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Large-scale trade-off between agricultural intensification and crop pollination services

Nicolas Deguines[1*], Clémentine Jono[1], Mathilde Baude[2,3], Mickaël Henry[4,5], Romain Julliard[1], and Colin Fontaine[1]

Unprecedented growth in human populations has required the intensification of agriculture to enhance crop productivity, but this was achieved at a major cost to biodiversity. There is abundant local-scale evidence that both pollinator diversity and pollination services decrease with increasing agricultural intensification. This raises concerns regarding food security, as two-thirds of the world's major food crops are pollinator-dependent. Whether such local findings scale up and affect crop production over larger scales is still being debated. Here, we analyzed a country-wide dataset of the 54 major crops in France produced over the past two decades and found that benefits of agricultural intensification decrease with increasing pollinator dependence, to the extent that intensification failed to increase the yield of pollinator-dependent crops and decreased the stability of their yield over time. This indicates that benefits from agricultural intensification may be offset by reductions in pollination services, and supports the need for an ecological intensification of agriculture through optimization of ecosystem services.

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The development of new farming methods since the 1960s, such as increased mechanization, monoculture systems, higher levels of inputs (ie water, chemical fertilizers, pesticides), and selection of high-yield crop strains (Tilman *et al.* 2002), has promoted agricultural intensification. As limits to crop productivity were raised, agricultural intensification increased global food production and reduced world hunger (Tilman *et al.* 2002).

However, these benefits came at a cost to biodiversity (Krebs *et al.* 1999), as agricultural intensification reduced habitat quality at local scales and resulted in simplified agricultural landscapes with lower habitat diversity and availability (Tscharntke *et al.* 2005). Habitat degradation results in a decrease in biological diversity, which may in turn reduce the provision of ecosystem services (Cardinale *et al.* 2012). In particular, there is evidence that pollinator diversity has declined over time (eg Biesmeijer *et al.* 2006), in part driven by agricultural intensification (Potts *et al.* 2010). A meta-analysis of local-scale experiments found that pollination services delivered to crops (Figure 1) decrease with isolation from natural habitats, lowering both crop yields and the stability of those yields over time (Garibaldi *et al.* 2011).

These findings are a matter of concern in terms of future food security (Allen-Wardell *et al.* 1998), since 35% of global crop production grown for human consumption derives from crops that depend to some extent on pollination services (Klein *et al.* 2007). Aizen *et al.* (2009) estimated that 3–8% of world crop production could be lost in the absence of pollinators. To date, however, such estimates remain speculative because locally declining pollination services do not seem to translate into a global decrease in the yield of pollinator-dependent crops (Aizen *et al.* 2008; Ghazoul and Koh 2010). From both the conservation and food security perspectives, it appears critical to ascertain whether the local effects of agricultural intensification on the yield of pollinator-dependent crops and yield stability could scale up, to become a matter of national political concern. The country-level scale is particularly relevant since directives regarding agricultural and conservation objectives are often issued nationally.

In the present study, we undertake a country-wide assessment of the productivity of crops with various degrees of pollinator dependence and cultivated across a gradient of agricultural intensification. We discuss the implications of our results for the management of agricultural lands and practices in Western Europe.

Methods

As the aim of agricultural intensification is to enhance crop productivity (Tilman *et al.* 2002), we would expect increases in yield and decreases in yield variability with rising levels of agricultural intensification. Because intensification methods also have negative impacts on pollinator communities (Garibaldi *et al.* 2011), we would expect to see effects on both yield and yield variability to diminish with increasing crop dependence on pollinators. We tested these hypotheses using a long-term, large-scale crop production dataset from France.

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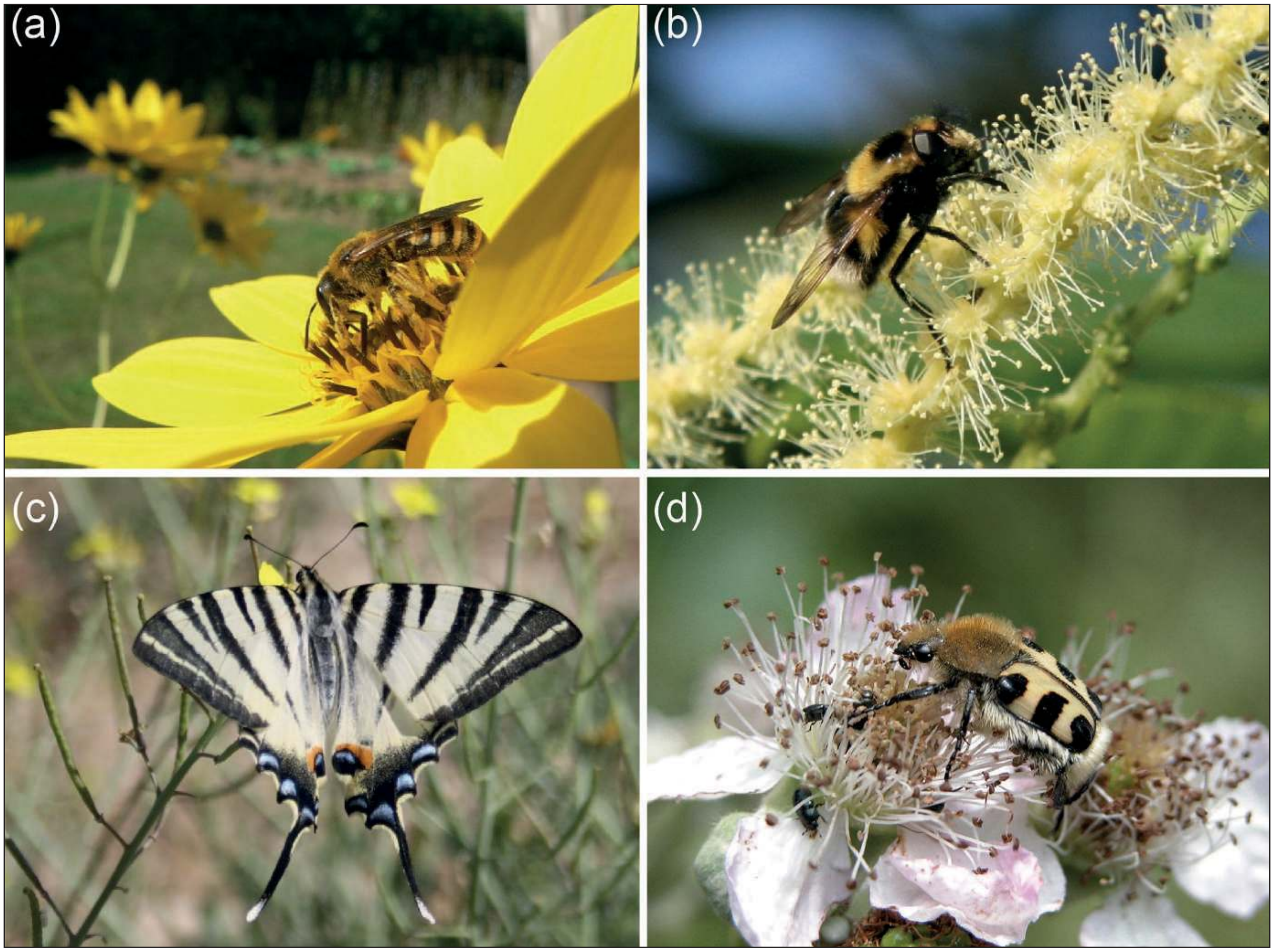

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Figure 1. *Pollination services are provided by pollinators visiting flowers of pollinator-dependent crops: (a) halictid bee (Halictidae, Hymenoptera) on Jerusalem artichoke (*Helianthus tuberosus*); (b) syrphid fly (Syrphidae, Diptera) on chestnut tree (*Castanea sativa*); (c) scarce swallowtail (*Iphiclides podalirius*, Lepidoptera) on rapeseed (*Brassica napus*); and (d) scarab beetle (*Trichius zonatus*, Coleoptera) on bramble (*Rubus *sp). In Europe, these four Orders of insects – Hymenoptera, Diptera, Lepidoptera, and Coleoptera – are the main pollinators.*

Crop dataset, measures of productivity, and pollinator dependence

From 1989 to 2010, statistics for the annual yields of 68 crops were provided by the Service de la Statistique et de la Prospective du Ministère de l'Agriculture et de l'Agroalimentaire (http://acces.agriculture.gouv.fr/disar/faces/) for each of the 22 regions of France (average area of administrative areas: 24 974 km²). We selected 54 crops that had been grown in a minimum of ten regions and for at least 10 years within each region, during the 1989–2010 period (see WebTable 1 for details).

For each crop, we estimated the regional yield and yield instability using the mean annual yield and the coefficient of variation of the yield (hereafter called "mean yield" and "yield variability", respectively). Specifically, for each crop in each region, we first performed a linear regression of crop yield against years. To account for annual yield improvement, we extracted the residuals from the regression, to which we added the predicted yield at year "1999.5" (ie the middle of our dataset's time frame) to avoid negative yield values. Mean yield was calculated as the mean of the residuals, whereas yield variability was the standard deviation of the residuals divided by the mean yield times 100. Finally, separately for each crop, mean yield and yield variability across the 22 regions were standardized (ie *z*-transformed) to allow comparisons among crops:

$$z\text{-scores} = \frac{y_i - \bar{y}}{\mathrm{SD}_y}$$

where y_i is either the regional mean yield or yield variability, $\bar{y}$ is the average of either the regional mean yield or yield variability across the 22 regions, and SD_y is the standard deviation of either the regional mean yield or yield variability across the 22 regions.

We followed Klein *et al.* (2007) by classifying crops based on their level of pollinator dependence. On the basis of the percentage of yield reduction resulting from an absence of pollinators, we classified crops into one of

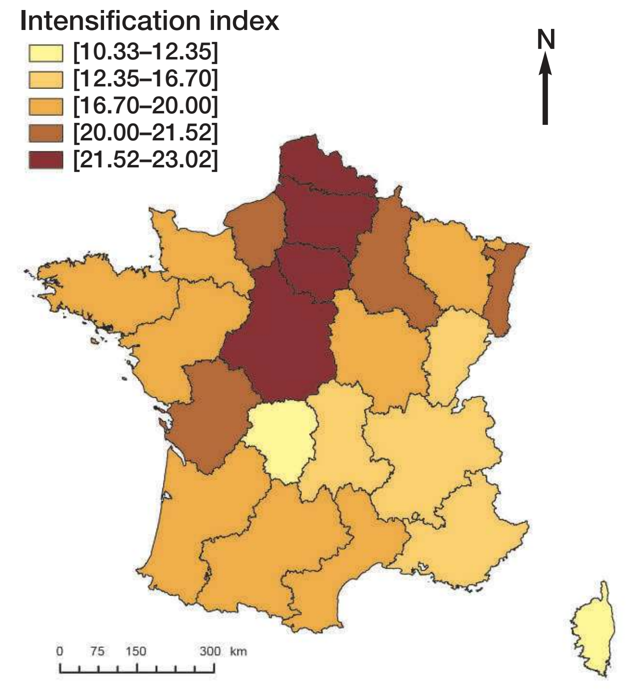

***Figure 2.** Map showing levels of agricultural intensification (intensification index) in the 22 administrative regions of France (areas range from 8336–45 723 km^2).*

the following dependence categories: none–0 (0% yield reduction), little–5 (< 10% yield reduction), modest–25 (10–39% yield reduction), great–65 (40–89% yield reduction), and essential–95 (≥ 90% yield reduction) (Table 1; WebTable 1).

Regional level of agricultural intensification

The level of agricultural intensification for each region (hereafter "intensification index") was derived from the High Nature Value indicator (Pointereau *et al.* 2007, 2010). The intensification index aggregates three components estimated at the municipality level (administrative areas within regions; average area: 15 km^2): "Crop diversity" (a proxy for the crop rotation system), "Extensive farming practices" (an estimation of pesticide inputs, levels of irrigation, and use of mineral fertilizers), and "Landscape elements" (an estimation of semi-natural habitat availability; eg hedgerows, forests, traditional orchards). Each component is scored from 0 (low intensity; ie high diversity of crops and large crop rotation system, low levels of inputs, or high availability of semi-natural habitats) to 10 (high intensity; ie low diversity of crops and short crop rotation system, high level of inputs, or poor availability of semi-natural habitats). The three scores are summed to obtain the intensification index (at the municipality level, intensification index averages 17.81 and ranges from 0 to 29). Because both local- and landscape-scale characteristics of agricultural intensification are included (Tscharntke *et al.* 2005), this index constitutes a comprehensive index of agricultural intensification.

To obtain the intensification index for each of the 22 regions of France (Figure 2), we calculated the mean intensification index of municipalities in a region, weighted by their agricultural area. Crops from all five levels of pollinator dependence covered areas involving very similar, large-scale gradients of intensification index (Table 1).

Data analyses

We tested our hypotheses using linear mixed models that included as the response variable either mean yield or yield variability, and as explanatory variables the level of pollinator dependence of crops (as a continuous variable), the intensification index, and the interaction between pollinator dependence and intensification. To take into account that crops may respond differently to agricultural intensification and that some crops originated from the same species, we included crop name nested within crop species as a random term on the intercept and the slope of the intensification index variable. Assumptions of homoscedasticity (homogeneity of variance) and normality of the residuals of our models were met. Residuals of the models were spatially independent. We performed *F* tests within Type III univariate analysis of variance to investigate the effects of the explanatory variables.

Results

We found a significant effect of the interaction between crop pollinator dependence and the intensification index on mean yield (degrees of freedom [df] = 1, $F = 22.365$, $P < 0.001$; WebTable 2), indicating that changes in mean yield with the intensification index depend on the crop's level of pollinator dependence (Figure 3, a–e). As expected, the mean yield of pollinator-independent crops increased with increasing intensification index, but this relationship weakened with increasing level of pollinator dependence, with the mean yield of highly pollinator-dependent

Table 1. Five levels of crop pollinator dependence together with a set of variables associated with their extent in France

Level of pollinator dependence	*Number of crops*	*Mean number of regions growing these crops*	*Mean total area under these crops (ha)*	*Mean (min–max) intensification index where these crops are grown*
0	12	20.67	776 298.47	18.94 (10.03–23.02)
5	5	16.60	12 025.21	18.96 (10.03–23.02)
25	10	17.90	304 738.75	18.98 (10.03–23.02)
65	23	17.52	8265.64	18.93 (10.03–23.02)
95	4	15.25	6027.51	18.55 (10.03–23.02)

Notes: The "intensification index" is the level of agricultural intensification at the regional scale. Particulars for individual crops are provided in WebTable 1. For more details, data are freely available from http://acces.agriculture.gouv.fr/disar/faces/.

crops remaining unchanged along the gradient of the intensification index. In other words, intensive agriculture increased the mean yield of crops with little or no pollinator dependence but failed to do so for highly pollinator-dependent crops.

Regarding yield stability, we also found a significant effect of the interaction between crop pollinator dependence and the intensification index on yield variability (df = 1, $F = 29.486$, $P < 0.001$; WebTable 2), showing that changes in yield variability with the intensification index depend on the level of pollinator dependence of the crop (Figure 3, f–j). Yield variability of pollinator-independent crops decreased with increasing intensification index, but increased for crops with high levels of pollinator dependence. This suggests that agricultural intensification led to crops with low pollinator dependence having more stable yields across years. However, intensive agriculture decreased yield stability in highly pollinator-dependent crops, strongly suggesting that a key resource needed by these crops is destabilized by agricultural intensification.

There appears to be a gradual shift along the gradient of crop pollinator dependence in the response of mean yield and yield variability to the intensification index, in spite of an "inversion" between regression lines of level 5% and 25% (the 25% regression slopes being steeper than the 5% regression slopes; Figure 3).

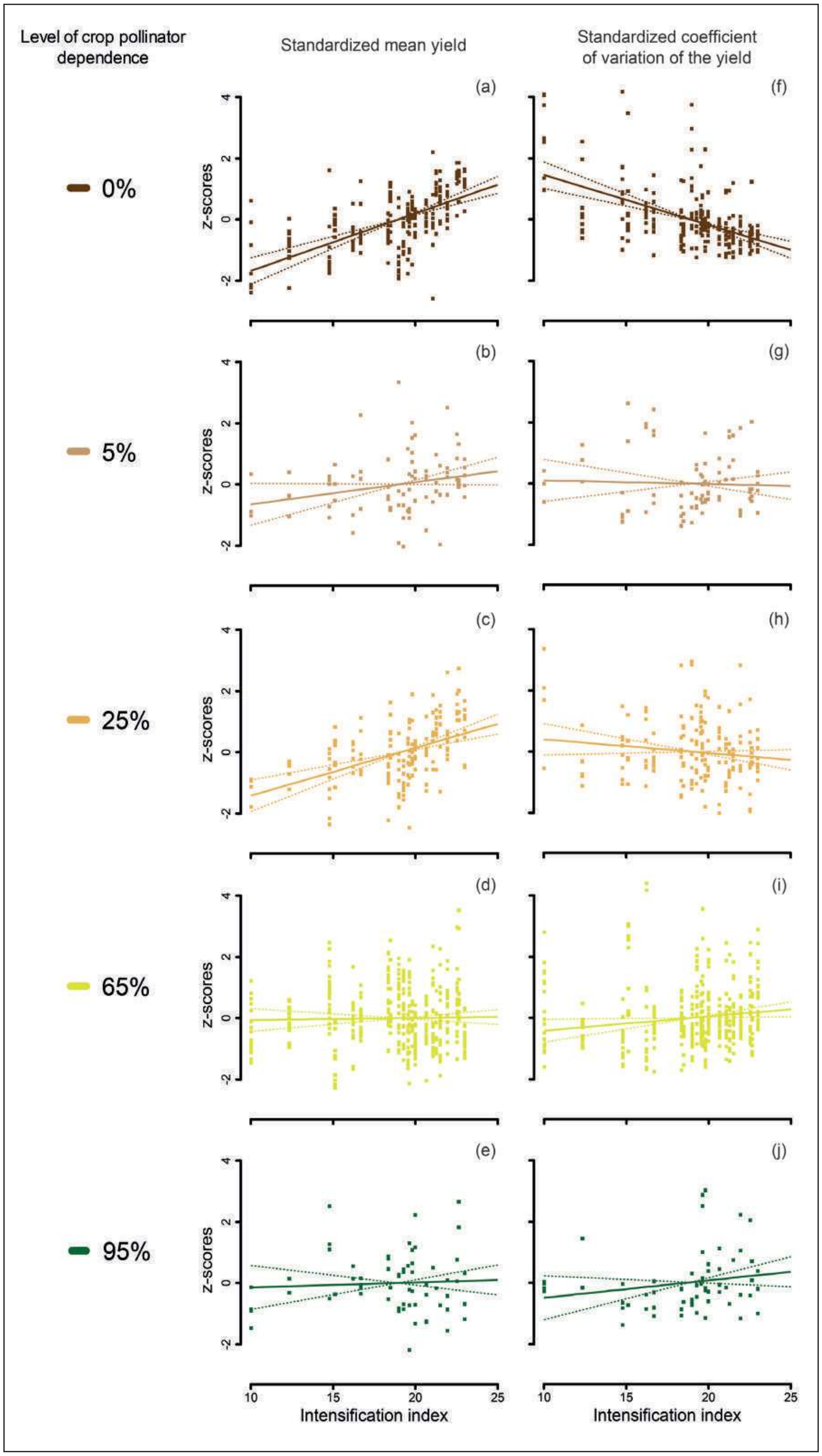

Figure 3. *Changes in mean yield (a–e) and yield variability (f–j) along the intensification index for each level of crop pollinator dependence. Squares represent crop data, solid lines represent the regression lines for each level of crop pollinator dependence, and dotted lines delineate the 95% confidence intervals of each regression slope. To represent data with high accuracy, we retrieved estimates of solid and dotted lines from linear mixed models similar to the ones described in the methods but included the level of crop pollinator dependence as a factor variable with five levels (Table 1). WebFigures 1 and 2, respectively, depict changes in mean yield and yield variability along the intensification index for each of the 54 crops.*

Discussion

Our results revealed that at the national scale, agricultural intensification increases the yield of crops with low or no pollinator dependence but failed to increase the yield of highly pollinator-dependent crops. Similarly, the effect of agricultural intensification on yield temporal stability ranges from positive for crops with little or no pollinator dependence to negative for crops that are highly dependent on pollinators. Although we did not directly assess the effect of agricultural intensification on pollinator diversity and abundance, the clear link with pollinator dependence strongly suggests a trade-off between agricultural intensification and crop pollination services across France; for pollinator-dependent crops, the expected benefits from agricultural intensification are offset by the reduction in pollination services. This finding is further supported by numerous studies highlighting a negative impact of agricultural intensification on local pollinator communities (Kennedy *et al.* 2013). Moreover, given the wide range of climatic conditions occurring in France (across the Atlantic, Continental, Mediterranean, and Alpine biogeographic regions), the similarities in agricultural intensity (as indicated by levels of fertilizers and pesticides, according to the UN Food and Agriculture Organization [FAOSTAT 2013]), and the set of crops (~70% of French crops considered are also cropped in one-half of the European countries; FAOSTAT 2013), our results may be representative of Western European agriculture as a whole. At the scale used in our analysis, the three components of the intensification index ("Crop diversity", "Extensive farming practices", and "Landscape elements") were highly correlated, making their respective effects indistinguishable from each other. To overcome this problem, researchers will need to conduct such large-scale analysis at finer spatial resolutions. Changes through time in the impact of agricultural intensification on pollination services are another key aspect to investigate if we are to anticipate future limitations on the productivity of pollinator-dependent crops.

Whether a decline in pollinator diversity and abundance translates into a decrease in the production of pollinator-dependent crops, which would define a state of "pollination crisis" (Ghazoul 2005), is an ongoing debate (eg Allen-Wardell *et al.* 1998; Steffan-Dewenter *et al.* 2005; Ghazoul and Koh 2010). So far, global assessments have not shown any negative effects on pollinator-dependent crop productivity as a result of a pollination shortage (Aizen *et al.* 2008) or agricultural intensification (Ghazoul and Koh 2010). This could be attributed to spatial and temporal variations in climate, soil fertility, and pollination management that are encompassed by global-scale datasets and that might mask any differences in the provision of pollination services by wild pollinators. Additionally, overlooking the varying levels of pollinator dependence (ie solely contrasting pollinator-independent versus pollinator-dependent crops; Aizen *et al.* 2008; Ghazoul and Koh 2010) prevented the detection of the gradual changes revealed in our study, from pollinator-independent to highly dependent crops. Here, we have demonstrated how the trade-off between the delivery of pollination services and the provision of other resources through intensive agriculture is consistent enough to limit crop yield and yield stability at a national scale. This underlines how the negative effects of agricultural intensification on biological diversity can result in changes to the factors limiting crop production, from nutrients, water, and pest control to pollination services (Bommarco *et al.* 2013), and suggests that further conventional agricultural intensification would be an inefficient method to increase the production of pollinator-dependent crops. Furthermore, for many crops, because the loss of pollination services cannot be compensated by managed honeybees (*Apis mellifera*), wild pollinators remain essential (Breeze *et al.* 2011; Garibaldi *et al.* 2013).

The global challenge of balancing food production with biodiversity conservation is linked to the question of whether natural areas and agricultural lands should be kept separated (the "land-sparing" approach) or integrated (the "land-sharing" approach) (Tscharntke *et al.* 2012). Proponents of land sparing argue for an increase in crop yield per area through farming intensification, thereby *sparing* natural areas from conversion to agricultural lands, whereas land-sharing advocates believe that both agriculture and biodiversity can exist on the same land. Our findings suggest that for highly pollinator-dependent crops, land sparing would not lead to higher yields, and that land sharing would increase yield stability over time. Different approaches to agricultural land management should therefore be developed based on each crop's level of pollinator dependence. The national scale of our findings is of particular relevance here, since country-level decisions are needed to respond to this global issue.

Our results add to the growing body of work suggesting that conventional intensive agriculture is not always necessary to maximize crop production efficiency (Seufert *et al.* 2012) and supports the need for a sustainable agriculture approach that can meet the dual challenge of feeding humanity without further diminishing Earth's biodiversity (Tilman *et al.* 2002; Tscharntke *et al.* 2012). Researchers and policy makers must develop ecologically based agricultural intensification that would maximize yield by taking full advantage of both ecosystem services and anthropogenic practices (Bommarco *et al.* 2013). The next steps should be to focus on understanding how enhanced pollination and other ecosystem services (Isaacs *et al.* 2009) affect various crop production systems, and how these can be integrated into sustainable agricultural strategies.

Acknowledgements

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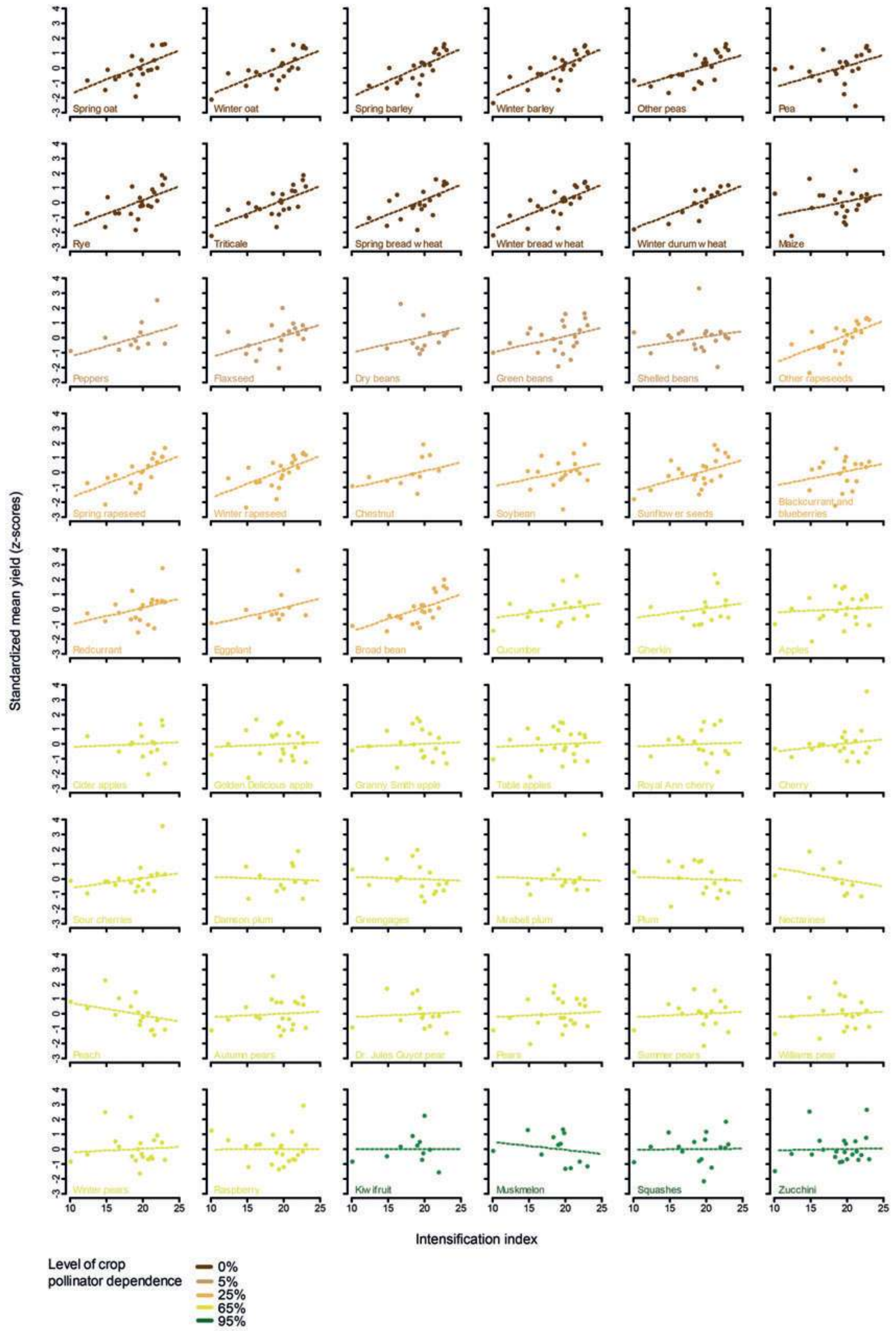
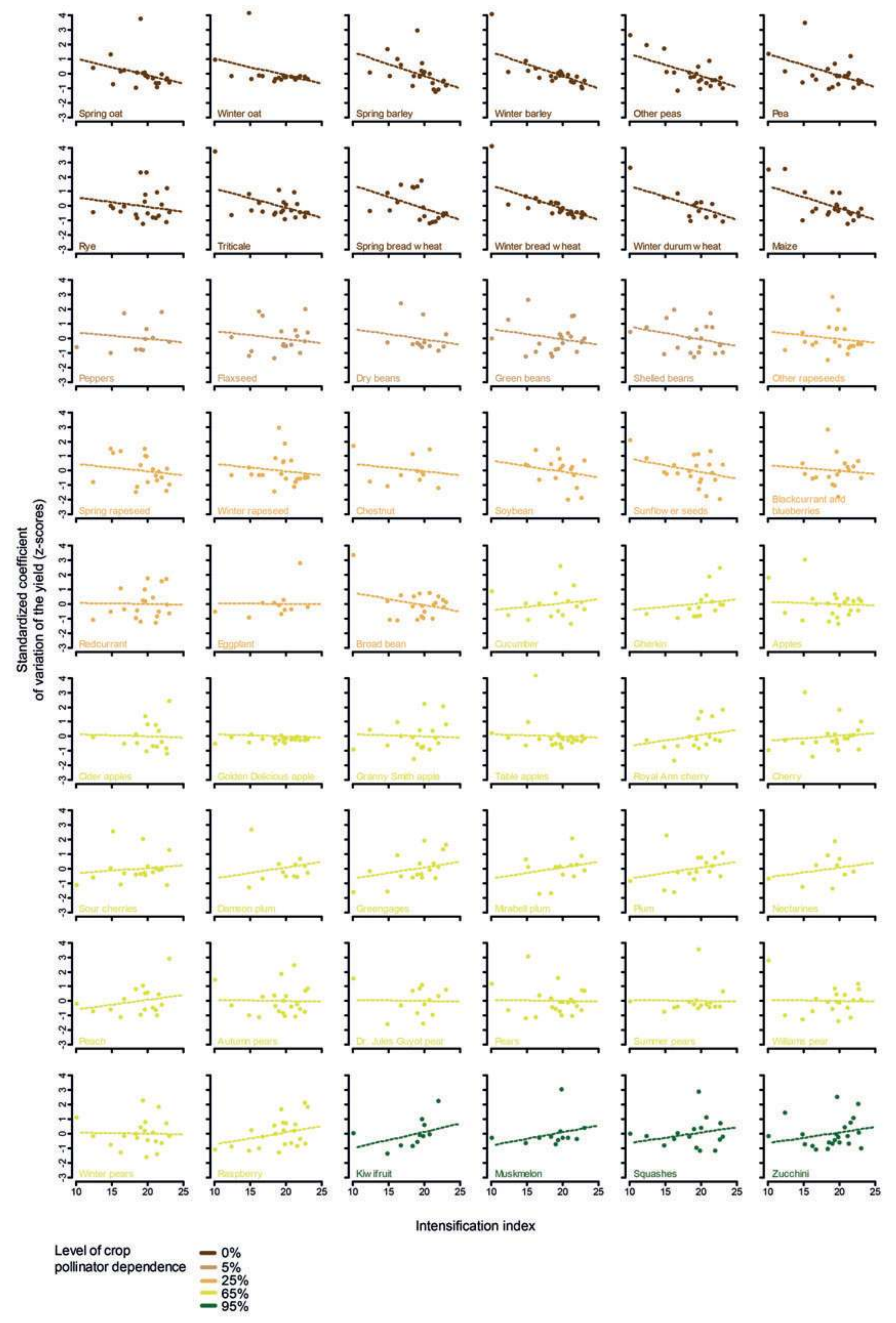


WebFigure 1. *Changes in mean yield with increasing level of agricultural intensification for each of the 54 crops. Dots represent crop data and the line indicates the estimate from the linear mixed model described in the main text.*



WebFigure 2. *Changes in yield variability with increasing level of agricultural intensification for each of the 54 crops. Dots represent crop data and the line indicates the estimate from the linear mixed model described in the main text.*

WebTable 1. List of the 54 crops grown in at least ten regions and for at least 10 years in each region during the 1989–2010 period

Crop name	*Crop species*	*Positive impact of animal pollination on production*	*Level of pollinator dependence*	*Number of regions growing the crop*	*Mean (min–max) intensification index where these crops are grown*	*Mean total area under the crop (ha)*	*Mean production per ha (kg ha^{-1})*
Kiwifruit	*Actinidia deliciosa*	essential	95	11	18.20 (10.03 – 21.94)	4311.20	153.55
Spring oat	*Avena sativa*	no increase	0	21	19.24 (12.35 – 23.02)	65 061.32	41.41
Winter oat	*Avena sativa*	no increase	0	21	18.79 (10.03 – 23.02)	74 878.41	44.79
Spring rapeseed	*Brassica napus*	modest	25	19	19.37 (12.35 – 23.02)	12 185.98	25.18
Winter rapeseed	*Brassica napus*	modest	25	21	19.24 (12.35 – 23.02)	1 047 054.86	30.00
Other rapeseeds	*Brassica napus*	modest	25	21	19.24 (12.35 – 23.02)	1 058 020.77	29.85
Peppers	*Capsicum annuum*	little	5	11	18.48 (10.03 – 23.02)	765.46	372.87
Chestnut	*Castanea sativa*	modest	25	11	17.51 (10.03 – 21.94)	6755.77	19.11
Muskmelon	*Cucumis melo*	essential	95	12	18.60 (10.03 – 23.02)	15 214.06	172.54
Cucumber	*Cucumis sativus*	great	65	16	18.50 (10.03 – 23.02)	98.23	1256.32
Gherkin	*Cucumis sativus*	great	65	15	19.91 (12.35 – 23.02)	518.01	145.32
Squashes	*Cucurbita maxima*	essential	95	16	18.56 (10.03 – 23.02)	1320.46	308.17
Zucchini	*Cucurbita pepo*	essential	95	22	18.82 (10.03 – 23.02)	3264.29	333.43
Soybean	*Glycine max*	modest	25	17	19.46 (14.78 – 23.02)	75 876.56	25.46
Sunflower seeds	*Helianthus annuus*	modest	25	21	18.64 (10.03 – 23.02)	798 337.32	24.37
Spring barley	*Hordeum vulgare*	no increase	0	21	19.24 (12.35 – 23.02)	493 756.14	47.88
Winter barley	*Hordeum vulgare*	no increase	0	22	18.82 (10.03 – 23.02)	1 154 051.50	57.95
Flaxseed	*Linum usitatissimum*	little	5	18	19.19 (12.35 – 23.02)	12 665.79	18.81
Apples	*Malus domestica*	great	65	22	18.82 (10.03 – 23.02)	25 199.82	275.18
Cider apples	*Malus domestica*	great	65	15	20.00 (12.35 – 23.02)	8248.84	178.68
Golden delicious apple	*Malus domestica*	great	65	22	18.82 (10.03 – 23.02)	21 847.17	332.51
Granny Smith apple	*Malus domestica*	great	65	19	18.69 (10.03 – 23.02)	4869.15	320.51
Table apples	*Malus domestica*	great	65	22	18.82 (10.03 – 23.02)	51 912.55	298.82
Shelled beans	*Phaseolus vulgaris*	little	5	20	18.67 (10.03 – 23.02)	9590.30	51.36
Dry beans	*Phaseolus sp*	little	5	12	19.66 (14.78 – 23.02)	3341.46	27.61
Green beans	*Phaseolus sp*	little	5	22	18.82 (10.03 – 23.02)	33 763.05	88.64
Other peas	*Pisum sativum*	no increase	0	22	18.82 (10.03 – 23.02)	454 363.19	40.37
Pea	*Pisum sativum*	no increase	0	22	18.82 (10.03 – 23.02)	31 918.77	60.32
Cherry	*Prunus avium*	great	65	20	18.72 (10.03 – 23.02)	12 283.54	49.05
Royal Ann cherry	*Prunus avium*	great	65	16	19.17 (12.35 – 23.02)	11 167.00	45.66
Sour cherries	*Prunus avium* and *P cerasus*	great	65	18	18.44 (10.03 – 23.02)	1101.18	45.01
Damson plum	*Prunus domestica*	great	65	12	19.71 (14.78 – 23.02)	487.82	72.21
Greengage	*Prunus domestica*	great	65	17	18.64 (10.03 – 23.02)	2427.65	79.11
Mirabelle plum	*Prunus domestica*	great	65	13	19.61 (14.78 – 23.02)	1941.32	75.46
Plums	*Prunus domestica*	great	65	16	18.75 (10.03 – 23.02)	2644.68	85.76
Nectarines	*Prunus persica*	great	65	10	18.04 (10.03 – 21.94)	8362.00	142.24
Peach	*Prunus persica*	great	65	17	18.56 (10.03 – 23.02)	13 700.25	105.97
Autumn pears	*Pyrus communis*	great	65	21	19.00 (10.03 – 23.02)	3812.23	198.71
Dr Jules Guyot pear	*Pyrus communis*	great	65	13	18.79 (10.03 – 23.02)	2677.45	185.29
Pears	*Pyrus communis*	great	65	22	18.82 (10.03 – 23.02)	11 000.59	196.83
Summer pears	*Pyrus communis*	great	65	16	19.01 (10.03 – 23.02)	199.52	185.64
Williams pear	*Pyrus communis*	great	65	19	18.90 (10.03 – 23.02)	3386.40	183.62
Winter pears	*Pyrus communis*	great	65	20	18.82 (10.03 – 23.02)	923.99	185.17
Blackcurrant and blueberries	*Ribes nigrum* and *Vaccinium myrtillus*	modest	25	18	19.31 (14.78 – 23.02)	2290.25	34.97
Redcurrant	*Ribes rubrum*	modest	25	19	19.43 (12.35 – 23.02)	324.43	51.52
Raspberry	*Rubus idaeus*	great	65	22	18.82 (10.03 – 23.02)	1300.31	50.33
Rye	*Secale cereale*	no increase	0	21	19.24 (12.35 – 23.02)	38 648.59	46.83
Eggplant	*Solanum melongena*	modest	25	11	18.48 (10.03 – 23.02)	574.18	378.41
Triticale	× *Triticosecale*	no increase	0	22	18.82 (10.03 – 23.02)	249 264.90	51.59
Spring bread wheat	*Triticum aestivum*	no increase	0	19	19.11 (12.35 – 23.02)	21 165.12	53.39
Winter bread wheat	*Triticum aestivum*	no increase	0	22	18.82 (10.03 – 23.02)	4 706 328.14	62.96
Winter durum wheat	*Triticum durum*	no increase	0	13	18.73 (10.03 – 23.02)	346 932.85	49.62
Broad bean	*Vicia faba*	modest	25	21	19.13 (10.03 – 23.02)	45 967.35	32.79
Maize	*Zea mays*	no increase	0	22	18.82 (10.03 – 23.02)	1 679 212.73	83.61

Notes: The "Positive impact of animal pollination on production" and the "Level of pollinator dependence" follow the classification of Klein *et al.* (2007). The "Number of regions growing the crop", the "Mean total area under the crop", and the "Mean production per ha" were provided by the Service de la Statistique et de la Prospective du Ministère de l'Agriculture et de l'Agroalimentaire. "Intensification index" is the level of agricultural intensification at the regional level (SOLAGRO; see main text for index computation).

WebTable 2. Type III ANOVA (*F* tests) results for the linear mixed models testing for an effect of crop level of pollinator dependence ("Dependence"), the regional level of agricultural intensification (Intensification index) and their interaction ("Dependence:Intensification index") on either mean yield ("Standardized mean yield") or yield variability ("Standardized coefficient of variation of the yield") of the 54 crops

Response variable	*Effect*	*df*	F *value*	P *value*
Standardized mean yield	Dependence	1	22.167	<0.001***
	Intensification index	1	61.415	<0.001***
	Dependence:Intensification index	1	22.365	<0.001***
Standardized coefficient of variation of the yield	Dependence	1	29.136	<0.001***
	Intensification index	1	29.959	<0.001***
	Dependence:Intensification index	1	29.486	<0.001***

Notes: df = degrees of freedom.

WebReferences

Klein AM, Vaissière BE, Cane JH, *et al*. 2007. Importance of pollinators in changing landscapes for world crops. *P Roy Soc B* **274**: 303–13.