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Opportunities to reduce pollination deficits and address production shortfalls in an important insect pollinated crop

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Abstract

Pollinators face multiple pressures and there is evidence of populations in decline. As demand for insect-pollinated crops increases, crop production is threatened by shortfalls in pollination services. Understanding the extent of current yield deficits due to pollination and identifying opportunities to protect or improve crop yield and quality through pollination management is therefore of international importance. To explore the extent of 'pollination deficits', where maximum yield is not being achieved due to insufficient pollination, we use an extensive dataset on a globally important crop, apples. We quantified how these deficits vary between orchards and countries as well as compare 'pollinator dependence' across different apple varieties. We found evidence of pollination deficits and in some cases, risks of over-pollination were even apparent where fruit quality could be reduced by too much pollination. In almost all regions studied we found some orchards performing significantly better than others, in terms of avoiding a pollination deficit and crop yield shortfalls due to sub-optimal pollination. This represents an opportunity to improve production through better pollinator and crop management. Our findings also demonstrate that pollinator dependence varies considerably between apple varieties in terms of fruit number and fruit quality. We propose that assessments of pollination service and deficits in crops can be used to quantify supply and demand for pollinators and help target local management to address deficits although crop variety has a strong influence on the role of pollinators.

Keywords

Apples, agro-ecology, *malus domestica*, pollinators, sustainable crop production

Introduction

Demand for crops which rely on insect pollinators is increasing on a global scale (Aizen *et al.*, 2019). Yet due to multiple threats (Vanbergen & Initiative, 2013; Potts *et al.*, 2016), populations of both wild and managed pollinators may not meet present or future demands for pollination service provision, compromising production by limiting yield and quality of crops. We are increasingly aware of the significant contribution pollinators make to global food production, particularly of nutritionally important crops (Smith *et al.*, 2015). In addition, as evidence of yield deficits emerge (Garibaldi *et al.*, 2016), there is a need to ensure pollination services are supported through policy and practice (Dicks *et al.*, 2016; Potts *et al.*, 2016; Garibaldi *et al.*, 2019). Avoiding mismatches between the supply of, and demand for, this valuable ecosystem service is vital for future sustainable food production.

Cost effective management of insect-pollination services by farmers, land managers and policy makers requires coordinated action at field, farm and landscape scales (Garibaldi *et al.*, 2019), and both wild and managed pollinators may be required to ensure adequate pollen transfer and optimal crop production (Garibaldi *et al.*, 2014; Isaacs *et al.*, 2017). However, matching pollination supply and demand in order to optimise yield and quality is not always straightforward as it requires combined knowledge of both a crop's breeding system (Hudewenz *et al.*, 2013; Benjamin & Winfree, 2014; Garratt *et al.*, 2016), as well as the influence of environmental and management context on pollination. For example, agronomic inputs including fertilisers and irrigation (Klein *et al.*, 2015; Garratt *et al.*, 2018), biological factors such as pest pressure (Barber *et al.*, 2012; Bartomeus *et al.*, 2015; Sutter & Albrecht, 2016; Samnegård *et al.*, 2019), and even environmental and climatic variables (Bishop *et al.*, 2016), can result in complex interactions that affect the contribution of pollinators to crop yield (Tamburini *et al.*, 2019).

Apples are a globally significant crop valued at US$45bn annually (FAOStat, 2018), with high economic and nutritional value. They are grown by large scale commercial operations and small scale farmers alike. Apple production relies on insect pollination (Ramírez & Davenport, 2013; Cross *et al.*, 2015; Demestihas *et al.*, 2017), but the degree of pollination by either managed or wild pollinators varies (Stern *et al.*, 2001; Martins *et al.*, 2015; Földesi *et al.*, 2016; Joshi *et al.*, 2016; Geslin *et al.*, 2017), and the delivery of pollination service has been found to depend on apple variety (Garratt *et al.*, 2016). Despite relatively few reported examples (Garratt *et al.*, 2014; Blitzer *et al.*, 2016), pollination deficits could arise due to pollinator loss, poor weather during flowering, insufficient availability of compatible pollen or a number of other factors. Yet we are not sure in which regions and varieties this is indeed a potential hazard, or if in fact deficits already exist.

Sustainable crop production depends on approaches that help predict potential and actual risks of yield losses arising from pollination shortfalls and identifying orchards where production is limited in order to target interventions. Using a global dataset, we set out to answer the following research questions: i) how widespread are pollination deficits in apples and to what extent do these vary among orchards and countries, ii) how does crop variety influence dependence on pollinators and pollination deficits, and iii) how does pollination effect aspects of both fruit yield and fruit quality across different apple varieties.

Materials and Methods

Datasets

We gathered datasets on insect pollination in apples from regions around the world, including intensive commercial orchards and low intensity smaller scale production. The analysis involved working with raw datasets and data holders were identified and approached following a workshop held on apple pollination as part of the 'Sustainable Pollination in Europe' Super-B COST Action Project to which European and other international researchers were invited. Studies were included if they involved manipulation of apple blossoms. Manipulations included pollinator exclusion using net bags, supplementary pollination, whereby pollen was applied by hand using compatible pollen from local polliniser trees or neighbouring varieties, and open 'controls' accessible to insect visits. Studies recorded metrics of apple pollination, including early fruit set and seed number per apple, or apple production such as fruit set at harvest and fruit quality in terms of apple size (max width mm), weight (g), firmness (kg/cm measured using a penetrometer) and sugar content (%brix measured using a refractometer). The analyses in which each study was involved depended on data availability and metrics taken, so not all studies were incorporated into all analyses. In total we analysed data from 14 countries and five continents, comprising 36 apple varieties across 356 orchards (Appendix S1: Table S1).

Calculating pollinator dependence, service and deficits

Using data from pollinator exclusion, open pollination and supplementary hand pollination (hereafter supplementary pollination) techniques we assessed levels of pollinator dependence, pollination service and pollination deficit across orchards, countries and apple varieties for a number of apple response metrics. These response metrics can be divided into two broad categories: 'pollination' and 'production'. We used early fruit and seed number to represent 'pollination' as they reflect the level of compatible pollen delivery to apple flowers but are not intrinsically of value to farmers. Final fruit set at harvest, yield (fruit set x fruit weight), and apple quality (size, sugar content, firmness) represent final crop outputs for farmers and were considered as 'production' metrics. 'Pollinator dependence' represents the potential contribution of insect pollinators to these metrics, and was calculated by subtraction of the output achieved following the exclusion of insect pollinators, from the maximum achievable by supplementary pollination. ‘Pollination service’ represents the realized contribution of insects to pollination at any given place and time. It was calculated by subtracting the output in pollinator exclusion treatments from that recorded under open pollination treatments. Finally, ‘Pollination deficit’ represents a shortfall in output due to a lack of pollination and was calculated by subtracting outputs from open pollination treatments from those achieved under supplementary pollination (fig 1).

Pollination service and deficits across countries, orchards and varieties

To assess the extent of yield loss in orchards resulting from insufficient pollination (a pollination deficit), we analysed datasets that had implemented supplementary pollination and open pollination treatments in at least three orchards of the same variety in the same country and included production variables, namely final fruit set and fruit weight. This included data for eleven apple varieties across five countries. Pollination service and deficit were calculated as a proportion of maximum yield achieved in either open or supplementary treatments, whichever was greatest. To compare between countries and varieties, we calculated the pollination deficit (± 95% confidence limits) across orchards for each country and variety combination. Countries and varieties for which confidence limits fell outside a zero deficit were considered to have a significant system-level deficit for yield.

To identify orchards with a significant pollination deficit relative to other orchards in that country growing the same apple variety, we used data from orchards where supplementary and open pollination treatments were implemented on at least three replicate locations within the orchard. We then calculated mean pollination deficits for each orchard. If the 95% confidence limits for each orchard did not include the mean of the orchard with the pollination deficit closest to zero within that variety and country, the orchard was considered as having a significant yield deficit requiring pollination management. Due to the effects of experimental scale on assessments of pollination (Bishop *et al.*, 2020; Webber *et al.*, 2020) we only compared orchards within each country and variety when experimental manipulations employed the same unit of assessment (e.g. tree branch). In order to assess the relationship between the extent of pollination deficits and the level of pollination service measured in each orchard, a linear mixed effect model was used, with orchard, apple variety, study and country as nested random effects.

Differences in pollination dependence between varieties

Linear mixed effects models were used to compare pollinator dependence of both pollination and production metrics between apple varieties. Seventeen studies involving 26 apple varieties included a supplementary pollination treatment and pollinator exclusion treatment and recorded at least one pollination or production metric. Pollination treatment (pollinator exclusion or supplementary pollination), variety, and their interaction were included as fixed effects in the model. Study, orchard, and sampling location within orchards were included as nested random effects. To test for a significant interaction between pollination treatment and apple variety ($p>0.05$) model with and without the interaction term were compared using a maximum likelihood ratio test. Both early and final percent fruit set were arcsine transformed, and seed number and firmness log transformed prior to analysis. Model residuals were checked to ensure they met model assumptions. To assess for significant treatment effects on pollination and production metrics for each variety, post-hoc Tukey tests were carried out.

Relationships between pollination and production

To examine relationships between pollination and production, the relationships between seed number and final fruit set on apple size were investigated using linear mixed effects models. Variety and either seed number or percentage fruit set and their interaction were included in the models as fixed effects. Study, orchard and sampling location within orchard were treated as random effects. Again, seed number was log transformed prior to analysis. All statistical analyses were carried out in R version 4.0.3 using packages *lme4* (Bates *et al.*, 2014), *nlme* (Pinheiro *et al.*, 2013), and *multcomp* (Hothorn *et al.*, 2008; R_Core_Team, 2017).

Results

Pollination service and deficits across countries, orchards and varieties

Data from 11 varieties and five countries included open, pollinator exclusion and supplementary pollination treatments with final fruit set and apple weight measured, allowing for orchard-level assessments of pollination service and pollination deficits for yield. Orchards growing three apple varieties from two countries showed a significant pollination deficit overall: Gala and Hastings orchards in the UK; as well as Braeburn orchards in Germany (fig 2). Orchards growing mixed varieties of apple in Kyrgyzstan had a significantly negative deficit indicating supplementary pollination reduced yield compared with open pollination. At least one orchard per country and apple variety showed significant pollination deficits relative to the best performing orchard in that country growing the same variety (fig 2), except for in Kyrgyzstan where multiple pollination assessments per orchard were not made, so individual orchard comparisons were not possible.

A negative linear relationship between pollination deficits and pollination service for yield was observed (t = -3.40, P <0.001) (Appendix S1: Table S2), indicating that orchards with high values of pollination service were less likely to have pollination deficits (fig 3).

Differences in pollinator dependence between varieties

The pollinator dependence of apples varied considerably among varieties for pollination metrics, with mean dependence ranging from 0.0 to 1.0 for early fruit set and 0.68 to 1.0 for seed number (fig 4). There was a significant interaction between variety and pollination treatment for both early fruit set (F = 18.79, P = <0.001) and seed number (F = 6.20, P = <0.001). A significant effect of pollination treatment was observed for 12 of 14 varieties for early fruit set and all 10 varieties for seed number (fig 4a; fig 4b; Appendix S1: Table S3; Table S4).

The pollinator dependence of apple production in terms of final fruit set and quality also varied considerably among varieties (fig 5). Mean dependence of final fruit set ranged from -0.42 and 1.0 depending on variety, with a significant interaction between experimental treatment and variety (F = 8.61, P = <0.001) and significant differences between pollination treatments were observed for 9 of 15 varieties (Appendix S1: Table S5). There was also an interactive effect of variety and pollination treatment on apple size (F = 8.20, P < 0.001), and firmness (F = 3.64, P =0.012) (Appendix S1: Table S6; Table S7). In contrast, interactive effects of variety and pollination treatment were not found for sugar content (F = 0.98, P = 0.42). When all varieties were considered together there was a significant difference in sugar content observed between pollination treatments (F = 7.19, P = 0.006) but not between apple varieties (F = 1.97, P = 0.09) (Appendix S1: Table S8).

Relationship between pollination and production

Metrics of pollination and production were interrelated, but the direction of these relationships varied among varieties. The relationship between seed number and fruit size depended on apple variety (F = 5.83, P < 0.001) (Appendix S1: Table S9). Seven varieties showed a positive relationship, where apples containing more seeds were also larger, while two varieties showed a negative relationship. The relationship between final fruit set and fruit size was also variety dependent (F = 3.45, P < 0.001) (Appendix S1: Table S10); some varieties exhibited a positive, some a negative, and others no relationship (fig 6).

Discussion

Individual orchards and regions experiencing pollination deficits (i.e. production shortfalls due to pollination) were identified in this study (fig 2) and point to an opportunity for optimising pollination management. Observed deficits could be the result of numerous factors, including insufficient abundance and diversity of wild pollinators (Martins *et al.*, 2015; Blitzer *et al.*, 2016; Grab *et al.*, 2019), a lack of availability or awareness of the need for managed pollinators (Stern *et al.*, 2001; Geslin *et al.*, 2017), sub-optimal fruit management practices such as thinning (Link, 2000) or lack of appropriate 'polliniser' trees providing compatible pollen (Ramírez & Davenport, 2013), agrochemicals impacts (Stanley *et al.*, 2015), or even over-pollination (Sáez *et al.*, 2014). In most study countries, we observed at least one orchard with optimal pollination services (i.e. deficits close to 0), which indicates that there are no regional constraints on achieving optimal pollination. These orchards with no or lower deficits could act as 'agroecological lighthouse' orchards (Nicholls & Altieri, 2018) providing a management and contextual role model for others to follow and help identify factors that limit production on farms with deficits, or provide a platform to share management practices that ensure optimal pollination in well-performing farms. This would allow for directed management towards achieving better pollination services. Best practices would need to be shared using effective tools and techniques, and exploit appropriate networks for each region and group of growers (Ingram, 2008; Klerkx & Jansen, 2010).

The link between pollination deficits in yield and level of pollination services across orchards demonstrated in this study indicates that an important driver of production deficits is low levels of insect pollination. These yield deficits could be addressed through habitat management (Blaauw & Isaacs, 2014; Földesi *et al.*, 2016; Sutter *et al.*, 2018), by avoiding pesticides harmful to wild pollinators (Park *et al.*, 2015; Stanley *et al.*, 2015) or through the effective use of managed pollinators (Stern *et al.*, 2001; Geslin *et al.*, 2017). In the past, the uptake of practices to promote biodiversity-based ecosystem services has been slow, however, identify deficits in production metrics such as yield and quality, familiar to farmers may encourage uptake of ecologically responsible practices (Kleijn *et al.*, 2019). To increase the likelihood of positive action taking place, farmers and their advisors can be encouraged to employ methods similar to those used in this study to assess their own levels of pollination service and deficit (i.e. by bagging flowers and carrying out supplementary pollination) thus becoming more engaged with the process and gathering targeted data on which they can make informed management decisions (Garratt *et al.*, 2019). The scale at which supplementary and pollinator exclusion techniques are employed and whether manipulations are carried out on the whole tree, single branches or groups of flowers can influence resulting deficits (Bishop *et al.*, 2020; Webber *et al.*, 2020), therefore widespread assessment should employ common protocols and focus on collecting production metrics relevant to growers, such as yield (Garratt *et al.*, 2019).

Our study has identified the yield deficits due to sub-optimal pollination in apple production and the extent to which these vary across orchards. Although we show that these deficits are likely a result of insufficient pollination by insects, additional research is required to identify exact causes. If, for example, it is a landscape-wide limitation in wild pollinator abundance (Martins *et al.*, 2015; Park *et al.*, 2015; Kremen & Merenlender, 2018; Winfree *et al.*, 2018), then the capacity of individual farmers to control this is limited. In such circumstances, amendments to policy may be necessary to promote large scale collaborative action (Garibaldi *et al.*, 2019). This is particularly relevant to regions in the UK and Germany and for the varieties Hastings and Braeburn, respectively, as a large proportion of these orchards appear to be experiencing a deficit, reflective of a regional or varietal, rather than orchard-scale challenge. That apples are effectively pollinated by a wide variety of insects (Pardo & Borges, 2020), even away from their native range meaning that management targeting different and locally available pollinators could deliver benefits.

Similarly to other insect-pollinated crops (Hudewenz *et al.*, 2013; Benjamin & Winfree, 2014) we observed that dependence on insect pollination varied considerably between apple varieties in both pollination, with seed number dependence ranging from 0.68 to 1.0, and production, with dependence of fruit set at harvest between -0.42 and 1.0. This negative dependence could indicate that some varieties are potentially at risk of over-pollination, although this negative dependence was not significant for any variety. It should also be noted that the response of a tree to supplementary pollination or pollinator exclusion may be influenced by external factors such as orchard management practice or seasonal conditions during the study year and could affect the level of dependence measured. Without measuring the dependence of different varieties across multiple regions and years it is not possible to account fully for these confounding effects. However, the extent of variation in pollinator dependence we present in this study demonstrates that variety is a key factor to consider when implementing pollinator management strategies in apple orchards. The level of dependence on insect pollinators will ultimately dictate vulnerability of production to pollinator declines or the extent of opportunities available to increase production. We found examples where varieties were entirely pollinator dependent for fruit and seed number, while a minority appear relatively self-compatible (e.g. Ingrid-Marie) due to unknown factors (e.g. partenocarpy, floral anatomy promoting self-pollination). Breeding self-compatibility into crops has been proposed as a possible strategy to reduce vulnerability to limited pollination provided by insects (Knapp *et al.*, 2017). Such an approach could be adopted for apples, targeting at-risk regions or varieties. However, self-pollination can potentially have an impact on the micro-nutritional and other quality parameters of fruit (Eilers *et al.*, 2011; Klatt *et al.*, 2014). Furthermore, self-incompatibility is the norm in commercial apple varieties (Matsumoto, 2014) and, as apples are a long-lived perennial crop, breeding takes decades. Also, perhaps more than any other crop, apple variety is a key component of consumer preferences so the continued demand for many current popular apple varieties which are self-incompatible is likely.

Over-pollination is a risk in some crops (Sáez *et al.*, 2014), and we found evidence for a risk of over-pollination in apples, with some individual orchards demonstrating significantly negative pollination deficits, indicating that enhancing pollination compared to current levels could harm production. Across our studies, compatible pollen was used and care was taken not to damage flowers when implementing supplementary pollination treatments, but ineffective manual pollination, poor pollen quality or stigmas clogging by incompatible pollen can lead to underestimates of deficits and if assessment of pollination services is to become widespread then methods should be standardised (Webber *et al.*, 2020). However, our results identified a mechanism for this apparent over-pollination in apples, as some varieties showed that increasing fruit set or seed number, metrics particularly responsive to insect pollination (Garratt *et al.*, 2014; Garratt *et al.*, 2016), resulted in reduced fruit quality in terms of size. This was particularly prominent for Bramley, Topaz and Golden delicious. This over-pollination is likely a result of resource limitation in trees; when fruit set is high, the maximum fruit size achieved by the tree is reduced. This is an example of a trade-off between pollination and other inputs (Garratt *et al.*, 2018; Tamburini *et al.*, 2019). In apples, growers are aware of this trade-off and employ mechanical and chemical flower and fruit thinning practices to optimise fruit number and, thus, fruit quality which underpins economic output in many regions (Link, 2000; Garratt *et al.*, 2014).

For other varieties, increasing seed number through better insect pollination increased apple size (e.g. Gala, Braeburn) and overall improvements in sugar content across all varieties was seen.

Optimising pollination services through abundant and diverse pollinator communities will likely ensure resilience in pollination services (Bartomeus *et al.*, 2013; Brittain *et al.*, 2013) and sufficient fruit set every year, provided thinning and pruning practices are effective in years with high fruit load. Our results highlight an opportunity for farmers to accrue benefits by monitoring pollination services and crop production on their farms (Garratt *et al.*, 2019) and by employing appropriate management practices in those apple varieties and individual farms to limit pollination deficits and over-pollination. Furthermore, consistent multi-year assessments of insect pollinated crops would expand our understanding of crop pollination and limits to yield across the globe and implementing standardised methods across more sites, more varieties, and more years would provide important insights on the changing status of pollination services across space and time (Breeze *et al.*).

Conclusions

In this study, adopting apple as an example of an important insect pollinated crop, we show how assessment of pollination services can be used to quantify and compare pollination deficits across orchards. Such approaches could be applied to other insect pollinated crops to understand the extent of pollination service limitations on production. Moreover, orchardists can follow the example of fields, farms and regions where pollination is optimal, taking them as model systems to help develop management approaches that improve pollination services. Such approaches to matching pollination supply and demand are most effective when farmers are able to assess their own crop pollination status, allowing them to make management decisions on a field-by-field, and season-to-season basis. Supplementary and pollinator exclusion techniques can be adapted and made user friendly, allowing farmers to employ these techniques for their own crops (Garratt *et al.*, 2019). Ultimately if we are to understand and mitigate the consequence of pollinator declines globally, then we need to make assessments and take action locally, and the approaches identified in this study are a step towards this.

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Supporting Information

Additional supporting information may be found online at: [link to be added in production]

Open Research

Data sets (Garratt et al. 2021) analysed in this current study are available through the University of Reading Data Archive at: http://dx.doi.org/10.17864/1947.314

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Fig 1. Theoretical output achieved under different experimental treatments. (a) pollinator dependence i.e. the level to which insects could contribute to pollination, (b) pollination service i.e. the extent to which pollinator dependence is met by ambient pollination conditions, and (c) pollination deficits in apple pollination or production, i.e. the shortfall of ambient pollination below maximum potential pollination.

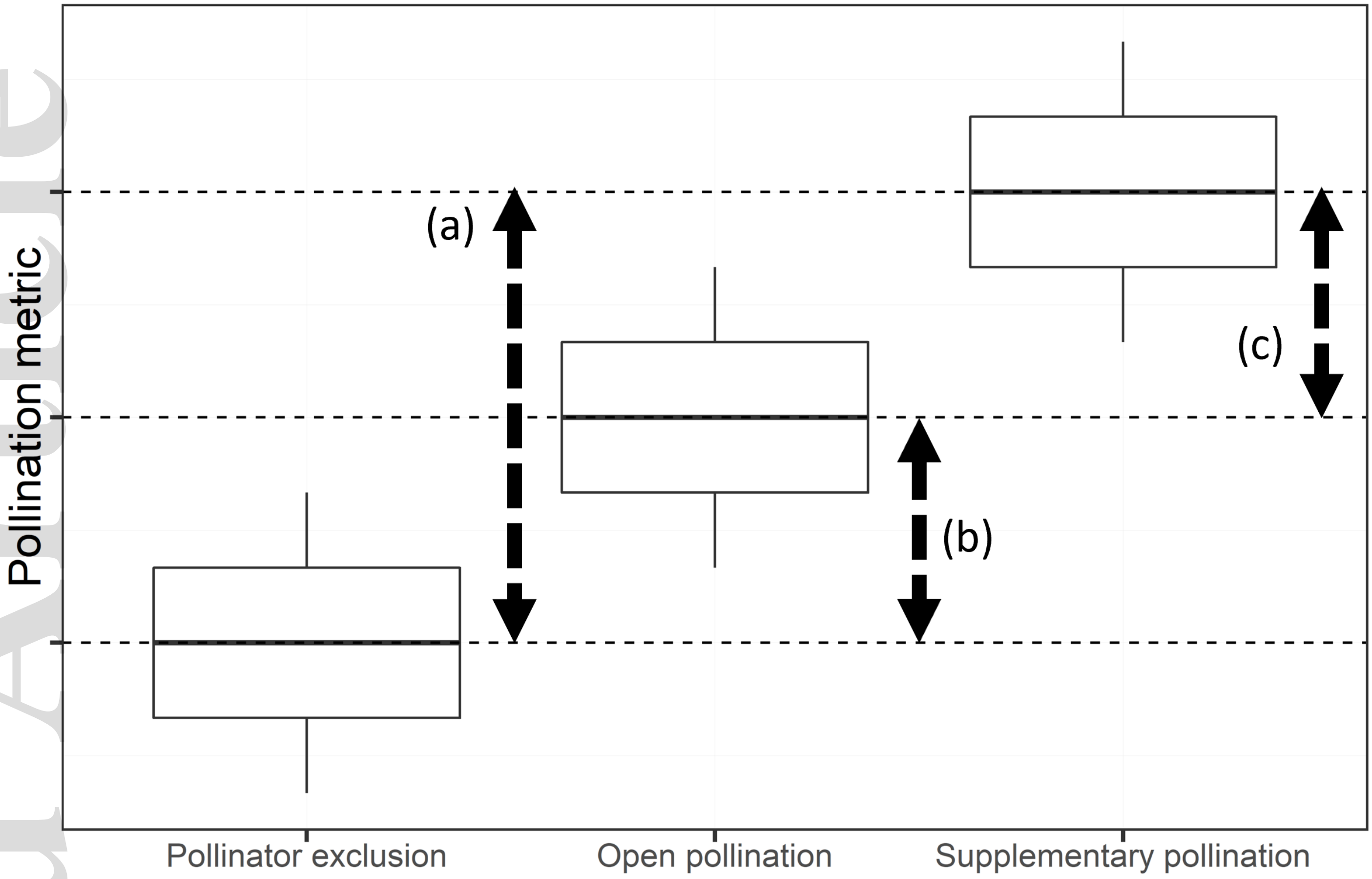
Fig 2. Deficits in yield due to sub-optimal pollination in orchards (individual points) separated by apple variety (colour) per country. Mean and 95% C.I. are shown for each variety within each country ('Various' refers to orchards made up of multiple varieties). A positive deficit occurs when yield is greater under supplementary pollination compared to open pollination treatments, and a negative deficit occurs when yield in open treatments is greater than for supplementary pollination. Points in circles represent individual orchards with a significant deficit in yield relative to the best performing orchard growing that variety in that country (i.e. the orchard with a pollination deficit closest to 0).

Fig 3. Relationship between pollination service (i.e. the current contribution of insects to yield) and pollination deficits (a shortfall in yield due to sub-optimal pollination) for apple orchards across countries and varieties. Linear model and 95% confidence limits shown.

Fig 4. The extent to which early fruit set (a) and seed number (b) of different apple varieties depend on pollination using available data from all orchards and countries. Mean pollinator dependence and 95% C.I. shown for each variety and grand mean across varieties shown as a dashed line. Varieties marked with '*' indicate those with significant differences found between supplementary pollination and pollinator exclusion treatments ($P < 0.05$).

Fig 5. The extent to which production of different apple varieties, measured as final fruit set (a), and fruit quality, in terms of firmness (b) and size (c), depend on pollination using available data from all orchards and countries. Mean pollinator dependence and 95% C.I. shown for each variety and grand mean for fruit set across varieties shown as a dashed line in (a). Varieties marked with '*' indicate significant differences between pollinator exclusion and supplementary pollination treatments ($P < 0.05$).

Fig 6. Relationship between metrics of pollination and production in different apple varieties including (a) seed number and apple size at harvest and (b) final fruit set and apple size at harvest for multiple apple varieties. Only varieties with greater than three data pionts included. Linear model and 95% confidence limits shown.



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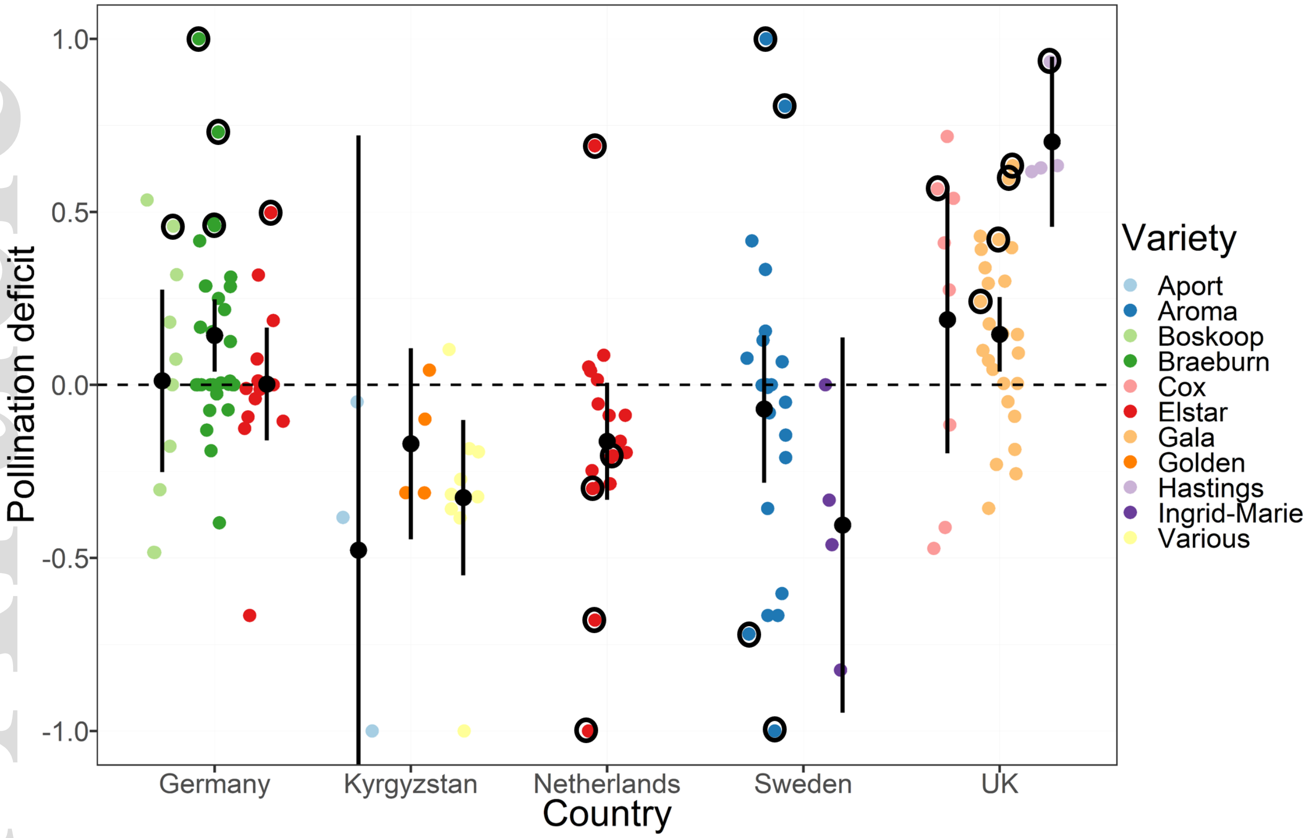

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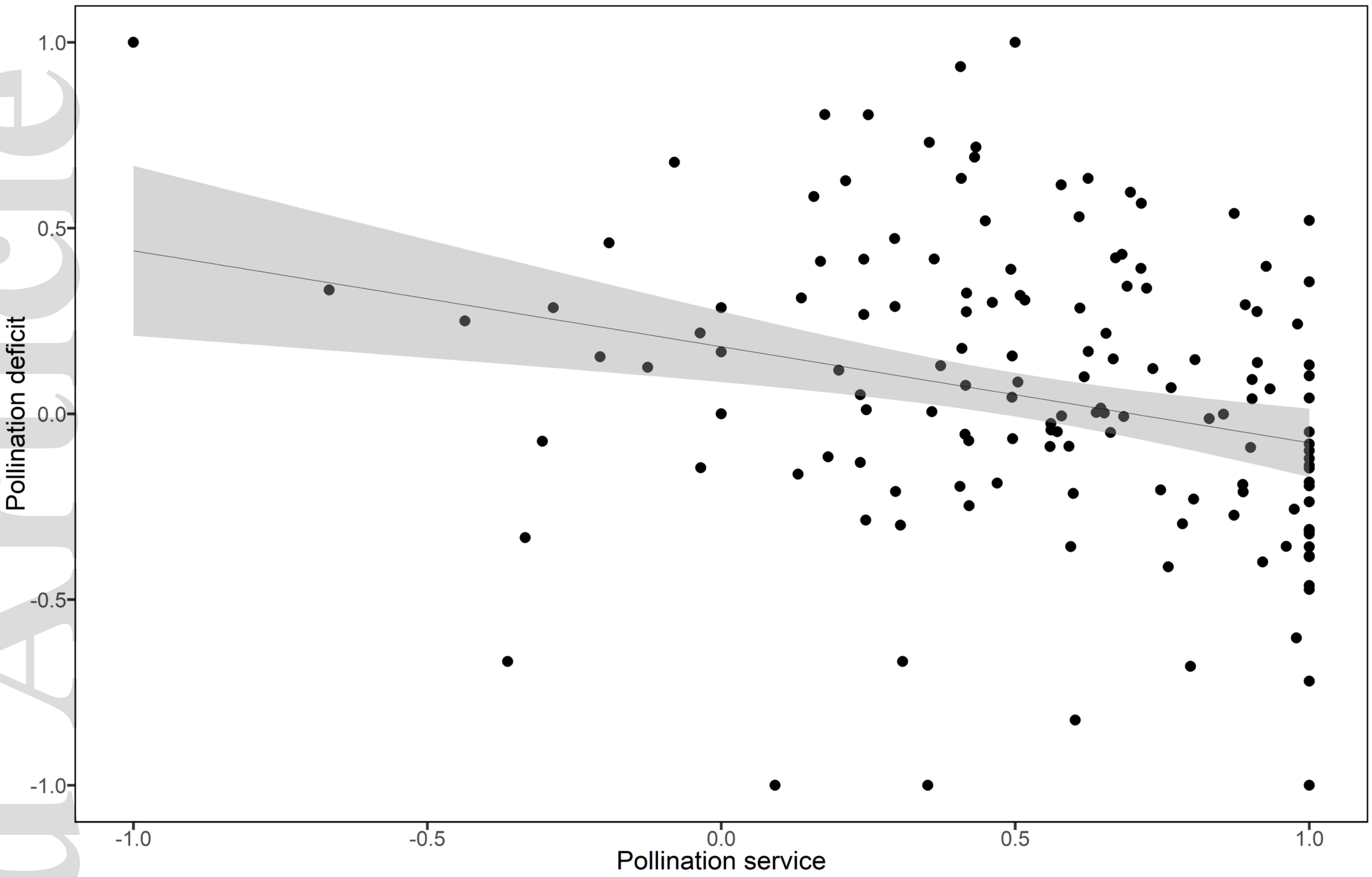

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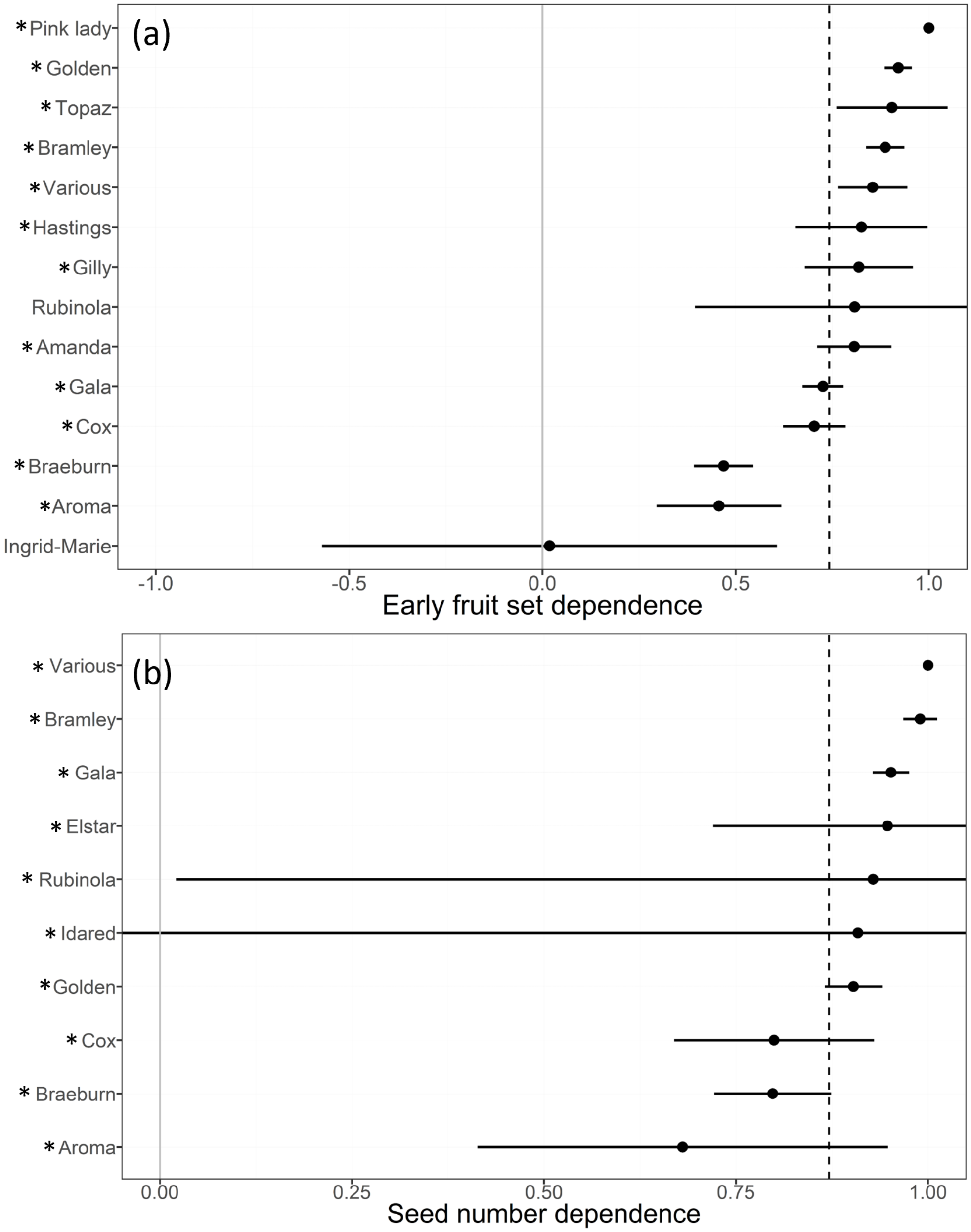

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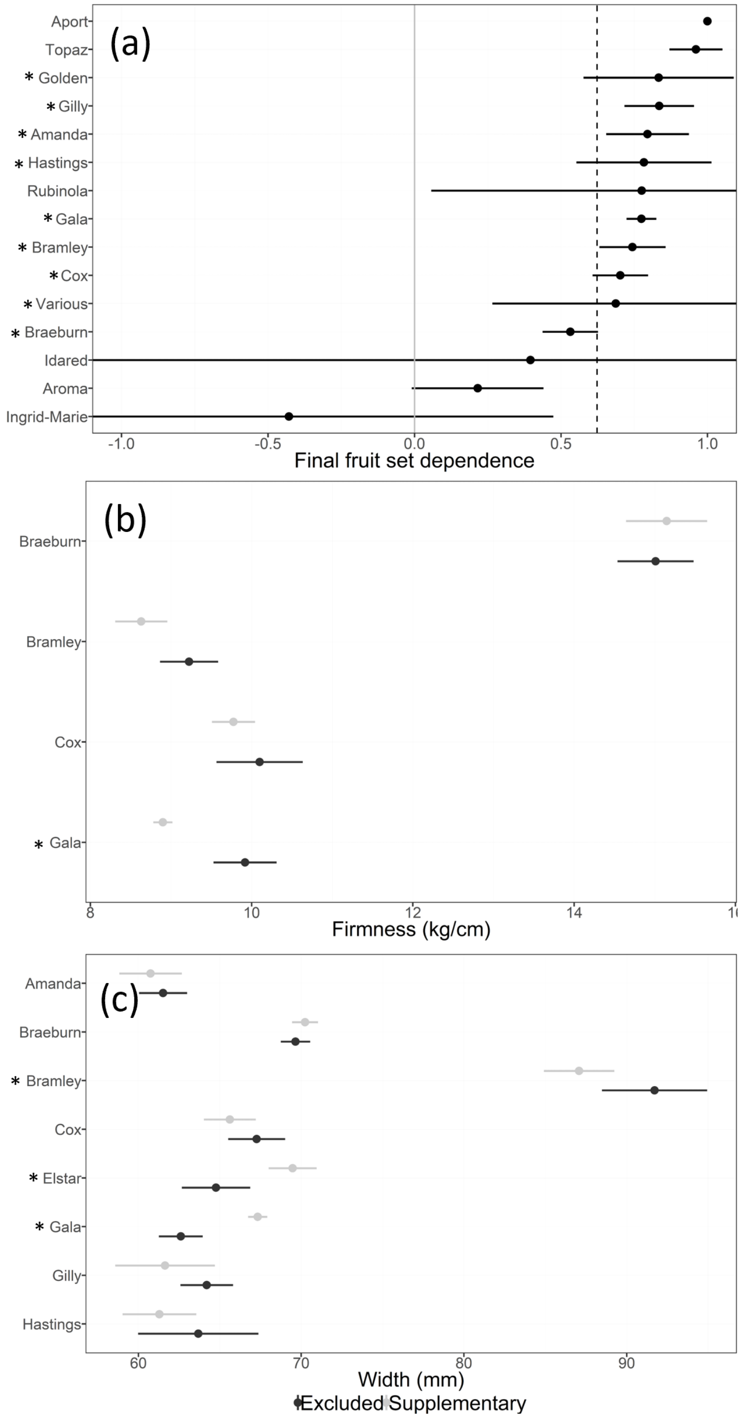

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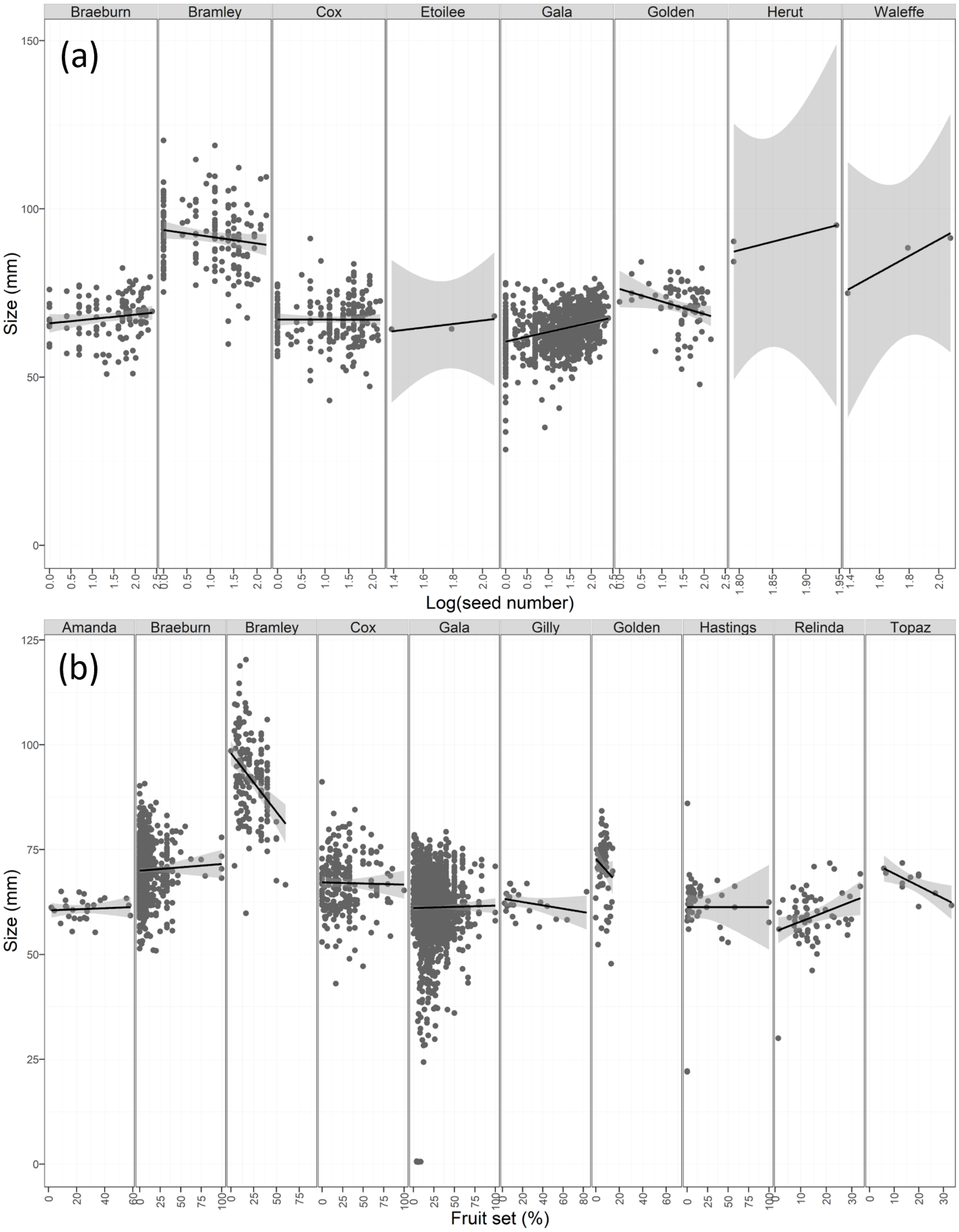

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