits between grain-crops and wild species. Previous, more focused, common-garden studies comparing putative grain-crop progenitors and wild relatives with archaeological evidence of harvesting, but not of domestication, detected differences consistent with progenitor filtering in Poaceae, but not in Fabaceae (Cunniff et al., 2014; Preece et al., 2015). Among the Poaceae considered by those studies, crop progenitors had larger seeds than wild species, but seed number of progenitors was either equivalent (Cunniff et al., 2014) or less than that of wild species (Preece et al., 2015). Additionally, Preece et al. (2015) found no difference in seed investment between related progenitor and crop species or subspecies (not examined by Cunniff et al., 2014). This heterogeneous evidence suggests that progenitor filtering may have contributed to distinctive seed characteristics of some grain crops, but it has not been involved universally.

4.2 | Domestication selection

Unlike assessment of progenitor filtering, intra-generic comparison of grain-crop and wild species revealed clear evidence of domestication selection on seed-production traits. The generally greater total

FIGURE 4 Comparison of variance components ($\pm 95\%$ confidence intervals) among species and among and within studies of individual species for seed number per plant, per-seed mass and total seed investment (the number-size product) between wild and grain-crop species. Based on 412 records for 87 wild species and 1,049 records for 49 grain-crop species



seed investment by grain-crop species is an expected outcome of artificial selection targeting increased collective yield (see Equation 2). Greater total investment in seed mass could arise from combined net increases in four components of plant resource economy; overall plant mass and the hierarchical relative allocations to reproductive versus vegetative function, female versus male function and seeds versus accessory tissues (Harlan, 1992; Milla & Matesanz, 2017; Preece et al., 2017; Stitzer & Ross-Ibarra, 2018). These changes can arise from direct selection for increased yield, or as a correlated response to selection for other traits. An example of the latter is increased relative allocation to female function resulting from selection for self-fertilizing varieties (see Charnov, 1987; Dempewolf et al., 2012; McKone, 1987). This variety of options suggests that the general increase in seed investment likely involved heterogeneous responses of resource investment and allocation to domestication among grain-crop lineages.

Although artificial selection that targets increased seed yield should not, by itself, have also selected for larger seeds (see explanation involving Equation 2), that change commonly distinguishes grain crops from wild relatives (Table 1, Obj. 2b; Figure 3: Preece et al., 2017; Purugganan & Fuller, 2009). Instead, increased per-seed mass could reflect additional aspects of artificial and natural selection during domestication. Artificial selection should have had contrasting consequences for seed number per plant and per-seed mass. Independent of its contribution to seed investment, seed number per plant may often be irrelevant to artificial selection of grain-crops, because agricultural propagation of the next generation involves a minor fraction of a crop's bulk production, the majority being used for human purposes. The heterogeneous changes in seed number during domestication (Figure 3) are consistent with this practice. In contrast, breeders could have imposed indirect artificial selection on per-seed mass by choosing propagation stock based on correlated aspects of seed quality related to seed growth capacity or nutritional value. Specifically, per-seed mass often varies positively within species with seedling emergence and establishment (Preece et al., 2017; Purugganan & Fuller, 2009; Sadras, 2007) and (or) with the concentrations of beneficial constituents of human and livestock diets (e.g. Kulwal & Mhase, 2017; Meru et al., 2018; Ries & Everson, 1973; Wang et al., 2020). Thus, artificial selection for seed quality could have induced evolution of larger seeds, even if seed size was not the explicit selection target.

Natural selection could also have contributed to the evolution of larger seeds in grain crops if domestication increased the optimal seed size that maximizes individual fitness, given the within-plant number-size allocation constraint. The general interspecific association of greater seed investment and seed mass by grain crops (Table 1, Obj. 1, 2b) suggests that artificial selection for enhanced yield shifted the seed-size optimum, causing coincident natural selection (see Venable, 1992). The novel agricultural environments experienced by crops could also have imposed unintended natural selection during domestication. In particular, the positive association of seed mass and seedling establishment (Leishman et al., 2000; Purugganan & Fuller, 2009; Sadras, 2007) could have favoured

natural selection of larger seeds to contend with aggravated intra-specific competition associated with cultivation (Preece et al., 2017; also see Turnbull et al., 1999). In either case, increased seed investment would have allowed evolution of seed size with heterogeneous change in seed number, despite individual plants being subject to a number-size trade-off.

4.3 | Boundaries of nature

During more than 10,000 years (generations) of domestication effort, seed evolution in annual grain-crop species has not expanded the phenotypic space they occupy compared to that of wild plants. Specifically, although grain crops generally produce large seeds relative to wild species, their mean per-seed mass does not lie disproportionately outside the 95% inclusion ellipse for wild species (Figure 2b). Explanation of this constrained evolution likely lies in the consistent interspecific seed number-size relation for both grain-crop and wild species, the slope of which largely parallels isoclines of fixed seed investment (Figure 2b). This consistency, despite the generally greater per-seed mass of grain crops, suggests a boundary of nature for annual plants associated with a pervasive upper limit on relative seed investment arising from the requirement that resources must also be expended on other plant functions. Such boundedness has also been reported for other trait relations, such as nitrogen content and specific leaf area (Milla et al., 2015), nitrogen use for photosynthesis (Rotundo & Cipriotti, 2017), and plant canopy height, leaf nitrogen content and seed dry mass (Milla et al., 2018).

4.4 | Domestication syndrome

Comparison of seed-production characteristics by congeneric wild and grain-crop species suggests that domestication of multiple annual grain crops has, at most, involved parallel, rather than convergent, evolution. Although grain-crop species generally produce a greater mass of larger seeds than related wild species (Figure 3), this evolution has not reduced interspecific variation among grain crops (Figure 4). The latter result is inconsistent with convergent evolution. Thus, the generally greater seed investment and per-seed mass for grain-crop species compared to wild relatives suggests roughly parallel evolution for these traits during domestication from contrasting initial states. These patterns are consistent with a general domestication syndrome (greater mass of larger seeds), rather than a specific syndrome represented by similar investment and per-seed mass among crop species.

5 | CONCLUSIONS

Results of this study suggest both common and heterogeneous aspects of the domestication of annual grain crops. Differences between wild and crop species in seed number and per-seed and total seed mass

seem to have arisen largely in response to domestication selection, rather than from initial progenitor filtering of candidate crops. In keeping with the general agricultural objective of enhancing yield, grain-crop evolution tended to increase total mass investment in seed production. However, yield improvement seems subject to an upper limit that is also evident among wild species (a boundary of nature). Within this apparent constraint, yield improvement typically involved increased per-seed mass, in contrast to varied changes among species in seed number per plant. The magnitude of shifts in seed-production characteristics differed considerably among clades, even among those with a long history of domestication (e.g. *Triticum* vs. *Hordeum*, Figure 3). Given this heterogeneity, fecundity characteristics seem to represent a minor component of an interspecific domestication syndrome.

ACKNOWLEDGEMENTS

We thank Adam Martin, Angela Moles and an anonymous reviewer for considered comments that improved this paper. Funding for this research was provided by the Argentine Agencia Nacional de Promoción Científica y Tecnológica (PICT 2013-1079 [L.A.G.] and PICT 2015-2333 [M.A.A.]) and Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 114-201101-00201: L.A.G.), the Universidad Nacional del Comahue (B152/04: M.A.A.), the Universidad Nacional de Río Negro (PI 40-B-399: L.A.G.) and the Natural Sciences and Engineering Research Council of Canada (RGPIN/107375-2012: L.D.H.).

AUTHORS' CONTRIBUTIONS

L.A.G., M.A.A. and L.D.H. designed the study; L.A.G., A.S. and M.M.S. collected the data; G.G. assembled the phylogenetic tree; L.A.G. and L.D.H. conducted the data analyses and wrote the initial draft, and all authors revised the final manuscript.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.jsxksn092> (Garibaldi et al., 2021).

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How to cite this article: Garibaldi LA, Aizen MA, Sáez A, Gleiser G, Strelin MM, Harder LD. The influences of progenitor filtering, domestication selection and the boundaries of nature on the domestication of grain crops. *Funct Ecol*. 2021;00:1–14. <https://doi.org/10.1111/1365-2435.13819>