Insect pollination enhances yield stability in two pollinator-dependent crops

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ABSTRACT

One of the most important challenges facing global agriculture is to ensure an adequate, stable food supply while conserving soil, water and biodiversity. The yield stability of pollinator-dependent crops, such as pear and apple, can be negatively affected by variability of the pollination service, which in turn can reduce mean yield. We explored how mean crop yield and yield variability were affected by pollinators and variability in their provision of the pollination service. Over four seasons we conducted a manipulative experiment in six pear and eight apple farms; fruit set (i.e., no. fruits/ no. flowers) was compared between flowers exposed to pollinators and those excluded from pollinators. We also recorded pollinator visitation rate to exposed flowers. We estimated the mean levels and spatial and temporal variability of both pollinator visitation and yield response by calculating the mean values per farm and the spatial (i.e., across trees within farm) and temporal (i.e., across seasons within farm) coefficients of variation (CV) for visitation rate and fruit set. Despite homogeneous irrigation and fertilization, we found strong variability in fruit set in both crops (pear spatial and temporal CV: 0.57 and 0.4, respectively; apple: 0.62 and 0.52). Pollinator exclusion reduced mean fruit set considerably in both crops (pears: a reduction of 50%, apples: 71–92%), and increased spatial and temporal variability (pears: 296% and 197% for spatial and temporal variability, respectively; apples: 385% and 329%). Visitation rates in pears were positively associated with mean fruit set and negatively related to its spatial CV. Also, in this crop we found a positive relation between the spatial CV of visitation rate and fruit set. However, there was no evidence that visitation rate in open-pollinated apple flowers affected either mean fruit set or its spatial or temporal variability. Apple trees received one order of magnitude more visits per flower than pear trees, suggesting that in this system the pollination service meets the pollination demand of the apple crop. Overall, our results highlight the importance of management practices that prioritize pollination service, thus ensuring a high, stable yield.

1. Introduction

Ensuring a stable, adequate food supply while minimizing environmental degradation is one of the most important challenges facing global agriculture today. In fact, conventional intensification of agriculture has been successful in increasing yields in the short term, but this has come at the cost of high external subsidies and the deterioration of ecosystem functions like nutrient cycling, biological pest control and pollination (Krebs et al., 1999; Matson et al., 1997; Foley et al., 2005). In this way, conventional agriculture compromises future yields, decreasing their spatial and temporal stability (Deguines et al., 2014). Improving knowledge of the relation between ecosystem functions and crop yield is therefore key to dealing with the challenges of increasing crop productivity and stability.

Globally, ~70% of cultivated species depend to some extent on insect pollination (Klein et al., 2007). Furthermore, global agriculture has become increasingly pollinator-dependent, cropland expansion having been driven mainly by increasing the area devoted to

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pollinator-dependent crops (Aizen et al., 2008, 2009). Although the importance of abundant, diverse pollinator assemblages for the yield of pollinator-dependent crops has been amply confirmed (Garibaldi et al., 2013; Dainese et al., 2019), their role in crop stability has received less attention (e.g., Kremen et al., 2004, Klein, 2009, Geeraert et al., 2020). Two studies have reported patterns that point to animal pollination as a driving factor of yield stability in pollinator-dependent crops. First, Garibaldi et al. (2011a) found on a global scale that lower mean yield and higher temporal variability were associated with a higher degree of pollination dependence in crops. Second, Deguines et al. (2014) reported patterns on a country scale of reduced mean yield and higher spatial variability in highly pollinator-dependent crops along gradients of increasing agricultural intensification. Therefore, addressing how pollination function affects crop yield and stability over space and time is of paramount importance.

This question should take into account not only how crop yields and their spatial and temporal variability respond to the provision of pollination service (i.e., mean values), but also how these responses are influenced by variability in the pollination service itself. For instance, Geeraert et al. (2020) showed that non-*Apis* diversity increased temporal stability in coffee yields, while Klein (2009) showed that lower variability in bee richness close to forest edges was associated with high coffee yields and reduced spatial yield variability. These results highlight the influence of pollinator diversity and its spatio-temporal stability on crop yields and their spatial and temporal stability. However, since under the current dominance of conventional agriculture a large proportion of commercial crops rely almost exclusively on few or even a single pollinator species (mostly honeybees, Klein et al., 2007), we need a broader conceptual framework within which to study the variation in crop yields associated with variation in the quantitative aspect of pollination function (e.g., pollinator abundance or visitation frequency). Such a framework could be applied to different crop systems, regardless of species diversity or composition. Here we applied a conceptual framework that enabled us to simultaneously evaluate the effect of spatial and temporal variability in pollinator visits on spatial and temporal variability in fruit set in the pear and apple, two crops with great pollinator dependence (Klein et al., 2007).

Yield typically increases asymptotically with the addition of resources such as nutrients, water or pollen (Fig. 1, Rubio et al., 2003). The shape of this response has several consequences. First, within a certain range, increases in mean resource supply are expected to enhance mean yield (Fig. 2-A1). Second, increases in mean resource supply are expected to reduce variability in crop yield (Fig. 2-B1). Third, for a certain mean resource supply, mean yield is lower when resource supply variability is higher (higher coefficient of variation – hereafter CV) than expected, for a stable resource supply (lower CV); this is a consequence of what is known as Jensen's inequality (Fig. 2-C1, Ruel and Ayres, 1999). Finally, a more direct and less empirically assessed consequence is that yield variability is expected to increase with high variability of

Fig. 1. - General relation of yield (e.g., fruit x flowerˆ−1) to resource availability.

resource supply (Fig. 2-D1). Although the enhanced yields at high pollination service levels predicted by Fig. 2-A1 have been broadly confirmed (Aizen et al., 2009; Garibaldi et al., 2013; Klein et al., 2007), few studies have tested the other three relationships (Fig. 2-B1,C1,D1). Since pollination is not as frequently managed as fertilization or watering, yield variation in pollinator-dependent crops could be more strongly linked to variation in pollen supply (Garibaldi et al., 2011a, 2011b).

We aim to explore the influence of pollinators and variability in the provision of pollination service on mean crop yield and its variability. To this end, we constructed a 4-year time series of pollinator visitation rates and fruit set in the pear and apple. We evaluated the effect of pollinator exclusion and mean levels of visitation rate, plus the spatial and temporal variability of visitation rate, on fruit set mean levels and spatial and temporal variability of fruit set. We expect that mean fruit set will increase with pollinator access to flowers and mean visitation rate (Fig. 2-A1), and decrease with the visitation rate spatial and temporal CV (Fig. 2-C1). In addition, we expect that fruit set CV will decrease with pollinator access to flowers and mean visitation rate (Fig. 2-B1), and increase with visitation rate spatial and temporal CV (Fig. 2-D1).

2. Material and methods

2.1. Study system

This study was carried out during the austral growing seasons of 2015–2016, 2016–2017, 2017–2018 and 2018–2019 (hereafter 2016, 2017, 2018 and 2019, respectively), from flowering in September to harvesting in March. The study area is an irrigation valley that lies in the arid region of northern Argentine Patagonia, known as the 'Alto Valle de Río Negro y Neuquén' (Cabrera and Willink, 1973). This region concentrates ~90% of Argentinean pear and apple production (Avellá et al., 2018). Typically, the farms are managed conventionally, with high use of pesticides and fertilizers. Watering is achieved by completely flooding the plot, and tillage of top soil between tree rows is a recurrent practice. Pollination management involves the deployment of honeybee (*Apis mellifera*) hives around the orchards. In December, chemical thinning is carried out on the apple trees in order to reduce the development of small fruits. The abundance of wild pollinators during the flowering period of pears and apples is close to zero on these farms (Geslin et al., 2017; Hünicken et al., 2020; Pérez-Méndez et al., 2020).

The farms selected are near the locality of 'San Patricio del Chañar', Neuquén province (approx. 38°37′ S, 68°18′ W, Fig. S1). We took measurements on six pear farms and eight apple farms, in ten trees per farm in 2016, 2018 and 2019 and five trees per farm in 2017. All the farms of each crop were separated from each other by at least 1.5 km. All farms used field flooding for irrigation (except one, which used drip irrigation) and applied the same fertilizers (manure and foliar fertilizer). The trees on each farm were distributed in rows, each row containing a single variety, and alternating rows were of different varieties. All selected trees were from the same row, so the effect of distance to another variety was controlled for. The crop varieties selected were Packhams' Triumph for pear, and Red Delicious for apple, two typical varieties grown in this region. Both crops have perfect flowers (i.e., female and male organs in the same flower); they are largely self-incompatible, and depend on cross-pollination to set the fruit (Jackson, 2003; Maccagnani et al., 2003; Ramírez and Davenport, 2013). According to the categories of Klein et al. (2007), both crops are greatly dependent on pollinators (i.e., production decreases by 40–90% in the absence of pollinators). Although the flowers of both crops have nectaries, the amount and concentration of sugar differs: apple flowers produce a higher volume of nectar with higher sugar concentration than pear flowers (Farkas and Orosz-Kovács, 2003; Jackson, 2003; Maccagnani et al., 2007; Díaz et al., 2013).
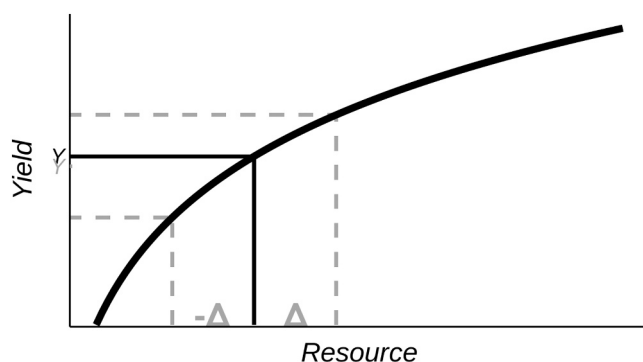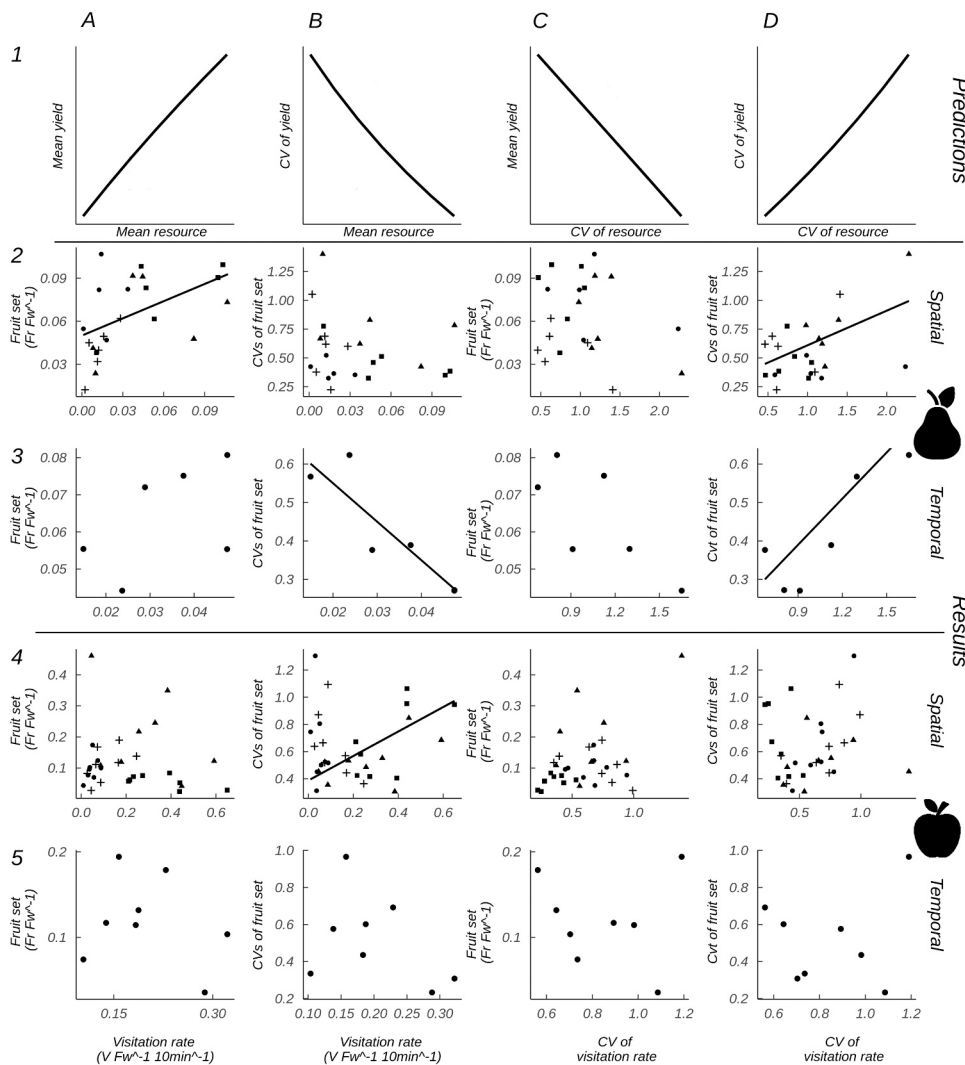
Fig. 2. - Predictions and results of the effect of visitation rate (mean and CV) on fruit set (mean and CV) of pears and apples. Row 1 shows the relations predicted of (A) Mean yield to mean resource. (B) Coefficient of variation in yield to mean resource. (C) Mean yield to coefficient of variation of resource. (D) Coefficient of variation of yield to coefficient of variation of resource. Please note that the relations predicted are not linear. Rows 2–3: results for pear; 4–5: apple. Rows 2 and 4 reflect the data used for the 'spatial variation models' and each symbol refers to a season (cross: 2016, circle: 2017, triangle: 2018, square: 2019). Rows 3 and 5 reflect the data used for the 'temporal variation models'. Regression lines were added when the effect of visitation rate (mean or CV) is statistically significant (p < 0.05). Visitation rate = Visit x Flower^− 1 x 10 min ^− 1, Fruit set = Fruit x Flower^− 1. Note the difference in scales in the x and y axes between rows.

2.2. Pollination treatment

To evaluate the effect of insect pollination, on each tree we excluded a number of pear and apple flowers from visits (pear mean ± SD: 22.6 ± 0.5; apple: 18.1 ± 0.6) (exclusion treatment), and marked a number of exposed pear and apple flowers (pear mean ± SD: 65 ± 2; apple: 46.6 ± 0.9) (open treatment). Sampled inflorescences were randomly located in the middle section of each tree. Exclusion was performed by covering 2 or 3 inflorescences with tulle bags (mesh size 2 mm). In total we followed 8054, 4631, 4522 and 4829 pear flowers and 4793, 2909, 4578 and 5830 apple flowers during seasons 2016, 2017, 2018 and 2019, respectively. When fruits ripened in February, we counted the number that had developed from flowers assigned to our open and exclusion treatments; this enabled us to estimate fruit set, defined as the ratio of developed fruits to tagged flowers. Beehives were placed on the road that separates the pear and apple trees, so distance to the hives was similar for both tree types.

2.3. Visitation rate

During each flowering season we surveyed flower visitation 2–6 times in all focal trees, between 9:00 am and 6:00 pm, when the temperature exceeded 15ºC. Two methods were used to assess visitation rate. In 2016 and 2017 we took measurements only in the flowers tagged for the 'open' treatment and recorded the number of visits made by each

insect over 10 min. Because of the low sensitivity of this method in detecting visits, in 2018 and 2019 we took measurements in a larger number of randomly selected inflorescences, counting the number of flowers and recording the number of visits made by each insect over 10 min. We categorized the visitors into the following functional groups: *A. mellifera*, bumblebees (*Bombus* sp.), hoverflies (Syrphidae), and other species. Over the first two seasons a mean ± SD of 16.7 ± 0.3 and 9.6 ± 0.2 flowers per tree were observed in each census on pear and apple, respectively. Over the second two seasons a mean ± SD of 34.1 ± 0.8 and 37 ± 1 flowers per tree were observed in each census on pear and apple, respectively.

2.4. Spatial and temporal variability

For both the variables measured (fruit set and visitation rate), we calculated the mean value across trees for each farm and season. In addition, we calculated the respective coefficients of variation (CV) by dividing the standard deviation by the mean value. We called this new variable spatial CV, since it reflects variation among trees within a farm. We used the mean values for each farm in each year to calculate the mean value by farm over the four seasons, and its respective CV. The latter was called temporal CV, as it reflects the variation among seasons within a farm. The scales selected (i.e., for both spatial and temporal variation within a farm) are relevant from an agronomic perspective, since producers are able to modify possible sources of this variation via

changes in their management practices.

2.5. Statistical analyses

We estimated linear mixed-effects models (LMM) and linear models (LM) with the 'nlme' package and 'base' package of R program, respectively (Pinheiro et al., 2016; R Core Team, 2018). We included the factor "Season" as a composite variable to control for climatic effects. Climatic variables for the years of our study are described in Table S1.

To analyze the effects of pollination on mean fruit set and its spatial variability, we performed two sets of models (Table 1 and S2). In the first we tested the effect of exclusion treatment, season, and the interaction between these variables, on mean fruit set and spatial CV of fruit set. In the second set of models, using data from only exposed flowers, we tested the effect of mean visitation rate, season, and the interaction between these variables, on mean fruit set and spatial CV of fruit set. We also tested the effect of visitation rate CV, season, and the interaction between these variables on mean fruit set and its spatial CV. Farm was set as a random factor in all models.

Regarding the effects of pollination on the levels and temporal variability of fruit set, we also performed two sets of models (Table 2 and S3). In the first we tested the effect of exclusion treatment on fruit set (mean and CV), and Farm identity was modeled as a random effect. In the second set of models, using data from only exposed flowers, we tested the effect of visitation rate (mean and CV) on fruit set (mean and CV).

The assumptions of normality, independence and homoscedasticity of all the models were visually checked (QQ-plot, predicted vs. residuals and histogram of residuals). Some variables were log transformed to achieve normality. We tested the significance ($p < 0.05$) of variables using the *Anova* function of 'car' package (Fox and Weisberg, 2011). When interaction was not significant, it was removed from the final model in order to make more accurate estimates of coefficients.

Table 1
– Chisq values of each predictor variable of the 'spatial variation' models. Chisq and p values were calculated with the *Anova* function of the car package. Chisq values whose p-values are lower than 0.05 are shown in bold type; chisq values whose p-values are lower than 0.1 are in italics. In the exclusion treatment model of apples, fruit set was log transformed to achieve normality.

		Pear		Apple	
	Predictor	Fruit set	Spatial CV of fruit set	Fruit set	Spatial CV of fruit set
Exclusion treatment models	Exclusion	**23.3*****	**59.0*****	**106*****	**301.3*****
	Season	**12.9****	7.0·	**15.2****	6.1
	Exclusion: Season	5.6	**14.5****	**28.8*****	**27.0*****
Visitation rate models	Visitation rate	**5.0***	3.6·	1.5	**7.2****
	Season	7.6·	**10.9***	**21.8*****	**8.4***
	Visitation rate: Season	0.5	0.3	2.7	4.2
Spatial CV of visitation rate models	Spatial CV of visitation rate	2.5	**6.5***	3.8·	3.4·
	Season	**13.4****	**10.3***	**15.6****	4.8
	Spatial CV of visitation rate: Season	1.3	7.1·	6.4·	**10.8***

· : $p < 0.1$;
* : $p < 0.05$;
** : $p < 0.01$;
*** : $p < 0.001$.

Table 2
– Chisq (exclusion models) and F- values (visitation rate – mean and CV – models) of each predictor variable of the 'spatial variation' models. Chisq, F- and p- values are calculated with the *Anova* function of the car package. Chisq or F-values whose p-values are lower than 0.05 are shown in bold type; chisq or F-values whose p-values are lower than 0.1 are in italics. In the exclusion treatment model of apples, fruit set was log transformed to achieve normality.

		Pear		Apple	
	Predictor	Fruit set	Temporal CV of fruit set	Fruit set	Temporal CV of fruit set
Exclusion treatment models	Exclusion	**28.4*****	**17.4*****	**52.4*****	**44.6*****
Visitation rate models	Visitation rate	1.9	**17.2***	0.4	1.2
Temporal CV of visitation rate models	Temporal CV of visitation rate	*5.1·*	**12.0***	0.1	0.2

· : $p < 0.1$;
* : $p < 0.05$;
*** : $p < 0.001$.

3. Results

3.1. Trends in visitation rate

The total number of observed visits differed greatly between the first two and the last two seasons, probably due to the different pollinator sampling methodologies. In flowering seasons 2016 and 2017, we observed a total of 548 visits to 45,810 flowers over a total of 2180 h of pear and apple flower monitoring, while in seasons 2018 and 2019 we observed a total of 10371 visits to 41,423 flowers over a total of 629 h. *Apis mellifera* accounted for almost all (99.7%) the visits to flowers of both crops. Visitation rate (visits per flower x 10 min^−1) was almost one order of magnitude higher in apple than in pear trees for both seasons 2016 and 2017 (apple mean ± SD: 0.092 ± 0.006, pear: 0.013 ± 0.001) and seasons 2018 and 2019 (apple mean ± SD: 0.36 ± 0.02, pear: 0.067 ± 0.006).

3.2. Effects of pollinator exclosure

In both crops the exclusion of pollinators had a statistically significant effect on mean fruit set (Tables 1 and 2, Fig. 3) and its spatial and temporal CV (Tables 1 and 2, Fig. 4). In pears we estimated a decrease of 50% in mean fruit set among pollinator-excluded flowers in both spatial and temporal models (Tables S2 and S3). In apples the exclusion treatment interacted with season (spatial models), so there were two years with reductions of almost 100% due to the exclusion (2016 and 2018) and one with a reduction of 30% (2019). Overall, we estimated a decrease in mean fruit set of 71% in excluded flowers (Table S2). In the temporal models, we estimated a decrease of 92% in the apple fruit set of excluded flowers (Table S3).

The spatial CV of fruit set strongly increased in both crops with pollinator exclusion, although this variable interacted with season (Fig. 4a, b). In pears we estimated an increase of between 155% and 496% in fruit set CV due to pollinator exclusion. In apples the estimated increase in the CV of fruit set due to exclusion was 248% and 495%, depending on the season (Table S2). Overall, the increase in fruit set spatial CV for the excluded flowers was 296% in pears and 385% in apples. The temporal CV of fruit set increased with exclusion by 197% for pears and 329% for apples (Fig. 4c,d, Table S3).

3.3. Effects of mean visitation rate

In the spatial models, the effects of mean visitation rate on fruit set (mean and spatial CV) were different in pears and apples. In pears we
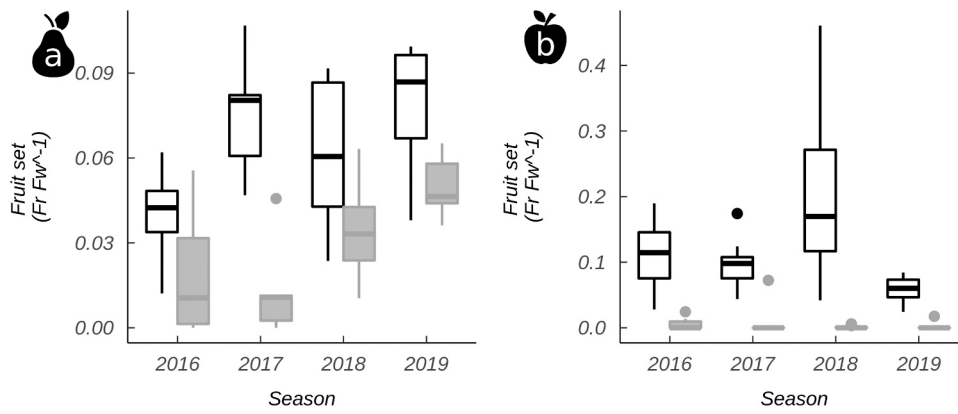
Fig. 3. - Effect of pollinator exclosure on mean fruit set of pears and apples. Left panels: pears, right panels: apples. (a) and (b) illustrate the data used for the 'spatial variation models'; (c) and (d) show the data used for the 'temporal variation models'. White boxes: open treatment, gray boxes: exclusion treatment. Boxes show the inter-quartile range (IQR), horizontal lines represent the median, and whiskers show the range of 1.5 *IQR. Mean fruit set = fruit x flower^−1. Note the difference in scales on the y axis between crops.
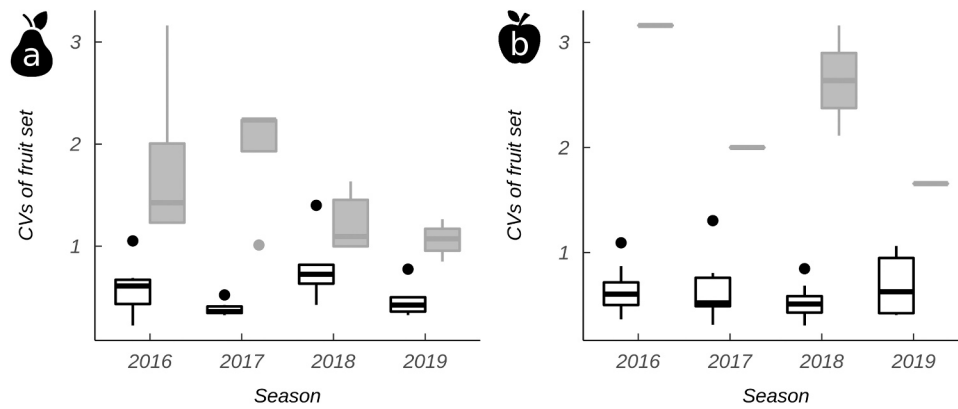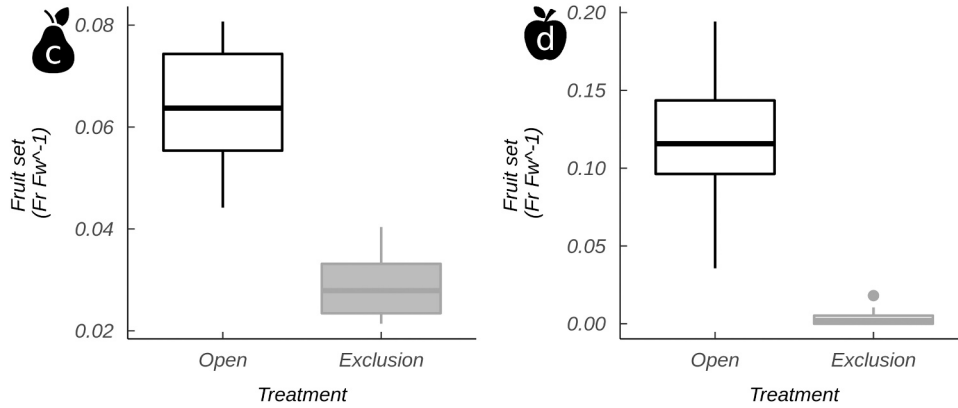

Fig. 4. - Effect of pollinator exclosure on the spatial and temporal coefficients of variation (CV) of fruit set in pears and apples. (a) and (b) illustrate the data used for the 'spatial variation models'; (c) and (d) show the data used for the 'temporal variation models'. White boxes: open treatment, gray boxes: exclusion treatment. Boxes show the inter-quartile range (IQR), horizontal lines represent the median, and whiskers show the range of 1.5 *IQR. Fruit set = Fruit x Flower^− 1, CV = standard deviation over mean.
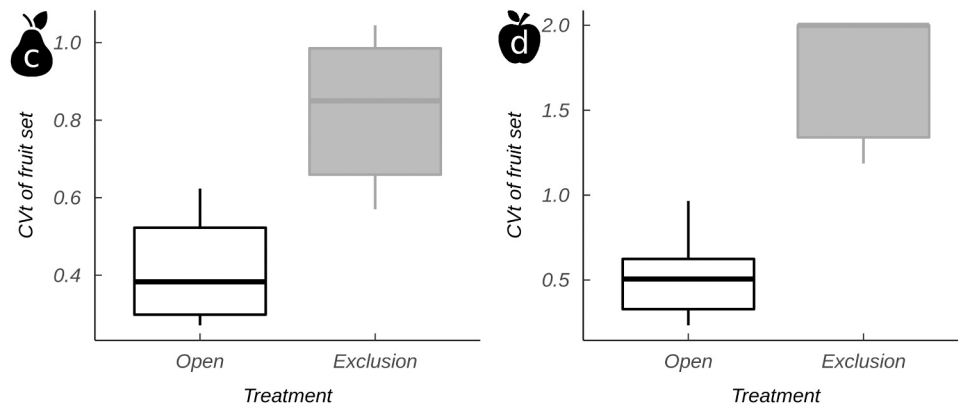
found a statistically significant increase in mean fruit set of 0.4 per unit of visitation rate (Fig. 2-A2, Table S2), while in apples mean visitation rate had a significant effect on the spatial CV of fruit set (Table 1, Fig. 2-B4). This effect was contrary to our predictions (i.e., spatial CV of fruit set increased 0.9 units per unit of visitation rate, Table S2). Interaction between mean visitation rate and season was non-significant for all models (Table 1).

Surprisingly, analysis of the temporal models did not show any significant effect of visitation rate on mean fruit set in either crop (Fig. 2-A3 and A5) or on the temporal CV of apple fruit set (Fig. 2-B5). However, we did find a statistically significant effect of mean visitation rate on the temporal CV of fruit set in pears (Fig. 2-B3, Table 2), as it decreased by 0.36 units per unit increase in visitation rate (Table S3).

3.4. Effects of CV of visitation rate

In the spatial models we found no statistically significant association between the spatial CV of visitation rate and the mean fruit set of either crop (Table 1 and Fig. 2-C2 and C4). Regarding the effect of the spatial CV of visitation rate on the fruit set CV, in pears we found a significant positive effect (an increase of 0.3 units per unit of visitation rate CV, Table S2, Fig. 2-D2) while in apples there was no significant effect (Table 1, Fig. 2-D4). Finally, in the temporal models the effect of the temporal visitation rate CV on fruit set (mean or temporal CV) was statistically significant only for the pear fruit set CV, showing an increase of 0.4 units per unit of visitation rate CV (Table 2, S3 and Fig. 2-C3, D3, C5 and D5).

4. Discussion

Our results show the important contribution of insect pollination to mean yield and yield stability over space and time in pears and apples. Despite homogeneous, managed watering and fertilization, large spatial and temporal variability was found in the pollination and yield of both crops. We found that the absence of pollinators decreased mean fruit set (Fig. 3) and increased its spatial and temporal variability (Fig. 4). Regarding the role of pollinator (honey bee) visits, the effect of mean visitation rate or their CVs on fruit set (mean and CVs) differed between the crops studied (Fig. 2).

The exclusion treatment simulates a "no pollinator" scenario. In the case of pears, we observed that it reduced fruit set by 50% in both spatial and temporal models. Moreover, this became more variable, the spatial and temporal CV of fruit set increasing by 296% and 197% with pollinator exclusion, respectively (Table S2 and Table S3). In apples, pollinator exclusion led not only to a greater reduction in fruit set than for pears (71% in spatial models and 92% in temporal models) but also to a more marked increase in spatial (385%) and temporal (329%) CV (Tables S2 and S3). This notable reduction in fruit set in both crops is consistent with their categorization as crops whose pollinator dependence is "great" (Klein et al., 2007). However, this category encompasses a wide range of pollinator dependencies (i.e., reductions in yield of between 40% and 90%). According to our results, fruit set in apples is more pollinator-dependent than in pears, almost reaching the category where the contribution of pollinators is "essential" (i.e., a reduction equal to or more than 90% in the absence of pollinators). Moreover, we showed that pollinators not only contribute to an increase in fruit set in both crops (Fig. 3), but also, and even more strongly, contribute to a reduction in spatial and temporal yield variability (Fig. 4). The difference in the magnitude of this effect between crops may suggest that the greater the contribution of pollinators to producing fruits in a crop, the greater their contribution to yield stability in space and time. While the correlation between crop pollinator dependence and the temporal variability of yield has been documented on a global scale (Garibaldi et al., 2011a), the relation with spatial variability shown here warrants further testing on different spatial scales.

Although the scenario of "no pollinators" is hypothetical, many

agricultural systems throughout the world are managed under conventional intensification, relying exclusively on hiring beehives to supply pollination demand (Klein et al., 2007, 2015; Ellis, 2012). This is the case of our study system, where ~99% of the insects visiting flowers were managed honeybees (Geslin et al., 2017; Hünicken et al., 2020; Pérez-Méndez et al., 2020). These results should serve as a warning that agricultural practices should be adjusted in order to ensure the presence of viable populations of wild pollinators, not only to increase crop yields but also to guarantee the spatial and temporal stability of these yields (see more detailed discussion below).

When we took the mean visitation rate or their CV as predictors, we found dissimilar effects between the fruit crops. In the case of pears, the effect of visitation rate on mean fruit set was statistically significant and consistent with our expectations (i.e., mean visitation rate increased mean fruit set (Fig. 2-A2, Table 1 and Table S2). Furthermore, the visitation rate spatial CV increased the fruit set spatial CV (Fig. 2-D2). A similar result was reported by Klein (2009) for bee-pollinated coffee: spatial variation in bee species richness on a farm scale decreased the mean fruit set and increased its spatial variation. In addition, the fruit set temporal CV decreases with an increase in visitation rate, and increases with an increase in the variability of visitation rate (Fig. 2-B3 and D3). Overall, the effects of pollination and its spatial and temporal variability in pears cannot be disregarded, as it is one of the major factors moderating fruit yield and stability, as shown here.

In the case of apples, the only statistically significant correlation between spatial variation in fruit set and visitation rate was contrary to our prediction (i.e., higher visitation rate was related to higher spatial CV in fruit set, Fig. 2-B4). One explanation could be that the visits received by apple blossoms were sufficient for optimal pollination, thus their high variation was compensated for. In fact, previous studies support this explanation, at least for the mean fruit set value. Hünicken et al. (2020) reported no effect of visitation rate on apple mean fruit set in this system, while the estimated visitation rate necessary for adequate pollination (0.092 visits per flower x 10 min^{-1}, Vicens and Bosch, 2000, Garibaldi et al., 2020) was exceeded by the first decile of visits to apple flowers in our study (0.14 visits per flower x 10 min^{-1}).

Our results suggest that producers should adopt practices that promote stability in visitation rates in order to improve mean crop yield and its stability. For instance, placing small groups of beehives throughout a farm could enhance the spatial stability of visits, as each tree would be close to a hive (Cunningham et al., 2016). A study in the faba bean (*Vicia faba*) found that yield was higher and its spatial variation lower in plants close to hives (Cunningham and Le Feuvre, 2013). Additionally, it is important to guarantee good quality beehives over the seasons, as this has a direct effect on the mean yield of pears and apples (Geslin et al., 2017). However, the management of honeybees alone is not sufficient for optimal pollination (Garibaldi et al., 2013, 2020).

While our study system relies exclusively on honey bee visits, a diverse pollinator assemblage can improve the mean yield and spatial or temporal stability of pollinator-dependent crops through several mechanisms. For example, spatial stability on a farm scale may be enhanced by different pollinator species since they are likely to have differing flight ranges and complement each other by visiting different sectors of the farm (Woodcock et al., 2013; Garratt et al., 2018). It is also possible that a species enhances its pollination efficacy in the presence of another species, via behavioral changes (Brittain et al., 2013; Eeraerts et al., 2020; Winfree and Kremen, 2009; Woodcock et al., 2013). Temporal stability between seasons could be improved due to natural uncoupled fluctuations in population abundance among different species (e.g., species that respond differently to rainy years) (Hoehn et al., 2008; Blüthgen and Klein, 2011). A previous study in this system reported that apple yield increased with the presence of both a native bumble bee and honeybees in comparison to honeybees alone (Pérez-Méndez et al., 2020). Furthermore, Kremen et al. (2004) found that both the amount and stability of watermelon pollination by native bees increased with the proportion of natural habitat in the landscape,

and recommended the conservation of these habitats to reduce farmers' reliance on managed honeybees; this would reduce both production costs and risks to farmers, while increasing not only food security for society (Garibaldi et al., 2011b), but also biodiversity in agricultural landscapes. All in all, high variability in yield can be reduced by boosting pollinator diversity, which highlights the importance of insect pollination, as shown by previous studies (Klein, 2009; Geeraert et al., 2020). Hence, producers should go beyond one species of managed pollinator and incorporate changes in land use to enrich the pollinator assemblage.

It is important to consider the social and economic consequences of yield variability, given that food stability is a dimension of food security (McGuire et al., 2015; Pinstrup-Andersen, 2009). On the producers' side, unstable harvests imply unpredictable monetary income and lead to variability in market supply. On the consumers' side, this instability has two major consequences: fluctuations in the offer of food and volatility of prices (Wheeler and von Braun, 2013; Wossen et al., 2018). While the effect of pollination on production has been evaluated in economic terms on different scales (Gallai et al., 2009; Giannini et al., 2020; Garratt et al., 2014; Borges et al., 2020; Geslin et al., 2017), the implications of variability in the pollination service for the farmers' profit and the market price warrants more attention.

5. Conclusion

Year after year, producers managing homogeneous crop systems invest strongly in fertilization and pest control. However, when cultivating pollinator-dependent crops, these systems seem to present great variability in yield due to fluctuations and deficiencies in pollinator visits to crop flowers. The results presented here demonstrate the importance of management practices that promote sufficient, stable pollination services that generate yields which are not only higher, but also more stable.

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CRediT authorship contribution statement

LAG and PLH conceived the idea and LAG, GA, NG and PLH designed the study. PLH, NG and GA collected the data. PLH analyzed the data with substantial input from LAG. PLH and CLM led the writing of the manuscript with input from MAA. All authors gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107573.

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