Ecological correlates of crop yield growth and interannual yield variation at a global scale

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Abstract. Artificial selection and genetic engineering plus an expanding repertoire and use of agrochemical inputs have allowed a rapid and continuous increase in crop yield (i.e., volume production per unit area) over the last century, which is needed to fulfill food demands from a growing human population. However, the first signs of yield deceleration and stagnation have already been reported for some globally important crops. Therefore, the study of the drivers of yield growth and its variation is essential for directing research and policies aiming at ensuring food security in the forthcoming years. We used data on mean and variability in annual yield growth for 107 globally important crops to assess the role of environmental (i.e., climatic region) and plant intrinsic traits (i.e., type of harvested organ, pollinator dependence, and life form) as drivers of change in yield growth and its stability. We applied a comparative approach to control for biases associated with phylogenetic non-independence among crops, an approach rarely used in agronomic studies. Average yield growth and its variation were not phylogenetically structured. Yield growth decreased with increasing pollinator dependence in tree crops but not in herbaceous and shrubby crops. Interannual yield variation tended to increase with increasing pollinator dependence, and it was higher in crops from temperate regions, in those cultivated for their reproductive organs, and in tree and shrubby crops as compared with herbaceous ones. Information on ecological correlates of crop yield growth and interannual yield variation can be used in the design of more sustainable and diversified agriculture schemes.

1 Introduction

Human population is increasing steadily, imposing greater demands on agricultural production (Godfray et al., 2010; Foley et al., 2011). Replacement of natural habitats by croplands, advances in crop breeding programs and genetic manipulation, a wider repertoire and more intensive use of agrochemicals (including pesticides, fungicides, herbicides, and fertilizers), and a widespread adoption of increasingly sophisticated irrigation systems have all allowed a rapid growth in total crop production and crop production per unit area (i.e., crop yield) during the last century (Miflin, 2000). This growth in yield has played a central role in fulfilling increasing food demands (Tilman et al., 2002; Aizen and Harder, 2009). However, human food security depends not only on crop yield but also on its interannual variation, which can slow down yield growth (Garibaldi et al., 2011), affecting food prices and limiting people's access to a broad nutritional diet, especially in developing countries (Ray et al., 2015; Schauberger et al., 2016). Indeed, first signs of yield deceleration and stagnation have already been reported for some globally important crops (Ray et al., 2012; Iizumi et al., 2014). In this context, bringing a comparative (i.e., including several species), ecological perspective into the crop science field can be crucial to broaden our knowledge of the factors limiting crop yield. More specifically, a phylogenetically framed approach is essential to avoid statistical biases associated with phylogenetic non-independence due to shared evolutionary history among crops (Revell, 2010; Symonds and Blomberg, 2014) and, thus, to accurately identify global

drivers and correlates of crop yield growth and growth stability (i.e., the inverse of interannual yield variation). Proper identification of these ecological drivers and correlates can be useful in designing national and supra-national policies aiming at guarantying food security in the forthcoming years. Yet, such an approach has been rarely applied in studies on crop biology (Kantar et al., 2015; Milla et al., 2015; Milla et al., 2018; Martin et al., 2019).

Plant growth depends directly on the photosynthetic rate, which is influenced by temperature as well as by light, water, and soil nutrient availability (Schulze et al., 2019). Therefore, all else being equal, tropical and subtropical crops might have higher yield growth than temperate crops because the effect of temperature on plant growth may impose an upper limit on yield in temperate zones. In addition, more pronounced daily and seasonal temperature fluctuations at higher latitudes, including the occurrence of frosts (Rodrigo, 2000), might predict lower crop yield stability. Furthermore, low solar radiation may affect soil nutrient uptake (Schauberger et al., 2016), reducing the potential for yield growth at higher latitudes. However, plant growing conditions may not be so benign in the tropics. For instance, an excess of solar radiation towards lower latitudes could be detrimental for plant development because of increasing damage risk of the photosynthetic systems (Schauberger et al., 2016; Tan et al., 2020). Also, tropical soils in humid areas suffer from intense rainfall and nutrient lixiviation, often becoming nitrogen and phosphorous limited, and thus are commonly less productive than soils in temperate regions (Santiago, 2015; Jeffery et al., 2017). Moreover, indirect climate effects, via higher weed growth and pest occurrence, can also hamper yield growth at lower latitudes (Rosenzweig and Liverman, 1992). Hence, differences in yield growth and yield variability between tropical and temperate crops, if any, might provide first cues to the relative importance of climatic factors as proximate and ultimate modulators of the growth rate in crop productivity.

Fruit and seed production rely on available resources (i.e., fixated carbon, nitrogen, phosphorous, etc.) once investment in vegetative growth and maintenance is secured (Lacey, 1986; Obeso, 2002; Weiner et al., 2009; Tuller et al., 2018); on different pollen vectors like wind, in wind-pollinated plants; and on a diversity of animal pollinators, in pollinator-dependent plants (Willmer, 2011). Consequently, given the expected higher unpredictability associated with the production of reproductive organs, we might predict lower average yield growth and higher yield variability in those crops cultivated for their reproductive parts (i.e., either seeds or fruits) than in those cultivated for their vegetative parts (e.g., tubers, stems, leaves).

Among those crops that are cultivated for their reproductive parts, there is also a broad variability in pollinator dependence (Klein et al., 2007; Aizen et al., 2019), ranging from crops that are completely independent of animal pollinators (e.g., bananas, olives, walnuts, wheat) to crops that are com-

pletely dependent on pollinators (e.g., cocoa, kiwi, vanilla, watermelon). Globally, $\sim 75\%$ of the crops depend, to different degrees, on both wild and managed pollinators for seed and/or fruit quantity and/or quality maximization (Klein et al., 2007; Garibaldi et al., 2013; Rader et al., 2016). Because of evidence that wild and managed pollinator populations are declining in many regions (Potts et al., 2010) and that pollinator availability varies naturally over space and time (Horvitz and Schemske, 1990; Price et al., 2005), crops that rely more strongly on pollinators are expected to be more susceptible to pollinator shortages. Accordingly, Garibaldi et al. (2011) reported that crops that depended more heavily on pollinators had lower mean yield growth and lower yield stability. However, phylogenetic non-independence among crops was not accounted for, and the potential roles of more direct, confounded effects and interactions with associated factors were not evaluated.

Relative investment in reproduction also relates to plant growth form. Annual plants invest a large proportion of their total resource budget in reproduction during a single season, whereas shrubs and specially trees are long lived and make large investments to develop long-lasting supportive and protective tissues (Petit and Hampe, 2006; Weiner et al., 2009), even before any resources are devoted to reproduction (Harper, 1977; Kozlowski and Uchmanski, 1987). Also, fruit and seed production in long-lived plants are usually characterized by high interannual variation (i.e., masting) that is often determined by the overall plant's resource availability as affected by the environment, and possibly by intrinsic resource accumulation–depletion cycles (Bogdziewicz et al., 2019). Thus, genetic or cultivation improvements are probably reflected in faster and more constant yield growth in annual crops as compared to shrubs and trees, which have longer life cycles and more complex patterns of resource allocation (Cheplick, 2005).

Crop species sharing a common recent ancestor may also show more similar yield growth just by descent. Indeed, significant phylogenetic signal has been reported in traits related to photosynthesis and plant growth (Zheng et al., 2009). Therefore, any analysis of crop yield growth and stability involving several crops should be evaluated within a phylogenetic context. Furthermore, because environmental and plant intrinsic traits do not act independently, the evaluation of possible interactions between them is fundamental. For example, as previously mentioned, lower yield stability was reported for those crops that depend more heavily on pollinators (Garibaldi et al., 2011). However, this pattern may also depend on the region in which crops are being cultivated, as yield of pollinator-dependent crops may be more stable in the tropics due to pollinators being mostly active all year (Souza et al., 2018; Rabeling et al., 2019). Also, the effect of pollinator dependence on yield may be more important in trees than in annual plants, as the former depend more strongly on the amount and quality of the pollination service (Knight et al., 2005; Petit and Hampe, 2006; Brittain et al., 2014).

Here, we conducted a comparative analysis of crop yield growth and its variation over a 57-year time series for more than 100 globally important crops. By applying phylogenetically explicit analyses, we assessed the influence of climatic region (i.e., tropical vs. temperate) and plant intrinsic factors (i.e., type of harvested organ, pollinator dependence, and life form) on mean annual yield growth and its variability, as well as explored possible interactions between these factors. Specifically, we predicted higher yield growth and/or yield stability in tropical/subtropical than temperate crops, in crops cultivated for their vegetative parts, in short-lived crops, and in those with reduced dependence on pollinators. Our results supported several of these expectations and revealed interesting interactions, broadening our knowledge of the ecological factors that affect crop yield growth and stability.

2 Methods

2.1 Database and phylogeny construction

Data on crop yield (hectograms/hectare) were obtained from the United Nations Food and Agriculture Organization database for 113 crops and crop items (i.e., aggregations of different species; Aizen et al., 2019; Table A1) from 1961 to 2017 (FAOSTAT, 2019). Temporal series for three crops were shorter (cassava leaves, 1990–2017; kiwi, 1970–2017; triticale, 1975–2017). With these data we estimated, for each crop, the mean yield growth, Δyield, as

$$\Delta\text{yield} = \sum_{t=1}^{N-1} [\ln(\text{yield}_{t+1}) - \ln(\text{yield}_t)]/N - 1, \quad (1)$$

with t being a given year, N the total number of years with data (i.e., 57 years for most crops, starting from 1961), and $\ln(\text{yield}_{t+1}) - \ln(\text{yield}_t)$ the relative yield growth rate between year t and year $t+1$. Similarly, we estimated the variability in yield growth, $\text{SD}(\Delta\text{yield})$, as

$$\text{SD}(\Delta\text{yield})$$

$$= \sqrt{\frac{\sum_{t=1}^{N-1} \left\{[\ln(\text{yield}_{t+1}) - \ln(\text{yield}_t)] - \Delta\text{yield}\right\}^2}{N-2}}, \quad (2)$$

with $\text{SD}(\Delta\text{yield})$ being the standard deviation of $\ln(\text{yield}_{t+1}) - \ln(\text{yield}_t)$. This measure of variability in annual yield growth is basically a linearly detrended measure of interannual variation in (log) yield (hereafter "interannual yield variation") and thus an inverse measure of yield stability. Also, even though Eq. (1) can be simplified as $[\ln(\text{yield}_{2017}) - \ln(\text{yield}_{1961})]/56$, this more complex expression reveals that Eqs. (1) and (2) depict the first (position) and second (dispersal) moments of the distribution of annual yield growth, respectively. Since both Δyield and the $\text{SD}(\Delta\text{yield})$ are based on differences in log yields, they provide comparable relative estimates of yield growth and its

variation across crops, while increasing compliance of these response variables with normal-distribution assumptions underlying the linear tests used to analyze data. Also, these two measures are unitless, as the difference between log yields is the log of their ratio. In the case of mean yield growth, $100 \cdot (e^{\Delta\text{yield}} - 1)$ provides the mean annual percent increase in yield.

The crop climatic region of origin (i.e., tropical or temperate) was searched from the literature (Table A2); crops were categorized as belonging to the two main climatic regions: "tropical-subtropical" when their region of origin never exceeded 35° latitude and "temperate" when their region of origin extended above 35° (Jeffery et al., 2017). In general, tropical crops are being cultivated mainly in the tropics, while crops originating in temperate regions are being cultivated mainly in temperate zones (Leff et al., 2004). Even though some temperate crops like wheat are cultivated both in temperate and tropical latitudes, most of its production is accounted for by temperate countries (e.g., China, Russia, Ukraine, USA, Canada, Argentina). Similarly, a greater share of the global production of subtropical/tropical staple crops like maize and rice that are widely cultivated in temperate latitudes comes from tropical/subtropical countries or tropical/subtropical regions within countries (FAOSTAT, 2019). Therefore, we assume that crop climatic region of origin reflects the climatic region of cultivation. Also, for animal-pollinated crops, optimal yields are expected in the region of origin (Garibaldi et al., 2013; Brown and Cunningham, 2019). Data on type of harvested organ (i.e., vegetative or reproductive organs) and life form (i.e., herbs, shrubs, or trees) were also obtained from the literature (Milla, 2020). Pollinator dependence data for each crop were extracted from Klein et al. (2007) and Aizen et al. (2019), the latter for crops not included in the former study, where five classes were defined: "none", for no yield reduction in the absence of pollinators; "little", for the range 0 %–10 % of yield reduction without pollinators; "modest", for the range 10 %–30 % of yield reduction; "considerable" for the range 40 %–90 % of yield reduction; and "essential", for cases where yield reduction in the absence of pollinators exceeded 90 %.

A synthesis-based phylogeny (i.e., a phylogeny that is obtained by sub-setting an already available mega-phylogeny) was built to represent phylogenetic relations among crops. This kind of phylogenies has proved robust to detect even weak phylogenetic signals and to be useful in community phylogenetic analyses (Li et al., 2019). The first step to obtain the synthesis-based tree involved checking crop species names to match accepted names in The Plant List (Table A1). An initial phylogeny including all checked species was then obtained using the function "phylo.maker" from the R package *V.PhyloMaker*, using the GBOTB.extended mega-phylogeny (74 531 tips) as backbone, and the option "scenario 1", which adds missing species as basal polytomies within their genera or families (Jin and Qian, 2019). Missing species were identified by comparing the focal species list

with the tips in the mega-phylogeny. The phylogenetically closest taxa of these missing species were searched in the literature and were used as input information when running the function "phylo.maker". This procedure has been shown to improve the placement of missing taxa into the resulting phylogeny (Jin and Qian, 2019).

A phylogenetic tree with 157 tips was obtained with the methodology described above. This tree was then modified to match FAO crop items (i.e., 113 items) by collapsing those nodes that included species belonging to the same FAO items. Six FAO items (i.e., "anise, badian, fennel, and coriander", "nutmeg, mace, and cardamoms", "mangoes, mangosteens, and guavas", "green chilies and peppers", "dry chilies and peppers", and "millets") included species phylogenetically dispersed, even belonging to unrelated families (Table A1); these items were excluded from the analyses. In some cases, FAO items comprised species phylogenetically dispersed (Table A1) but that could be represented as soft polytomies including a few items (e.g., "Brassicaceae clade", which included the items "rapeseed", "mustard seed", "cauliflowers and broccoli", and "cabbages"); these cases were kept in the analyses (see Fig. A1). The clade comprising the crops "potatoes", "tomatoes", and "eggplants" was resolved according to Milla (2020).

2.2 Phylogenetic signal and phylogenetically controlled regressions

Phylogenetic signals in mean yield growth and interannual yield variation were calculated with Blomberg's K index (Blomberg et al., 2003). This index quantifies the amount of phylogenetic signal in the data relative to a Brownian motion (BM) model of trait evolution, with $K = 0$ indicating a random distribution of the trait along the phylogeny (i.e., absence of phylogenetic signal) and $K = 1$ reflecting a BM pattern of trait evolution (i.e., presence of phylogenetic signal). K estimates were obtained with the R package *phytools* (Revell, 2012), and their statistical significance was assessed by generating 10 000 randomized values of K. Furthermore, as phylogenetic signal may vary across the phylogeny, we looked for the existence of local hotspots of phylogenetic autocorrelation by estimating local indicators of phylogenetic association scores (LIPA scores hereafter) for each crop in the phylogeny (Anselin, 1995; Keck et al., 2016). Positive LIPA scores for a given trait of interest indicate that the phylogenetic neighborhood of a focus tip in the phylogeny is more similar for that trait than expected by chance. LIPA scores and their statistical significance were obtained with the R package *phylosignal*, on the basis of patristic phylogenetic distances and 999 randomizations (Keck et al., 2016).

Even in the absence of phylogenetic signal in the response variables, accounting for species-shared evolutionary history is recommended in interspecific comparisons (Felsenstein, 1985; Revell, 2010). Therefore, the associations of yield growth and interannual yield variation with climatic region, type of harvested organ, pollinator dependence, and life form were evaluated by conducting phylogenetic least squares (PGLS; Paradis, 2012) regressions, which account for phylogenetic non-independence among species. Phylogenetic correlations among species are made explicit in these regressions by including a residual variance–covariance matrix, which can be constructed by assuming different evolutionary models. PGLS regressions were ran using the *ape* v. 5.3 (Paradis and Schliep, 2019) and *nlme* v 3.1-140 (Pinheiro et al., 2019) R packages, and the fit of the residuals to different evolutionary models (as available in the *ape* R package) was compared in terms of the Akaike information criterion (AIC). Following a step-up analysis strategy (West et al., 2007), mean yield growth and interannual yield variation were regressed, alternatively, against single predictors (i.e., climatic region, type of harvested organ, pollinator dependence, or crop life form) and against combinations of two predictors to account for predictor interactions and potential confounding effects (Mazer, 1989). Higher factorial designs were not analyzed due to being too incomplete and unbalanced. Also, the tree category was excluded from the "type of harvested organ + life form" combination given that only reproductive organs (i.e., fruits or seeds) are harvested from the included tree crops. Finally, the two-predictor combination "type of harvested organ + pollinator dependence" was not tested, as the development of the vegetative organs that we consume does not depend on pollination, and thus these two factors do not cross. All predictors were treated as categorical variables in the analyses; however, the existence of a linear trend was evaluated for the relations between pollinator dependence and yield growth and yield stability given that pollinator dependence itself has an increasing (or decreasing) order across categories. In these cases, the five different categories of pollinator dependency were assigned discrete values from 0 to 4 for "none", "little", "modest", "considerable", and "essential", respectively. Model-estimated means and their standard errors were calculated using the R package *effects* (Fox and Weisberg, 2019).

3 Results

Mean annual yield growth was about 0.008 (equivalent to 0.802 % yr^{-1}) and highly variable across crops, ranging from an average logarithmic increase of 0.025 (2.546 % yr^{-1}) in kiwis to a decrease in yield of -0.037 (-3.614 % yr^{-1}) in currants (Table A3). The most stable crop in terms of yield variation was lettuce, with an interannual variation of 0.019, followed by sugar cane and rice (0.020 and 0.022, respectively). On the contrary, the greatest interannual yield variation, 0.425, was observed in jojoba, which could relate to the quite extreme arid conditions present in the regions where it is mostly grown (Al-Obaidi et al., 2017; FAOSTAT, 2019). This crop departed clearly from the rest (about 50 % more variable than Brazil nuts, 0.291, and pistachios, 0.282,

the following most variable crops; see Fig. A2), and thus it was considered as an outlier and excluded from the analyses of the determinants of yield growth stability. Mean annual yield growth and interannual yield variation were negatively, albeit weakly correlated across crops ($r = -0.362$, $p < 0.001$). Thus, those crops with more variable yields also tended to exhibit lower yield grow rates.

Differences in crop yield growth could not be explained by crop similarity due to common ancestry, as there was no evidence of an overall phylogenetic signal in this trait ($K = 1.426 \times 10^{-6}$, $p = 0.331$). Accordingly, only 6 % of all crops, mainly belonging to the *Prunus* clade, were surrounded by phylogenetic neighborhoods with similar yield growths (i.e., significant local positive phylogenetic autocorrelation; Fig. A3). Phylogenetically controlled regressions showed no significant effects of climatic region or type of harvested organ on the rate of yield growth (Table A4). Yield growth tended to decrease with pollinator dependence (Table A4; linear trend contrast: $\beta = -0.017$, SE $= 0.008$, $p = 0.047$) and was about 64 % and 88 % lower in shrubs and trees than herbs, respectively ($\beta = -0.008$, SE $= 0.003$, $p = 0.015$ for shrubs; and $\beta = -0.011$, SE $= 0.002$, $p < 0.001$ for trees). However, a significant statistical interaction between pollinator dependence and life form (Table A4) indicated that the reduction in yield growth associated with pollinator dependence is only evident in tree crops (Fig. 1; linear contrasts with $\beta = 0.005$, SE $= 0.011$, $p = 0.642$ for herbs; $\beta = 0.028$, SE $= 0.023$, $p = 0.225$ for shrubs; and $\beta = -0.037$, SE $= 0.013$, $p = 0.006$ for trees). Therefore, tree crops that are highly dependent on pollinators showed, on average, the lowest growth in yield.

Crop similarity due to common ancestry was not reflected in yield stability, as there was no evidence of phylogenetic signal in interannual yield variation globally ($K = 6.479 \times 10^{-7}$, $p = 0.651$). Local phylogenetic autocorrelation was detected but involved only ca. 10 % of all crops, with significant LIPA positive scores detected in all members of the [Amaryllidaceae + Asparagaceae] clade as well as in other six phylogenetically dispersed crops (Fig. A3). Interannual yield variation was 33 % higher in temperate than tropical crops ($\beta = 0.027$, SE $= 0.011$, $p = 0.020$; Fig. 2a) and 65 % higher in those crops cultivated for consumption of their reproductive organs than in crops cultivated for their vegetative organs ($\beta = 0.039$, SE $= 0.015$, $p = 0.010$; Fig. 2b). These results were not confounded by the inclusion of tree crops that are only harvested for their seeds or fruits, as a significant difference in yield variability persisted after excluding trees and controlling for the remaining growth forms (Table A4; Fig. A4). Interannual yield variation tended to increase with increasing pollinator dependence (Fig. 2c; linear contrast: $\beta = 0.105$, SE $= 0.048$, $p = 0.032$), despite the overall test not being statistically significant (Table A4). Crops highly dependent on animal pollination were, on average, about 50 % more variable in yield that those that do not depend, or depend little, on pollinators. Finally, in-

terannual yield variation was 37 % higher in trees than in herbaceous crops ($\beta = 0.030$, SE $= 0.013$, $p = 0.023$), with shrubs showing values of yield variability closer to trees than to herbs (Fig. 2d).

4   Discussion

Increasing crop yield to fulfill the continuous rising food demands from a growing human population, while minimizing the impact on natural ecosystems, is one the main challenges of modern agriculture (Tilman, 1999; Tilman et al., 2002; Foley et al., 2011; Bommarco et al., 2013). Genetic and management innovations have boosted a steady increase in crop yield since the middle of the last century (Evenson and Gollin, 2003; Garibaldi et al., 2011; Hatfield and Walthall, 2015). However, the first signs of yield deceleration and stagnation have already been reported for some globally important crops (Ray et al., 2012; Kucharik et al., 2020). Under this scenario, an ecological perspective can be crucial to broaden our knowledge of the factors affecting crop yield growth. By applying a comparative approach, here we uncovered the influence of environmental and plant intrinsic traits on average yield growth and on its interannual variation. Specifically, we found that yield growth decreased with increasing pollinator dependence in tree crops but not in herbaceous and shrubby crops. Interannual yield variation was higher in crops from temperate regions, in those cultivated for their reproductive organs, and in tree and shrubby crops as compared with herbaceous ones, and it tended to increase with increasing pollinator dependence. Unexpectedly, average yield growth and its variation were not phylogenetically structured. Therefore, our results revealed new and intriguing patterns, which we discuss below.

There was no evidence that climatic region was related to yield growth, with temperate crops exhibiting similar mean growth rates to tropical-subtropical crops (0.72 % yr^{-1} vs. 0.83 % yr^{-1}). Under the assumption that the climatic region where a crop (or its ancestors) originated reflects the climatic conditions where the crop is most commonly cultivated, higher temperature and an overall more benign environment for plant growth in the tropics was not reflected in significantly higher rates of yield growth. As proposed in the Introduction, it might well be that more intense weed competition and, perhaps, higher herbivore pressure at low latitudes counteract the positive effect of a more benign and stable climate on crop development (Rosenzweig and Liverman, 1992). Alternatively, crop genetic and management improvements could have been more prevalent and intense among temperate crops (e.g., wheat, canola). However, this seems unlikely as several tropical-subtropical crops have also been genetically manipulated intensively and are grown industrially (e.g., soybean, rice, maize; Aizen et al., 2019). Despite no apparent differences in yield growth, we did find that interannual yield variation was lower in tropical-subtropical
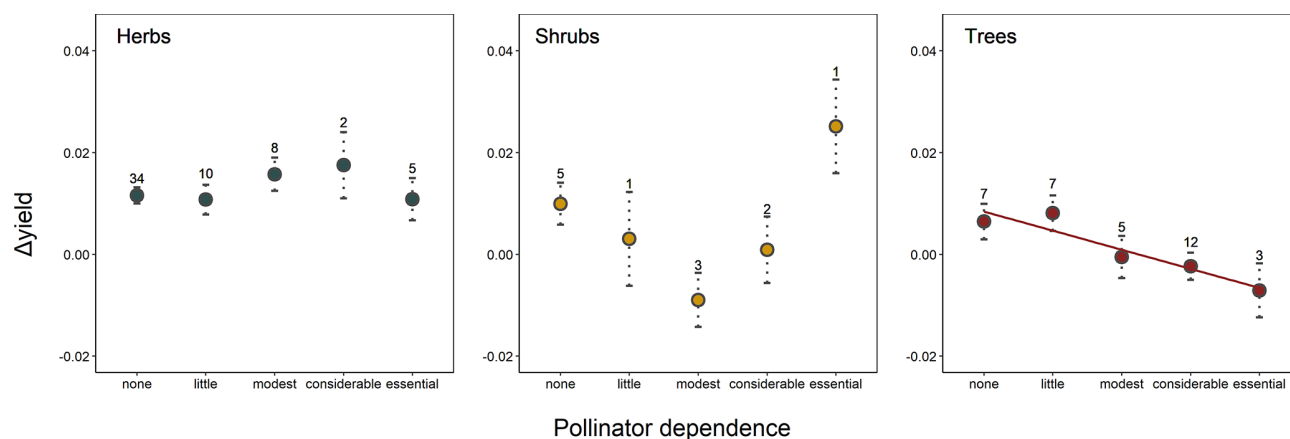
Figure 1. Joint effect of pollinator dependence and crop life form on mean yield growth (Δyield). The single significant linear trend found (in tree crops; see results) is indicated with a regression line. Points depict model-adjusted estimated means, while dotted lines model-adjusted standard errors. Sample sizes are shown for each category. Note that Δyield is unitless (see Methods).

than temperate crops, probably reflecting higher climatic stability at lower latitudes. Previous studies focusing in four of the most economically important crops (i.e., wheat, maize, soybean, and rice) have identified temperature and precipitation variability as the main factors explaining yield variation (Ray et al., 2015; Schauberger et al., 2016). While water availability may limit plant growth in both zones (Kramer, 2019), temperature amplitude is greater in temperate zones, and occasional extreme temperatures may occur more frequently in these zones (e.g., occurrence of frosts; Rodrigo, 2000; Snyder and de Melo-Abreu, 2005). The stability and performance of many physiological and biochemical processes affecting plant growth – including photosynthesis, stomatal conductance, and nutrient uptake – depend on an optimal temperature range and can be disturbed by the occurrence of temperatures outside this range (Schauberger et al., 2016; Slot and Winter, 2017). Given that the greater yield variability observed among temperate crops was independent of whether the crops were harvested for their vegetative or reproductive organs (Table A4), higher yield variation in temperate regions may be explained by extreme temperatures affecting biochemical processes involved in the development of both vegetative and reproductive organs.

Yield growth seems to be independent of whether a crop is cultivated for its vegetative or for its reproductive parts. However, crops cultivated for their vegetative parts show more stable yields than those cultivated for either their fruits or seeds. This lower variation may result from the fact that investment in vegetative parts (i.e., leaves, stems, roots, tubers, rhizomes) is quintessential to plant survivorship, and even though it can be regulated, it cannot be postponed (Horvitz and Schemske, 2002; Obeso, 2002). On the contrary, variable resource availability can determine high variability in fruit and seed production among reproductive seasons in iteroparous species (Weiner et al., 2009; Hulshof et

al., 2012), and even in annual plants, in which sexual reproduction in a given year can fail entirely (Kho, 2000). Besides resource availability as an intrinsic source of variability, most fruit and seed crops depend to different degrees on an external agent, either wind or insect pollinators, for pollen transfer between flowers (Klein et al., 2007). Particularly, restricted pollen transfer due to pollinator scarcity can be an important factor limiting fruit and seed set in a large fraction of wild plants and crops. In fact, pollen limitation (i.e., the failure of achieving maximum seed set as a consequence of inadequate pollination; Knight et al., 2005) affects more than a half of all crops (Aizen et al., 2008). As a consequence, pollinator availability, which is highly variable in time and space (Herrera, 1988; Price et al., 2005), can also determine high variability in yield. Agreeing with this hypothesis, we report a trend of increasing interannual yield variation with increasing dependence on animal pollination. This confirms results from previous reports (Garibaldi et al., 2011), although our conservative analysis controlled for phylogenetic non-independence among crops.

Pollen limitation has also been proposed to limit yield growth in addition to decreasing yield stability. In fact, a proposed global pollinator decline is expected to affect total agriculture production by decelerating yield growth or even decreasing the yield of pollinator-dependent crops (Aizen et al., 2008; Potts et al., 2010). Even though previous studies have reported that yield growth decreased with increasing crop pollinator dependence (Aizen et al., 2008; Garibaldi et al., 2009, 2011), these studies did not account for potentially confounding factors and phylogenetic non-independence. In particular, by accounting for growth form, we found that this trend was only apparent in trees, in which high pollinator dependence seems to hinder yield growth. In fact, several tropical-subtropical and temperate tree crops that depend to a large extent on pollinators to produce either fruits or seeds,
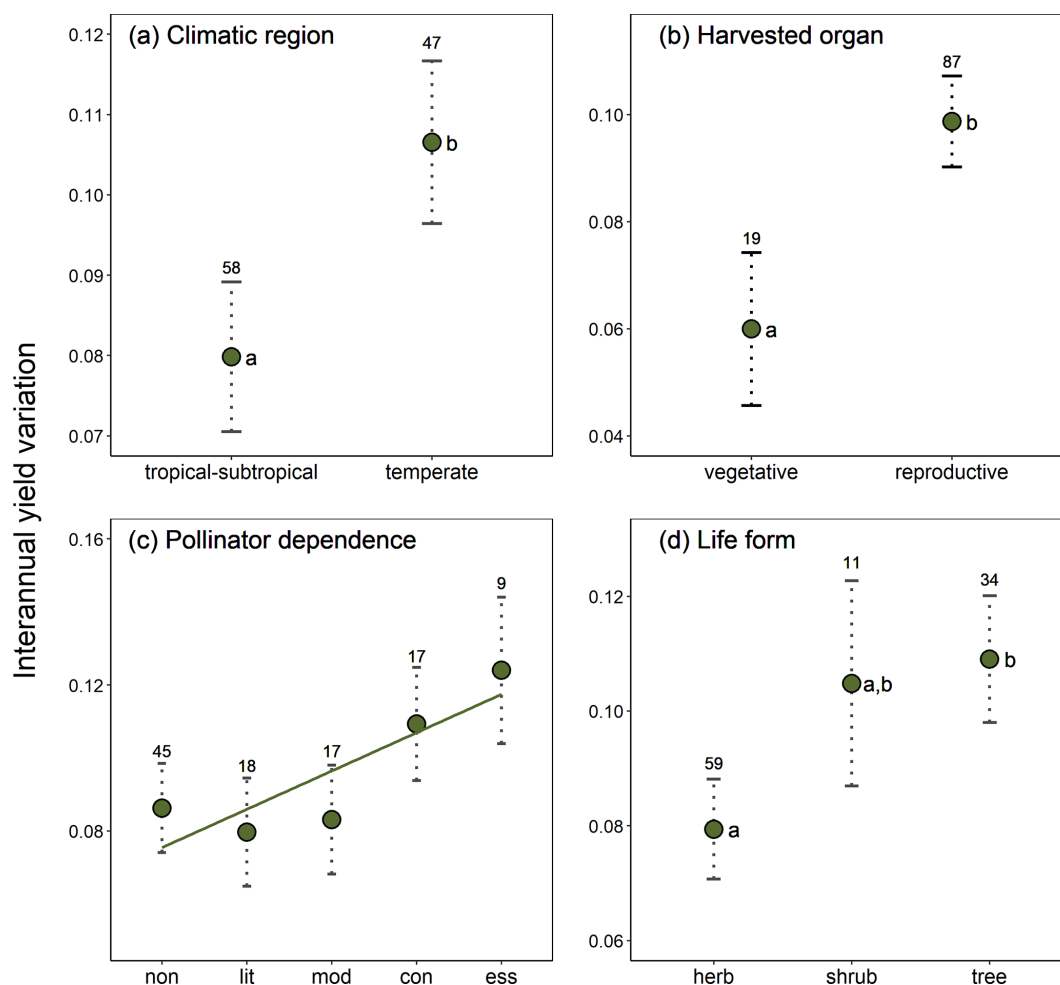
Figure 2. Effects of **(a)** climatic region, **(b)** type of harvested organ, **(c)** pollinator dependence, and **(d)** crop life form on interannual yield variation (SD(Δyield)). Model-adjusted estimated means are illustrated with points and standard errors with dotted lines. Sample sizes are shown for each category. The regression line in panel **(c)** illustrates the positive linear trend found for the relation between interannual yield variation and pollinator dependence (see Results). Significant differences among categories are indicated with different letters (Table A4). Pollinator dependence categories are abbreviated as "non" (none), "lit" (little), "mod" (moderate), "con" (considerable) and "ess" (essential). Note that SD (Δyield) is unitless (see Methods).

or even fail to produce fruits or seeds without pollinators, have shown negative growth rates during the last decades (e.g., Brazil nuts, kola nuts, cashew, plums, cherries, quinces, blueberries; Table A3), supporting the view that a global pollinator decline is affecting crop yield. However, it is puzzling that no trend for decreasing yield was observed among herbaceous crops, and apparently a concave trend was found for shrubs (Fig. 1). Several factors could explain these discrepancies. First, independent of their pollinator dependence, there seems to be lower pollen limitation in herbaceous than woody plants (Knight, 2005). Therefore, and perhaps associated with much larger floral displays and higher incidence of self-incompatibility, greater pollinator abundance is needed to maximize crop yield in trees than in herbaceous crops (Garibaldi et al., 2020). Second, hand and other forms of artificial pollination constitute a customary procedure in highly

valuable herbaceous and shrubby crops like vanilla and kiwi, respectively (Arditti et al., 2009, Sáez et al., 2019), which lowers their dependence on declining insect pollinators. Although there are some accounts of fruit production based on hand pollination for highly pollinator dependent tree crops (e.g., apples in China; Partap et al., 2001; Partap and Ya, 2012), this is a highly laborious and geographically restricted procedure.

It has been proposed that reduced yield growth could be a consequence of higher variability of a crop's input resource (i.e., pollinators) via what is known as Jensen's inequality (Jensen, 1906; Ruel and Ayres, 1999), which is predicted when there is a positive but saturating response of yield with an increase in an agriculture input (Garibaldi et al., 2011). In this case, variability in an agriculture input resource is expected to be reflected in higher yield variation, resulting in

a decrease in average yield over years. In fact, higher variability in yield associated with larger reproductive uncertainty has been proposed as an explanation of reduced yield in highly pollinator dependent crops (Garibaldi et al., 2011). Although here we report an overall negative relation between yield growth and variability, as expected due to Jensen's inequality, the interactive effects of growth form and pollinator dependence on yield growth still persisted after accounting for yield variation (Table A5). Thus, reduced yield growth in highly pollinator dependent trees can be interpreted as a direct consequence of their dependence on this external biotic input rather than of the yield uncertainty introduced by this dependence.

Lower pollen limitation in herbaceous than woody plants might also explain why in general yield growth and yield stability decreased along a gradient of crop increasing woodiness. Moreover, herbs and trees differ in the length of their life cycles, which influences the pattern of resource allocation between vegetative and reproductive structures. Life cycles are shorter in herbs, and resources are invested mainly in vegetative growth and reproduction. Trees have longer life cycles, they grow taller, and have higher costs of maintenance as resources are needed for the development of supportive and protective tissues, which reduces growth rates (Petit and Hampe, 2006). Furthermore, woody species are often characterized by a variable and synchronized reproductive behavior known as "masting", which may increase plant fitness by increasing either pollination success, seed dispersal, or offspring survival through predator satiation (Pearse et al., 2016). This reproductive strategy, although beneficial for wild plant populations, is highly undesirable in agriculture, as it can increase interannual yield variation and price peaks (Smith and Samach, 2013; Ray et al., 2015). All tree crops included in this study are being cultivated for exploitation of their fruits or seeds, and their interannual variation in yield may reflect, in addition to higher pollination limitation, yearly fluctuations in resources invested in reproduction.

Finally, it is interesting that neither mean yield growth nor its variation were conditioned by crop common ancestry in the majority of the analyzed crops. This is a meaningful finding that indicates that crop genetic and management improvements could overcome several developmental and ecological conditionings, besides those analyzed here, which may be phylogenetically structured. As a consequence, phylogenetically related crops that probably have been manipulated genetically to different extents can exhibit contrasting yield growth rates (e.g., apples vs. quinces; Table A3).

5   Concluding remarks

The strength of a comparative approach lies in revealing general patterns. This approach has been rarely applied in interspecific studies of crop yield, despite the need for identifying global factors limiting crop yield growth and yield sta-

bility. This is of paramount importance in a context of decelerating yield growth and increasing yield variability expected under climate change (Chalinor et al., 2014, Zhao et al., 2017) and global pollinator decline (Aizen et al., 2008; Potts et al., 2010). By analyzing yield growth and interannual yield variation of more than 100 globally important crops, here we identified ecological factors associated with climate, resource allocation, and pollination limitation that affect crop yield. Despite the ultimate processes and mechanisms underlying these patterns, the ecological correlates of yield growth and yield variation detected here provide a useful starting point for establishing management guidelines for crop selection. For instance, even though pollinator-dependent tree crops have relatively high market values (Bauer and Wing, 2016), agronomic schemes based solely on the cultivation of this type of crops is a risky business because of their reduced yield growth and high interannual variability, particularly in temperate regions. In any event, the relative reduced yield growth and high yield variability of highly pollinator dependent tree crops (i.e., those in the moderate and essential categories) call for the need to apply a more active and knowledge-based pollinator management than is commonly performed today. This requires not only the management of domesticated pollinators (e.g., *Apis mellifera*), but also the enhancement of wild pollinators through infield and outfield strategies that involve habitat management at different spatial scales (Garibaldi et al., 2014). On the other hand, agronomic schemes based exclusively on crops cultivated for either their vegetative parts or with low levels of pollinator dependence could show adequate levels of yield growth and stability, but their production is of a poorer nutritional quality and has lower market prices than the one represented by the seeds and fruits of many pollinator-dependent crops (Gallai et al., 2009; Eilers et al., 2011). Overall, our results advocate for more diverse agriculture that involves the cultivation of different crops with different ecological features, nutritional quality, and market value at all spatial scales. In addition to contributing to increasing food security in quantitative and qualitative terms, this more diversified agriculture will ensure a more sustainable agriculture and the preservation of different ecosystem services (Aizen et al., 2019).

Appendix A

Table A1. FAO crops/items included in the study, with their corresponding species names and family. Listed species names are accepted names according to The Plant List (TPL). Items indicated with an asterisk were not included in the analyses, as they include species phylogenetically dispersed.

Crop name	TPL accepted names	Family
almonds	*Prunus dulcis* var. *amara*	Rosaceae
anise, badian, fennel, and coriander*	*Pimpinella anisum*	Apiaceae
	Illicium verum	Schisandraceae
	Foeniculum vulgare	Apiaceae
	Coriandrum sativum	Apiaceae
apples	*Malus domestica*	Rosaceae
apricots	*Prunus armeniaca*	Rosaceae
areca nuts	*Areca catechu*	Arecaceae
asparagus	*Asparagus officinalis*	Asparagaceae
avocados	*Persea americana*	Lauraceae
Bambara beans	*Vigna subterranea*	Fabaceae
bananas	*Musa×paradisiaca*	Musaceae
	Musa cavendishi	Musaceae
barley	*Hordeum distichon*	Poaceae
berries	*Rubus idaeus*	Rosaceae
	Rubus chamaemorus	Rosaceae
	Rubus flagellaris	Rosaceae
	Rubus fruticosus (unresolved)	Rosaceae
blueberries	*Vaccinium corymbosum*	Ericaceae
Brazil nuts	*Bertholletia excelsa*	Lecythidaceae
broad beans	*Vicia faba*	Fabaceae
buckwheat	*Fagopyrum esculentum*	Polygonaceae
cabbages	*Brassica rapa*	Brassicaceae
	Brassica oleracea	Brassicaceae
carrots	*Daucus carota*	Apiaceae
cashew nuts	*Anacardium occidentale*	Anacardiaceae
cashew apples	*Anacardium occidentale*	Anacardiaceae
cassava	*Manihot esculenta*	Euphorbiaceae
	Manihot palmata	Euphorbiaceae
cassava leaves	*Manihot esculenta*	Euphorbiaceae
	Manihot palmata	Euphorbiaceae
castor oil seeds	*Ricinus communis*	Euphorbiaceae
cauliflowers and broccoli	*Brassica oleracea*	Brassicaceae
cherries	*Prunus avium*	Rosaceae
chestnuts	*Castanea sativa*	Fagaceae
chick peas	*Cicer arietinum*	Fabaceae

Table A1. Continued.

Crop name	TPL accepted names	Family
chicory roots	*Cichorium intybus*	Asteraceae
	Cichorium endivia	Asteraceae
cocoa beans	*Theobroma cacao*	Malvaceae
coconuts	*Cocos nucifera*	Arecaceae
coffee	*Coffea arabica*	Rubiaceae
	Coffea canephora	Rubiaceae
	Coffea liberica	Rubiaceae
cowpeas	*Vigna unguiculata*	Fabaceae
cranberries	*Vaccinium macrocarpon*	Ericaceae
	Vaccinium oxycoccos	Ericaceae
cucumbers and gherkins	*Cucumis sativus*	Cucurbitaceae
currants	*Ribes nigrum*	Grossulariaceae
	Ribes rubrum	Grossulariaceae
dates	*Phoenix dactylifera*	Arecaceae
dry beans	*Phaseolus acutifolius*	Fabaceae
	Phaseolus coccineus	Fabaceae
	Phaseolus lunatus	Fabaceae
	Phaseolus vulgaris	Fabaceae
	Vigna aconitifolia	Fabaceae
	Vigna angularis	Fabaceae
	Vigna mungo	Fabaceae
	Vigna radiata	Fabaceae
	Vigna umbellata	Fabaceae
dry chilies and peppers*	*Capsicum annuum*	Solanaceae
	Pimenta dioica	Myrtaceae
dry peas	*Pisum sativum*	Fabaceae
dry onions	*Allium cepa*	Amaryllidaceae
eggplants	*Solanum melongena*	Solanaceae
figs	*Ficus carica*	Moraceae
garlic	*Allium sativum*	Amaryllidaceae
gooseberries	*Ribes uva-crispa*	Grossulariaceae
grapefruits	*Citrus paradisi*	Rutaceae
	Citrus maxima	Rutaceae
grapes	*Vitis vinifera*	Vitaceae
green beans	*Vigna unguiculata*	Fabaceae
	Vigna subterranea	Fabaceae
green chilies and peppers*	*Capsicum annuum*	Solanaceae
	Pimenta dioica	Myrtaceae
green maize	*Zea mays*	Poaceae
green onions and shallots	*Allium cepa*	Amaryllidaceae
	Allium ascalonicum	Amaryllidaceae
	Allium fistulosum	Amaryllidaceae
green peas	*Pisum sativum*	Fabaceae

Table A1. Continued.

Crop name	TPL accepted names	Family
groundnuts	*Arachis hypogaea*	Fabaceae
hazelnuts	*Corylus avellana*	Betulaceae
jojoba seeds	*Simmondsia chinensis*	Simmondsiaceae
karite nuts	*Vitellaria paradoxa*	Sapotaceae
kiwi	*Actinidia deliciosa*	Actinidiaceae
kola nuts	*Cola nitida*	Malvaceae
	Cola acuminata	Malvaceae
leeks	*Allium ampreloprasum*	Amaryllidaceae
	Allium spp.	Amaryllidaceae
lemons and limes	*Citrus limon*	Rutaceae
	Citrus aurantiifolia	Rutaceae
	Citrus medica	Rutaceae
lentils	*Lens culinaris*	Fabaceae
lettuce	*Lactuca sativa*	Asteraceae
linseed	*Linum usitatissimum*	Linaceae
maize	*Zea mays*	Poaceae
mandarins, tangerines, clementines, and satsumas	*Citrus reticulata*	Rutaceae
	Citrus limon	Rutaceae
	Citrus hystrix	Rutaceae
mangoes, mangosteens, and guavas*	*Mangifera indica*	Anacardiaceae
	Garcinia×mangostana	Clusiaceae
	Psidium guajava	Myrtaceae
melons and cantaloupes	*Cucumis melo*	Cucurbitaceae
	Cucumis metuliferus	Cucurbitaceae
melonseed	*Cucumis melo*	Cucurbitaceae
millet*	*Echinochloa frumentacea*	Poaceae
	Eleusine coracana	Poaceae
	Eragrostis tef	Poaceae
	Panicum miliaceum	Poaceae
	Paspalum scrobiculatum	Poaceae
	Pennisetum glaucum	Poaceae
	Setaria italica	Poaceae
mustard seed	*Sinapis alba*	Brassicaceae
	Brassica nigra	Brassicaceae
nutmeg, mace, and cardamoms*	*Elettaria cardamomum*	Zingiberaceae
	Myristica fragrans	Myristicaceae
oats	*Avena sativa*	Poaceae
okra	*Abelmoschus esculentus*	Malvaceae
olives	*Olea europaea*	Oleaceae
oranges	*Citrus sinensis*	Rutaceae
palm fruit oil	*Elaeis guineensis*	Arecaceae
papayas	*Carica papaya*	Caricaceae
peaches and nectarines	*Prunus persica*	Rosaceae

Table A1. Continued.

Crop name	TPL accepted names	Family
pears	*Pyrus communis*	Rosaceae
pepper	*Piper nigrum*	Piperaceae
	Piper longum	Piperaceae
persimmons	*Diospyros kaki*	Ebenaceae
	Diospyros virginiana	Ebenaceae
pigeon peas	*Cajanus cajan*	Fabaceae
pineapples	*Ananas comosus*	Bromeliaceae
pistachios	*Pistacia vera*	Anacardiaceae
plums and sloes	*Prunus domestica*	Rosaceae
	Prunus spinosa	Rosaceae
poppy seeds	*Papaver somniferum*	Papaveraceae
potatoes	*Solanum tuberosum*	Solanaceae
pumpkins, squash, and gourds	*Cucurbita maxima*	Cucurbitaceae
	Cucurbita argyrosperma	Cucurbitaceae
	Cucurbita moschata	Cucurbitaceae
	Cucurbita pepo	Cucurbitaceae
quinces	*Cydonia oblonga*	Rosaceae
quinoa	*Chenopodium quinoa*	Chenopodiaceae
rapeseed	*Brassica napus*	Brassicaceae
rice	*Oriza* spp.	Poaceae
rye	*Secale cereale*	Poaceae
safflower seeds	*Carthamus tinctorius*	Asteraceae
seed cotton	*Gossypium hirsutum*	Malvaceae
	Gossypium barbadense	Malvaceae
	Gossypium arboreum	Malvaceae
	Gossypium herbaceum	Malvaceae
sesame seeds	*Sesamum indicum*	Pedaliaceae
sorghum	*Sorghum bicolor*	Poaceae
sour cherries	*Prunus cerasus*	Rosaceae
soybeans	*Glycine max*	Fabaceae
spinach	*Spinacia oleracea*	Amaranthaceae
strawberries	*Fragaria* spp.	Rosaceae
string beans	*Lablab purpureus*	Fabaceae
	Phaseolus coccineus	Fabaceae
	Phaseolus vulgaris	Fabaceae
	Vigna unguiculata	Fabaceae
sugar beet	*Beta vulgaris*	Amaranthaceae
sugar cane	*Saccharum officinarum*	Poaceae
sunflower seeds	*Helianthus annuus*	Asteraceae
sweet potatoes	*Ipomoea batatas*	Convolvulaceae
taro	*Colocasia esculenta*	Araceae

Table A1. Continued.

Crop name	TPL accepted names	Family
tomatoes	*Solanum lycopersicum*	Solanaceae
triticale	*Triticum aestivum×Secale cereale*	Poaceae
vanilla	*Vanilla planifolia*	Orchidaceae
	Vanilla pompona	Orchidaceae
walnuts	*Juglans regia*	Juglandaceae
	Juglans nigra	Juglandaceae
	Juglans cinerea	Juglandaceae
watermelons	*Citrullus lanatus*	Cucurbitaceae
wheat	*Triticum* spp.	Poaceae
yams	*Dioscorea* spp.	Dioscoreaceae
yautia	*Xanthosoma sagittifolium*	Araceae

Table A2. Bibliographical sources for the climatic region of origin of the crops included in the study.

Crop name	Climatic region of origin	Reference
almonds	temperate	Zeinalabedini et al. (2010), Khoury et al. (2016)
apples	temperate	Harris et al. (2002)
apricots	temperate	Decroocq et al. (2016)
areca nuts	tropical-subtropical	Khoury et al. (2016)
asparagus	temperate	Milla (2020)
avocados	tropical-subtropical	Khoury et al. (2016)
Bambara beans	tropical-subtropical	Milla (2020)
bananas	tropical-subtropical	Khoury et al. (2016)
barley	temperate	Milla (2020)
berries	temperate	Milla (2020)
blueberries	temperate	Milla (2020)
Brazil nuts	tropical-subtropical	Milla (2020)
broad beans	tropical-subtropical	Caracuta et al. (2016)
buckwheat	tropical-subtropical	Gondola and Papp (2010)
cabbages	tropical-subtropical	Arias et al. (2014)
carrots	temperate	Milla (2020)
cashew nuts	tropical-subtropical	Milla (2020)
cashew apples	tropical-subtropical	Milla (2020)
cassava	tropical-subtropical	Milla (2020)
cassava leaves	tropical-subtropical	Milla (2020)
castor oil seeds	tropical-subtropical	Khoury et al. (2016), van der Vossen and Mkamilo (2007)
cauliflowers and broccoli	tropical-subtropical	Arias et al. (2014)
cherries	temperate	Milla (2020)
chestnuts	temperate	Milla (2020)
chick peas	temperate	Milla (2020)
chicory roots	temperate	Milla (2020)
cocoa beans	tropical-subtropical	Milla (2020)
coconuts	tropical-subtropical	Khoury et al. (2016), Milla (2020)
coffee	tropical-subtropical	Khoury et al. (2016), Milla (2020)
cowpeas	tropical-subtropical	Milla (2020)
cranberries	temperate	Khoury et al. (2016), Milla (2020)
cucumbers and gherkins	tropical-subtropical	Sebastian et al. (2010), Milla (2020)
currants	temperate	Milla (2020)
dates	tropical-subtropical	Milla (2020)
dry peas	temperate	Milla (2020)
dry onions	temperate	Khoury et al. (2016), Milla (2020)
eggplants	tropical-subtropical	Milla (2020)
figs	tropical-subtropical	Khoury et al. (2016)
garlic	temperate	Khoury et al. (2016), Milla (2020)
gooseberries	temperate	Milla (2020)
grapefruits	tropical-subtropical	Milla (2020)
grapes	temperate	Toffolatti et al. (2018), Milla (2020)
green beans	tropical-subtropical	Milla (2020)
green maize	tropical-subtropical	Khoury et al. (2016), Milla (2020)
green onions and shallots	temperate	Milla (2020)
green peas	temperate	Milla (2020)
groundnuts	tropical-subtropical	Khoury et al. (2016), Milla (2020)
hazelnuts	temperate	Milla (2020)
jojoba seeds	temperate	Kumar et al. (2012)
karite nuts	tropical-subtropical	Milla (2020)
kiwi	tropical-subtropical	Milla (2020)
kola nuts	tropical-subtropical	Milla (2020)
leeks	temperate	Hirschegger et al. (2010), Milla (2020)
lemons and limes	tropical-subtropical	Khoury et al. (2016), Wu et al. (2018)
lentils	temperate	Milla (2020)
lettuce	tropical-subtropical	Křístková et al. (2008)

Table A2. Continued.

Crop name	Climatic region of origin	Reference
linseed	temperate	Milla (2020)
maize	tropical-subtropical	Khoury et al. (2016), Milla (2020)
mandarins, tangerines, clementines, and satsumas	tropical-subtropical	Wang et al. (2018), Wu et al. (2018)
melons and cantaloupes	tropical-subtropical	Khoury et al. (2016), Milla (2020)
melonseed	tropical-subtropical	Khoury et al. (2016), Milla (2020)
mustard seed	temperate	Milla (2020)
oats	temperate	Khoury et al. (2016) Milla (2020)
okra	tropical-subtropical	Milla (2020)
olives	temperate	Milla (2020)
oranges	tropical-subtropical	Wu et al. (2018)
palm fruit oil	tropical-subtropical	Milla (2020)
papayas	tropical-subtropical	Khoury et al. (2016), Milla (2020)
peaches and nectarines	temperate	Faust and Timon (1995)
pears	temperate	Milla (2020)
pepper	tropical-subtropical	Milla (2020)
persimmons	temperate	Guo et al. (2006), Soriano et al. (2006)
pigeon peas	tropical-subtropical	Milla (2020)
pineapples	tropical-subtropical	Khoury et al. (2016), Milla (2020)
pistachios	temperate	Milla (2020)
plums and sloes	temperate	Milla (2020)
poppy seeds	temperate	Teteni (1995)
potatoes	tropical-subtropical	Khoury et al. (2016), Milla (2020)
pumpkins, squash, and gourds	tropical-subtropical	Sanjur et al. (2002), Khoury et al. (2016), Milla (2020)
quinces	temperate	Milla (2020)
quinoa	tropical-subtropical	Milla (2020)
rapeseed	temperate	Milla (2020)
rice	tropical-subtropical	Milla (2020)
rye	temperate	Milla (2020)
safflower seeds	tropical-subtropical	Milla (2020)
seed cotton	tropical-subtropical	Milla (2020)
sesame seeds	tropical-subtropical	Bedigian et al. (1985), Milla (2020)
sorghum	tropical-subtropical	Milla (2020)
sour cherries	temperate	Milla (2020)
soybeans	tropical-subtropical	Guo et al. (2010), Khoury et al. (2016), Milla (2020)
spinach	temperate	Milla (2020)
strawberries	temperate	Khoury et al. (2016), Milla (2020)
string beans	tropical-subtropical	Milla (2020)
sugar beet	temperate	Milla (2020)
sugar cane	tropical-subtropical	Khoury et al. (2016), Milla (2020)
sunflower seeds	temperate	Khoury et al. (2016), Milla (2020)
sweet potatoes	tropical-subtropical	Khoury et al. (2016), Milla (2020)
taro	tropical-subtropical	Khoury et al. (2016), Milla (2020)
tomatoes	tropical-subtropical	Khoury et al. (2016), Milla (2020)
triticale	temperate	
vanilla	tropical-subtropical	Khoury et al. (2016), Milla (2020)
walnuts	temperate	Milla (2020)
watermelons	tropical-subtropical	Chomicki and Renner (2015), Milla (2020)
wheat	temperate	Milla (2020)
yams	tropical-subtropical	Milla (2020), APG IV.
yautia	tropical-subtropical	Milla (2020)

Table A3. Mean yield growth (Δyield), interannual yield variation (SD(Δyield)), and mean annual percent increase in yield (% Δyield) for the FAO crops/items included in the study. Data were obtained from the FAOSTAT database and covered a 57-year period (from 1961 to 2017) for all but three crops (see Methods for details).

Crop name	Δyield	SD(Δyield)	% Δyield
almonds	0.00217058	0.16500452	0.21729338
apples	0.00948692	0.07662275	0.95320648
apricots	0.00449209	0.1181696	0.45021993
areca nuts	0.0120489	0.05365916	1.21217782
asparagus	0.01380359	0.03621639	1.38993015
avocados	0.00183314	0.05121231	0.18348198
Bambara beans	−0.00038776	0.12635301	−0.03876825
bananas	0.01139601	0.03171601	1.14611969
barley	0.01533921	0.0740192	1.54574621
berries	0.00193931	0.09090424	0.19411926
blueberries	−0.01350698	0.16181083	−1.34161701
Brazil nuts	−0.02728997	0.2906871	−2.6920963
broad beans	0.014011	0.07798472	1.4109615
buckwheat	0.01067132	0.13617233	1.07284578
cabbages	0.00888201	0.04706542	0.89215756
carrots	0.01500502	0.03339517	1.51181651
cashew nuts	0.00346746	0.07339473	0.34734748
cashew apples	−0.00887508	0.18441034	−0.88358149
cassava	0.00720464	0.02623632	0.72306554
cassava leaves	0.00049446	0.05998736	0.04945847
castor oil seeds	0.01845184	0.09573532	1.86231314
cauliflowers and broccoli	0.00458121	0.02600946	0.45917179
cherries	−0.01541209	0.1356929	−1.52939281
chestnuts	−0.00720649	0.10026083	−0.71805809
chick peas	0.00797888	0.11653123	0.80107912
chicory roots	0.01107802	0.16175596	1.113961
cocoa beans	0.00886955	0.07294877	0.8909006
coconuts	0.00153597	0.04564775	0.15371504
coffee	0.01080565	0.09231583	1.08642432
cowpeas	0.00877164	0.15937423	0.88102203
cranberries	0.01529573	0.09702625	1.5413304
cucumbers and gherkins	0.0243494	0.04007409	2.46482683
currants	−0.03681024	0.20700515	−3.61409772
dates	−0.00401493	0.07389119	−0.40068783
dry beans	0.00995793	0.04150106	1.00076774
dry peas	0.01278227	0.13759495	1.28643156
dry onions	0.00843938	0.02306261	0.84750883
eggplants	0.02062972	0.05014455	2.08439831
figs	0.00658167	0.07525325	0.6603379
garlic	0.02077647	0.03700207	2.09938068
gooseberries	0.00699571	0.06086436	0.70202393
grapefruits	0.00353658	0.08649643	0.35428455
grapes	0.01507857	0.07408466	1.51928241
green beans	0.0190214	0.03288979	1.92034544
green maize	0.0111837	0.06031723	1.12464724
green onions and shallots	0.01183165	0.03928078	1.19019227
green peas	0.00517291	0.0380565	0.51863108
groundnuts	0.01224044	0.05579314	1.23156561
hazelnuts	0.0160642	0.26202516	1.61939188
jojoba seeds	0.00849108	0.42483628	0.85272309
karite nuts	−0.01426026	0.06379342	−1.41590673
kiwi	0.02514235	0.1507326	2.54610831
kola nuts	−0.01630822	0.12361623	−1.61759574
leeks	0.00321461	0.04575138	0.3219782

Table A3. Continued.

Crop name	Δyield	SD(Δyield)	% Δyield
lemons and limes	0.00391987	0.05923242	0.39275624
lentils	0.01395521	0.07720088	1.40530396
lettuce	0.0064908	0.0188423	0.65119091
linseed	0.0163961	0.10216615	1.65312496
maize	0.01939543	0.06773364	1.95847432
mandarins, tangerines, clementines, and satsumas	0.00813799	0.09846082	0.8171193
melons and cantaloupes	0.01523815	0.02764863	1.53548469
melonseed	−0.00368031	0.16040998	−0.3673541
mustard seed	0.00968023	0.1905356	0.97272304
oats	0.01205159	0.06566067	1.21244981
okra	0.00297939	0.09356481	0.29838309
olives	−0.00870367	0.20172565	−0.86658988
oranges	0.00722409	0.05250987	0.72502428
palm fruit oil	0.02452654	0.04470793	2.4829791
papayas	0.01671554	0.05205554	1.68560251
peaches and nectarines	0.00961111	0.06859212	0.96574497
pears	0.00917736	0.09477455	0.92196006
pepper	0.01713192	0.10635009	1.72795082
persimmons	−0.00738406	0.0861261	−0.73568611
pigeon peas	0.00305091	0.1511845	0.30555716
pineapples	0.01566351	0.04952555	1.57868253
pistachios	0.01615674	0.28230055	1.62879686
plums and sloes	−0.02221958	0.13529796	−2.19745443
poppy seeds	0.00457541	0.13960183	0.4585889
potatoes	0.00890241	0.05664544	0.89421546
pumpkins, squash, and gourds	0.01934329	0.04959308	1.95315795
quinces	−0.00281892	0.09398141	−0.28149458
quinoa	0.00565192	0.19193331	0.56679232
rapeseed	0.02398523	0.07585527	2.42751895
rice	0.01608759	0.02205044	1.62176955
rye	0.01733697	0.08186681	1.74881273
safflower and seeds	0.01148734	0.12901911	1.15535747
seed cotton	0.01716008	0.05191093	1.73081567
sesame seeds	0.01180364	0.06690349	1.18735767
sorghum	0.00830287	0.07352281	0.8337432
sour cherries	−0.00531848	0.1607349	−0.53043584
soybeans	0.01656652	0.06522905	1.67045047
spinach	0.021734	0.14531135	2.19719053
strawberries	0.01905668	0.06263665	1.92394179
string beans	0.01074331	0.04143396	1.08012242
sugar beet	0.01743104	0.06127232	1.75838492
sugar cane	0.00613899	0.02032183	0.61578703
sunflower seeds	0.01013751	0.07956927	1.01890654
sweet potatoes	0.0091435	0.06615356	0.91854323
taro	0.000032	0.07881259	0.00322584
tomatoes	0.01477903	0.02546481	1.48887824
triticale	0.00891108	0.16885613	0.89508998
vanilla	−0.00023624	0.22315504	−0.02362095
walnuts	0.00222087	0.12323914	0.22233346
watermelons	0.02351296	0.04440071	2.37915679
wheat	0.02100839	0.05267996	2.1230618
yams	0.00294095	0.09174646	0.29452742
yautia	0.01490923	0.09241804	1.50209298

Table A4. Analysis of variance of PGLS fitted models for **(a)** mean yield growth (Δyield) and **(b)** interannual yield variation (SD(Δyield)), with climatic region, type of harvested organ, pollinator dependence, and crop life form as sources of variation. Marginal sums of squares (type III) were estimated for models with more than one source of variation by applying the R function "anova" (with the option "type = marginal") on the PGLS fitted objects. Interaction terms were only kept in the models when their inclusion increased model fit in terms of AIC (ΔAIC $\geq$ 2); all interactions between predictors not informed were statistically non-significant ($p > 0.05$). Significant tests ($p < 0.05$) are indicated in bold type.

(a)

Source of variation	DF_{num}	DF_{den}	F	p
Climatic region	1	104	0.240	0.625
Harvested organ	1	105	0.323	0.570
Pollinator dependence	4	102	2.963	**0.023**
Life form	2	102	13.448	**< 0.001**
Climatic region + harvested organ				
Climatic region	1	103	0.287	0.593
Harvested organ	1	103	0.377	0.540
Climatic region + pollinator dependence				
Climatic region	1	100	0.224	0.637
Pollinator dependence	4	100	2.795	**0.030**
Climatic region + life form				
Climatic region	1	100	0.511	0.476
Life form	2	100	13.250	**< 0.001**
*Harvested organ + life form**				
Harvested organ	1	68	0.665	0.418
Life form	1	68	8.066	**0.006**
Pollinator dependence + life form				
Pollinator dependence	4	90	0.588	0.672
Life form	2	90	0.908	0.407
Pollinator dependence · life form	8	90	2.873	**0.007**

Table A4. Continued.

(b)				
Source of variation	DF_{num}	DF_{den}	F	p
Climatic region	1	103	5.611	**0.020**
Harvested organ	1	104	6.908	**0.010**
Pollinator dependence	4	101	1.404	0.238
Life form	2	101	3.035	0.052
Climatic region + harvested organ				
Climatic region	1	102	6.605	**0.012**
Harvested organ	1	102	8.066	**0.005**
Climatic region + pollinator dependence				
Climatic region	1	99	5.841	**0.017**
Pollinator dependence	4	99	1.416	0.234
Climatic region + life form				
Climatic region	1	99	5.894	**0.017**
Life form	2	99	3.117	**0.049**
Harvested organ + life form*				
Harvested organ	1	67	5.649	**0.020**
Life form	1	67	2.197	0.143
Pollinator dependence + life form				
Pollinator dependence	4	97	1.034	0.394
Life form	2	97	2.157	0.121

* Tree crops were not included in the analysis.

Table A5. Analysis of variance of a PGLS fitted model constructed to assess whether the slowdown in mean yield growth found in tree crops could be explained by Jensen's inequality effect. Interannual yield variation was used as a proxy reflecting the effect of variable pollen delivery (i.e., a resource needed for seeds or fruit production) on yield growth.

Source of variation	DF_{num}	DF_{den}	F	p
Pollinator dependence	4	88	0.785	0.538
Life form	2	88	0.079	0.924
Interannual yield variation	1	88	14.703	**< 0.001**
Pollinator dependence · life form	8	88	3.252	**0.003**
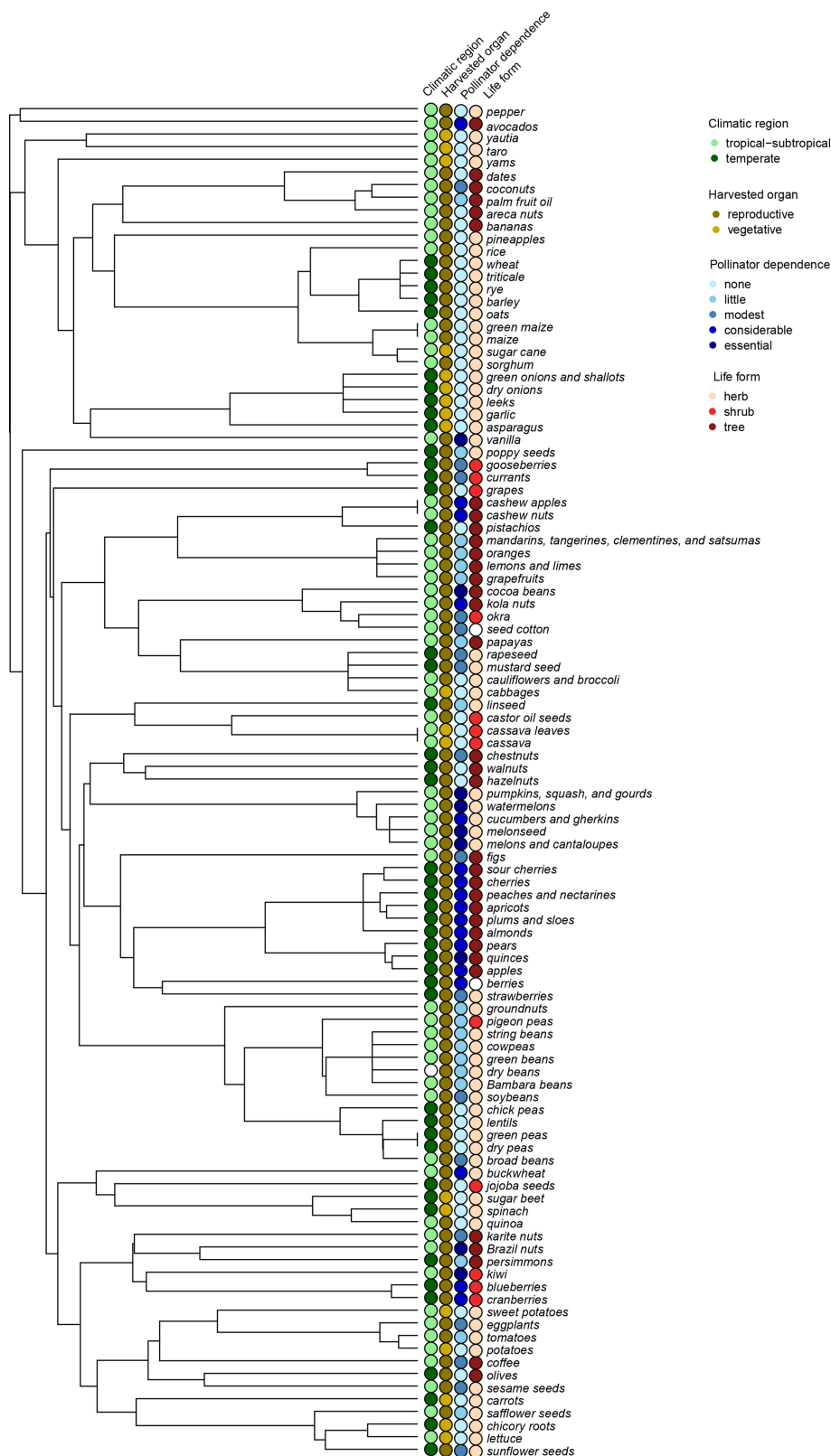
Figure A1. Phylogenetic relationships among all FAO items included in the study. Data on climatic region, harvested organ, pollinator dependence, and crop life form are indicated for each tip. Unfilled circles depict tip data that have been excluded from the analyses, as they corresponded to FAO items comprising species that differ in a given trait.
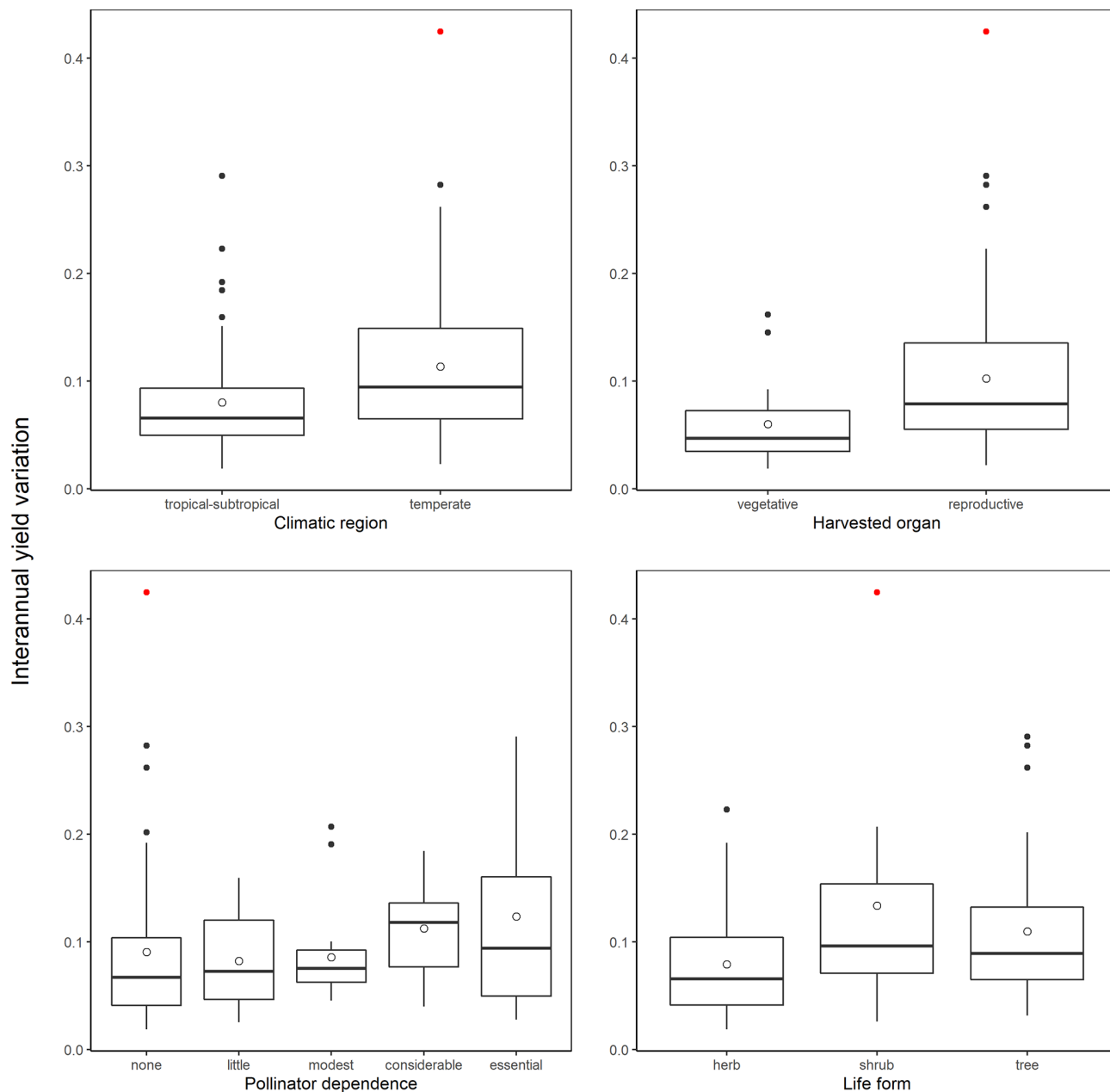
Figure A2. Boxplots showing the distribution of the interannual yield variation against climatic region, type of harvested organ, pollinator dependence, and crop life form. Boxes delimit the lower and upper quartiles; the black horizontal line within the boxes shows the median, the white circle the mean, the vertical lines the whiskers, and the points outside the boxes the outlying points. The red outlying points correspond to the FAO item "jojoba seeds".
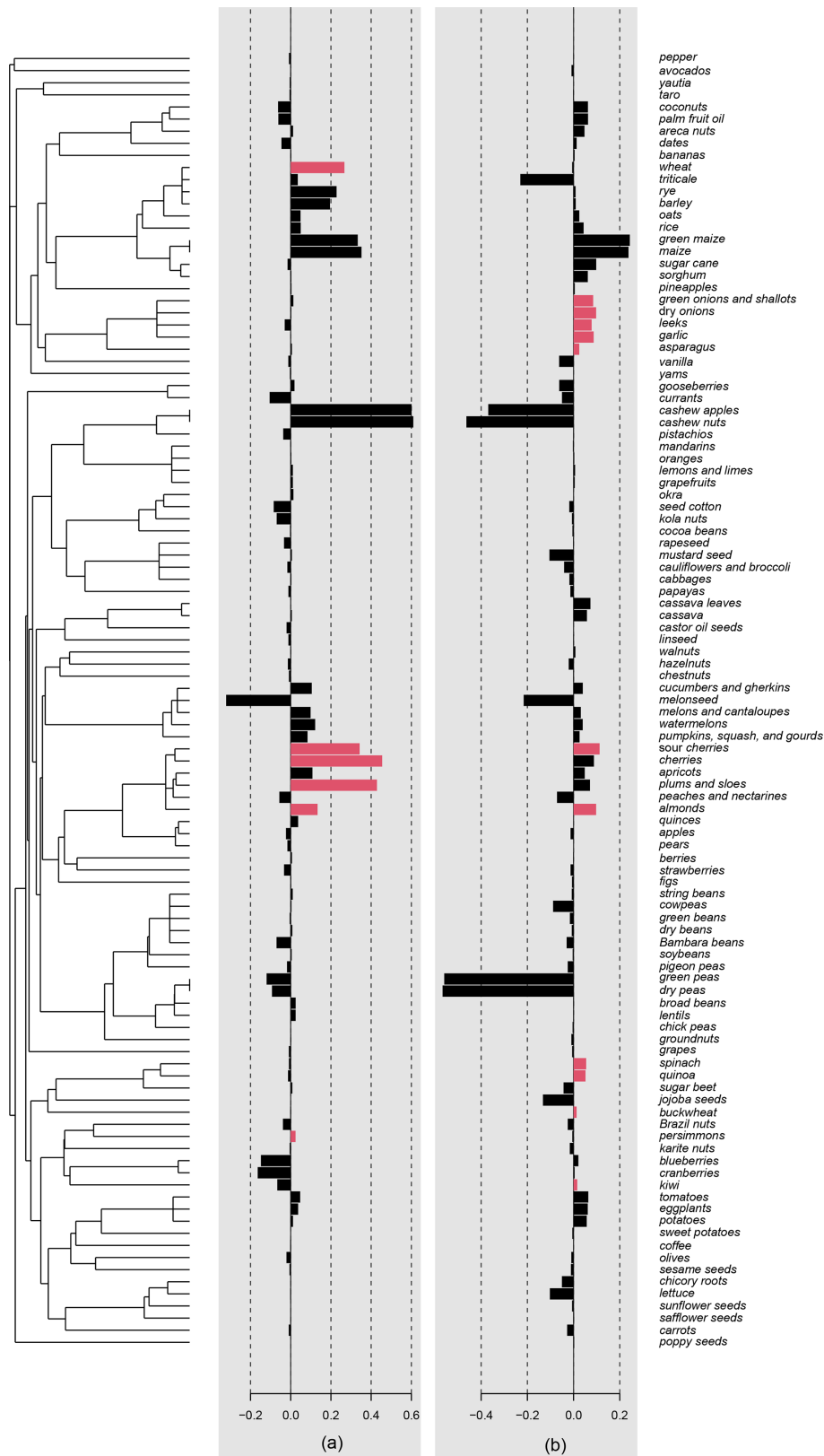
Figure A3. Local indicators of phylogenetic association (LIPA) scores for **(a)** Δyield and **(b)** SD(Δyield), depicted with a bar for each crop. Significant values ($p < 0.05$) are indicated with colored bars.
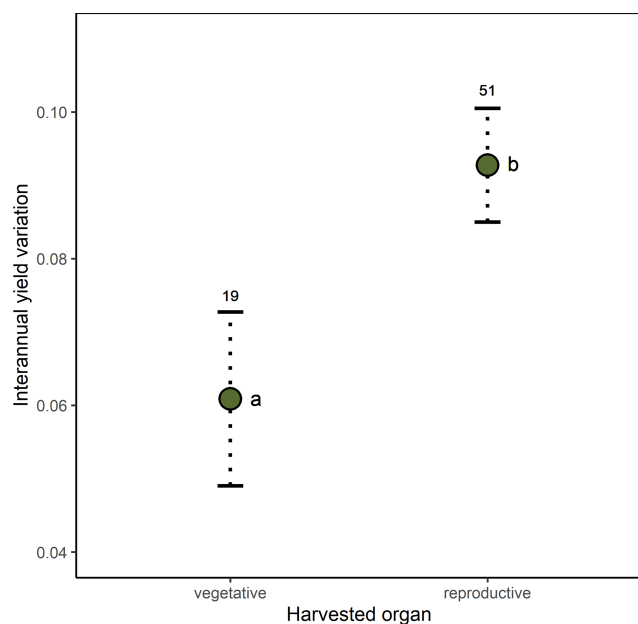
Figure A4. Effect of type of harvested organ on interannual yield variation, SD(Δyield), for herbaceous and shrubby crops. Model-adjusted estimated means are illustrated with points and standard errors with dotted lines. Sample sizes are shown for each category. Significant differences are indicated with different letters (see Table A4).

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