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1 New indices for rapid assessment of pollination services based on crop yield data: France as a
2 case study

3

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23

24 **Abstract**

25 Local studies indicate that animal pollination is essential for crop productivity, but its
26 effectiveness and temporal stability vary broadly across regions. However, there is no simple
27 and rapid method to assess the pollination services over large areas. Here, we introduce two
28 new indices to measure pollination services and its temporal stability in farmland, the
29 Pollination Services Index and the index of Temporal Variation in Pollination Services, that
30 only require readily available data, namely crop yield and crop pollinator dependence. The
31 philosophy of these indices is to compare at a given site the standardized yield, or the
32 temporal variation in yield, among crops that have different levels of dependence on animal
33 pollinators for their production. We expect that where there is a shortage of pollinators,
34 standardized crop yields should decrease, and temporal variation in crop yields should
35 increase, with increasing dependence on pollinators. The Pollination Services Index in a given
36 area is thus defined as the slope of the linear regression between standardized crop yield
37 and crop pollinator dependence; the Temporal Variation in Pollination Services is defined as
38 the slope of the linear regression between the inter-annual coefficient of variation of crop
39 yield and crop pollinator dependence. We calculated these two indices in France, where we
40 show extensive spatial variation in the estimated pollination services. We further show that
41 this variation in the Pollination Services Index is negatively correlated with the index of
42 Temporal Variation in Pollination Services, and positively correlated with habitat quality for
43 pollinators. At a spatial resolution of administrative departments (ca. 5800 km²), the results
44 show that intensive farming is positively correlated with higher Temporal Variation in
45 Pollination Services but is not significantly associated with the Pollination Services Index,
46 probably due to multicollinearity issues. Despite some limitations that deserve further
47 attention, these indices may constitute promising, cost-effective tools to highlight regions of

48 pollination deficit over large areas.

49

50 **Highlights**

51 -We introduce indices for rapid assessment of pollination services over large areas.

52 -The two new indices only require data on crop yield and crop pollinator dependence.

53 -Pollination services correlates positively with habitat quality for pollinators.

54 -Pollination stability correlates negatively with intensive farming.

55 -The two indices are used to map pollination services for the first time in France.

56

57 **Keywords:** Pollination services; Pollination stability; Relative Pollination Potential; Crop yield;

58 Ecosystem services; Intensive farming.

59

60 **1. Introduction**

61 There is strong evidence that wild (Biesmeijer et al., 2006) and managed (Potts et al., 2010;
62 vanEngelsdorp et al., 2011) insect pollinators have declined in abundance and diversity over
63 the past few decades in Europe and North America (Potts et al., 2016). The main recognized
64 drivers of such a decline include land-use change and the resulting loss and fragmentation of
65 semi-natural habitats, environmental pollution, due to e.g. pesticides, decreasing resource
66 diversity and/or abundance, alien species, spread of pathogens and climate change (see
67 Potts et al., 2016 for a synthesis). Decline in pollinators has raised much attention because
68 animal pollination is essential for the persistence of wild plant communities (Aguilar et al.,
69 2006; Ashman et al., 2004; Biesmeijer et al., 2006; Fontaine et al., 2005), and because it is
70 considered an important ecosystem service (Millennium Ecosystem Assessment, 2005),
71 defined by Daily (1997) as “the conditions and processes through which natural ecosystems,
72 and the species that make them up, sustain and fulfill human life”. For example, the yield of
73 ca. 75% of crop species representing 35% of global food production is improved by animal
74 pollination (Klein et al., 2007). In Europe, the proportion of crop species (partially)
75 dependent on pollinators reaches 84% (Williams, 1994).

76
77 The actual contribution of pollinators to crop yields is however known to vary through space
78 and time depending on the abundance, composition or diversity of pollinator communities
79 (Garibaldi et al., 2011b). Assessing the pollination services over large areas is crucial to
80 quantify the provision of these services, to identify general spatial patterns, temporal trends
81 and potential drivers of pollination services, as well as to inform land-management decisions
82 and to achieve conservation objectives. Moreover, the assessment of the spatial distribution
83 of the pollination services over large spatial extents has become a policy priority in the last

84 years (see e.g. “Action 5” of the EU biodiversity strategy, European Commission, 2011).
85 However, so far there is no simple means to evaluate this variation over large areas.
86 Numerous local scale studies have demonstrated a positive effect of wild pollinator
87 abundance or diversity on crop production and its temporal stability (Garibaldi et al., 2016,
88 2013, 2011b). Most of these field-scale studies use data-intensive experimental methods to
89 collect detailed information on flower-visitor richness, visitation rates, and seed or fruit set,
90 thereby providing precise estimates of the pollination services at a local scale. Although they
91 are fundamental for an accurate measure of animal pollination, these methods cannot easily
92 be used to assess the pollination services over larger areas, because they are expensive and
93 extremely time-consuming.

94 To our knowledge, a single, indirect measure of the pollination services exists at the
95 European scale: Zulian et al. (2013) introduced the Relative Pollination Potential index,
96 defined as the potential of ecosystems to support crop pollination by wild bees. The Relative
97 Pollination Potential combines literature and expert-assessed parameters on the ecology of
98 wild bee species, with spatial information on resource availability for such pollinators (i.e.,
99 food and nesting sites). The Relative Pollination Potential decreases with the distance to
100 semi-natural habitats (a proxy of the bee visitation rate) and increases with annual
101 temperature (a proxy of wild bee activity). The mapping of this index shows an increase in
102 pollination potential along a North-South gradient following the temperature gradient in
103 Europe (Zulian et al., 2013). However, the indicator only uses a-priori and expert-based
104 assumptions on wild bee ecology, it is not based on observations of pollinators or pollination,
105 and has not been validated against data. For this reason, its interpretation as an indicator of
106 the pollination service might be questionable.

107

108 In this study, we introduce and test two new indices based on the direct measure of crop
109 yield, which, although influenced by numerous additional factors, is the measurable final
110 output of pollination services. The general idea of these new indices is to quantify for
111 different areas (i) the relative effectiveness in animal pollination, defined here as a
112 quantitative measure of the amount of successful pollen deposition and (ii) the temporal
113 instability in animal pollination. We call these two new indices (i) the Pollination Services
114 Index and (ii) the Temporal Variation in Pollination Services, respectively. Our approach
115 elaborates on that of Garibaldi et al. (2011a), who examined the correlations between (1)
116 standardized crop yield or crop yield coefficient of variation and (2) crop pollinator
117 dependence to demonstrate the impact of pollinator limitation on agricultural production at
118 a global scale. Here, we show that this approach can be adapted to assess the spatial
119 distribution of pollination services over large areas.

120 We used a dataset reporting the yield of 56 crops between 2000 and 2010, available at the
121 spatial resolution of administrative departments in France and we combined it with
122 information on crop pollinator dependence to produce maps of Pollination Services Index
123 and index of Temporal Variation in Pollination Services. We calculate and examine the spatial
124 patterns of these two indices over the French territory. We test their ecological relevance by
125 examining their correlations with two known indicators of drivers of pollinator communities
126 and activities: the Relative Pollination Potential (Zulian et al., 2013), an indicator based on
127 habitat and climate suitability for wild bees; the High Nature Value index, an indicator of
128 extensive agricultural practices. We discuss the potential limitations and biases of this new
129 approach for the assessment of the pollination services. We conclude that our approach,
130 which is easily transferable to other datasets, could be used to monitor spatial and temporal
131 variation in the pollination services from local to regional scales, depending on availability

132 and spatial resolution of crop yield data.

133

134 **2. Materials and methods**

135 Countless definitions of the pollination services exist (see e.g. Liss et al., 2013). In the
136 following, pollination services are defined as the relative increase in crop yield resulting from
137 pollen deposition by animal pollinators.

138

139 2.1. Crop dataset and pollinator dependence

140 Annual yields of 133 crops were retrieved from the *Service de la Statistique et de la*
141 *Prospective* of the French ministry of agriculture
142 (<http://acces.agriculture.gouv.fr/disar/faces/>) for each of the 95 administrative departments
143 of France (mean area = 5770 km²), except Paris, and for the years 2000 to 2010. We selected
144 59 crops that produce fruits or seeds for direct human consumption, therefore excluding
145 crops for which seeds are only used for breeding purposes or to grow vegetative parts for
146 direct human use or for fodder. We also excluded greenhouse production. These crops were
147 grown in a minimum of two departments (Avocados) and a maximum of 93 departments
148 (Apples) between 2000 and 2010, with an average of 64 departments. The annual area
149 grown with these crops varied between 8 ha (Avocados) and above 4 million ha (Bread
150 wheat) with an average of 242,676 ha (see Appendix A Table A1 in Supplementary data for
151 details). Following Klein et al. (2007), we classified crops on the basis of their level of
152 pollinator dependence, defined as the percentage of yield reduction resulting from an
153 absence of pollinators. The dependence categories were: none (0% yield reduction), little
154 (<10% yield reduction), modest (10 to 39 % yield reduction), great (40 to 89% yield
155 reduction), and essential ($\geq 90\%$ yield reduction). The level of pollinator dependence was

156 unknown for three of 59 crop classes (Oleaginous, Proteaginous, Other oleaginous), which
157 were excluded from the analysis. The levels of pollinator dependence contained between 5
158 (“essential”) and 21 (“none”) crops, representing respectively 20,000 ha and 9 million ha
159 each year in France (Table 1; see Appendix A Table A1 in Supplementary data).

160

161 2.2. Calculation of the Pollination Services and the Temporal Variation in

162 Pollination Services indices

163 As a preliminary step common to both indices, we performed for each crop a linear
164 regression of crop yield against years to account for annual yield increases due to genetic
165 progress and improvement of agricultural practices. We then extracted the residual yields
166 from the regression.

167

168 *Pollination Services Index*

169 For the Pollination Services Index, residual yields were standardized within each crop (i.e. z-
170 transformed) across the 95 departments to allow comparisons among crops. For each crop,
171 the z-transformed residual can be interpreted as the yield surplus or deficit in a department
172 with respect to the national mean. For each department, we then performed a linear mixed-
173 effects regression of standardized residual yields against the level of pollinator dependence
174 to describe the relative change in yield along a pollinator dependence gradient (Fig. 1). The
175 mixed-effect model also included a random effect of year, to account for non-independence
176 of crop yield data within a year. We chose a linear regression over more flexible models
177 because each crop pollinator dependence class is expected to be impacted by pollinator
178 shortage in direct proportion to its pollinator dependence, by definition of the latter. We
179 defined the Pollination Services Index as the slope of this linear regression. The use of z-

180 transformed residuals has two important implications for the interpretation of the index.

181 First, our approach does not compare absolute yields, but instead the position of crop yields
182 with respect to the national mean (for a given crop), across levels of pollinator dependence.
183 In other words, a positive slope in a department indicates that the pollinator-dependent
184 crops fare better than the national mean, while pollinator-independent crops have yield
185 equivalent to, or below, the national mean (Fig. 1, Bouches-du-Rhône department). Hence in
186 such department, pollination does not appear as a major limitation for crop yield. In
187 contrast, a negative slope in a department (e.g. Fig. 1, Eure department) tends to suggest
188 that pollinator-dependent crops fare worse there than the national mean, while pollinator-
189 independent crop yields are at or above the national mean. This could be interpreted as a
190 sign of pollination deficit (but see next paragraph for a more careful interpretation).

191 Second, the z-transformation of the residual yields of each crop at the national level implies
192 by definition that the distribution of z-transformed residual yields is centered on zero, with
193 95% of the distribution between -2 and 2 *for each crop*. Hence, when all z-transformed
194 residual crop yields, from all departments, are plotted together against pollinator
195 dependence (Fig. 1), the collection of points is centered on zero throughout the range of
196 pollination dependence values. If pollination services are equally effective across the study
197 area, i.e. with all departments experiencing the same levels of pollination, the yield of a
198 given crop in a given department should not depend on the pollinator-dependence of the
199 crop, but mostly on local environmental conditions and farming practices. As a result, the
200 slope of the linear regression of z-transformed residual crop yields against pollinator
201 dependence for a given department is expected to be zero on average, i.e. with small values
202 that do not differ significantly more zero more often than 5% of the time. In contrast, when
203 pollination services are variable through space, we expect frequent (>>5%) significant

204 positive and negative slopes for the linear regression between residual yields and pollinator
205 dependence. Because the z-transformed residual crop yield dataset is constrained mostly
206 between -2 and 2 throughout the whole range of pollinator dependence, by symmetry any
207 positive slope in one department will be compensated by a negative slope in another
208 department, and vice versa (Fig. 1). Hence the Pollination Services Index only provides a
209 relative, not an absolute, indicator of pollination services. It ranks the study area from sub-
210 areas (here departments) in which pollination is most limiting (departments with highly
211 negative slopes) to sub-areas in which pollination is less limiting (departments with highly
212 positive slopes). In the latter departments where pollination is less limiting, crop yield might
213 still be pollinator-limited, but to a lesser extent than in other departments.

214

215 *Temporal Variation in Pollination Services*

216 For the Temporal Variation in Pollination Services, we also worked with residual yields
217 obtained from the linear regression against years, but we added the mean yield in 2005 (the
218 median year for our dataset) to residual yields for each crop, to work with positive values
219 only. We then calculated for each crop and department the coefficient of variation of these
220 values, which provided a standardized measure of yield variation. We performed a linear
221 regression of the coefficient of variation of residuals yields against level of pollinator
222 dependence for each department. We retained the slope of the linear relationship between
223 yield variability and crop pollinator dependence as the departmental index of Temporal
224 Variation in Pollination Services. Positive relationships between yield variability and
225 pollinator dependence in a department indicate temporal instability of the pollination
226 services, i.e. the temporal variability of yield is larger for pollinator-dependent vs. pollinator-
227 independent crops during the study period. In contrast, a slope of zero suggests comparable

228 stability of the pollination services for pollinator-dependent and independent crops.

229

230 2.3. Correlations with the Relative Pollination Potential, another index of

231 pollination services, and the High Nature Value index

232 We examined, using the Spearman's rank correlation coefficient, all the pairwise correlations

233 between the Pollination Services Index, the Temporal Variation in Pollination Services, and

234 the Relative Pollination Potential of Zulian et al. (2013). For each department, the Relative

235 Pollination Potential is provided at a 100m x 100m pixel resolution; we calculated the

236 average Relative Pollination Potential in agricultural areas as the mean over all farmland

237 pixels of a department.

238 Both the Relative Pollination Potential and the Pollination Services Index exhibit a strong

239 latitudinal gradient (see below). To examine the spatial patterns in both Pollination Services

240 Index and Temporal Variation in Pollination Services, as well as their environmental

241 correlates, while checking for biases due to the latitudinal gradient and particularly for a

242 strong spatial autocorrelation in the data, we then used linear mixed models (Pinheiro and

243 Bates, 2000). These models included three fixed explanatory variables that are likely to drive

244 most of the latitudinal gradient, namely the Relative Pollination Potential (habitat

245 availability), agricultural intensity and temperature (climate). We also included administrative

246 regions ($n = 22$, i.e. administrative regions group about 4-5 neighboring administrative

247 departments) as a random variable in the model, to further account for unidentified drivers

248 of the latitudinal gradient. We then checked that the residuals of both models were spatially

249 uncorrelated using Moran's Index with inverse-distance weighting.

250 We used the High Nature Value index (Andersen et al., 2004; Pointereau et al., 2010, 2007)

251 to characterize agricultural intensity. The High Nature Value index is defined in areas where

252 agriculture is a major land use. It aggregates three components at the municipality level
253 (average area = 15 km²). The first component quantifies crop diversity and share of
254 permanent grasslands, a proxy for the rotation system and the diversity of agricultural
255 landscape. The second component characterizes extensive farming practices, defined by low
256 pesticide and mineral fertilizer inputs, as well as low irrigation; it includes permanent
257 grasslands and annual crops but not permanent crops. The third component estimates semi-
258 natural habitat availability in agricultural areas, via a combination of number of traditional
259 fruit trees, length of hedges and wood edges and number of farm ponds. All these
260 components are likely to influence habitat quality and availability for pollinators and we
261 expect the High Nature Value index to be positively related with the Pollination Services
262 Index and negatively related with the Temporal Variation in Pollination Services. In each
263 department, we calculated the average High Nature Value across all municipalities weighted
264 by their farmland area (Agreste, 2016), for each of the three components of the High Nature
265 Value index. Because the three components are strongly correlated with one another, we
266 performed a principal component analysis (PCA) on these three components. We retained
267 the first axis of the PCA only, which represents 69% of all variance and can be interpreted as
268 a South-North gradient of increasing agricultural intensity (see Appendix A Fig. A1 in
269 Supplementary data).

270 We calculated the mean annual temperature, a variable with major influence on insect
271 activity and their pollination potential (Corbet et al., 1993) and potentially contributing
272 strongly to the latitudinal gradient in pollination. For each department, we collected daily
273 mean temperature between 2000 and 2010 from the ENSEMBLES dataset (Haylock et al.,
274 2008), using data from the nearest E-OBS station in France on a 0.25 degree grid.

275

276 All analyses were performed using R version 3.2.4 (R Development Core Team, 2008). Indices
277 were calculated and mapped using R packages *ggplot2* version 2.1.0 (Wickham, 2009), *sp*
278 version 1.2.2 (Bivand et al., 2013; Pebesma and Bivand, 2005), *maptools* version 0.8.39
279 (Bivand and Lewin-Koh, 2016), *classInt* version 0.1.23 (Bivand, 2015), *RColorBrewer* version
280 1.1.2 (Neuwirth, 2014), *maps* version 3.1.0 (Becker and Wilks, 2016), *rgdal* version 1.1.3
281 (Bivand et al., 2015), *rgeos* version 0.3.17 (Bivand and Rundel, 2016), *rje* version 1.9.0 (Evans,
282 2014), *gridExtra* version 2.3.0 (Auguie, 2017), *nlme* version 3.1-131.1 (Pinheiro et al., 2017),
283 *geo* version 1.4-3 (Hoskuldur et al., 2015), *car* version 2.1-6 (Fox and Weisberg, 2011), *gstat*
284 version 1.1-5 (Pebesma, 2004) and *ape* version 5.1 (Paradis et al., 2004). Climate data were
285 extracted using the R package *climateExtract* (Schmucki, 2018), and *devtools* (Wickham and
286 Chang, 2016).

287

288 **3. Results**

289 3.1. Latitudinal gradient in the pollination services

290 We found a strong latitudinal gradient in the Pollination Services Index, with higher values in
291 southern vs. northern France (Spearman correlation with latitude $\rho = -0.64$, $n = 95$, $P <$
292 0.001). Overall, the Pollination Services Index, i.e. the slope of the linear regression between
293 standardized mean yield and level of pollinator dependence, varied between -1.78 ± 0.19
294 and 2.39 ± 0.16 , with significant negative values in 38 departments, most of them in northern
295 France, and significant positive values in 31 departments (Fig. 2a). Individual relationships
296 between standardized mean yield and level of pollinator dependence for all departments are
297 plotted in Appendix A Fig. A2 in Supplementary data.

298

299 3.2. Negative correlation between the pollination services and their temporal

300 variation

301 We found a significant negative but weak correlation between the Pollination Services Index
302 and the Temporal Variation in Pollination Services (Spearman's $\rho = -0.31$, $n = 95$, $P = 0.002$,
303 Fig. 3a), i.e. departments with higher pollination services also tended to exhibit more stable
304 pollination. The Temporal Variation in Pollination Services, i.e. the slope of the regression
305 between yield variation and level of pollinator dependence, was significantly positive in 16
306 departments (Fig. 2b, and see Appendix A Fig. A3 in Supplementary data for individual
307 relationships in each department). Such positive relationships suggest that in those
308 departments an appreciable fraction of the temporal variability in the yield of pollinator-
309 dependent crops is caused by temporal variation in pollinator availability or effectiveness. In
310 78 departments, the relationship was not significantly different from 0, indicating that
311 pollinators do not appear to contribute much to yield temporal variation. The relationship
312 between yield variability and level of pollinator dependence was significantly negative in a
313 single department (Haute-Pyrénées). Departments with strong pollination instability tended
314 to be located in northern France, as indicated by a weak latitudinal gradient (Spearman's $\rho =$
315 0.19 , $n = 95$, $P = 0.059$) that was however not significant.

316

317 3.3. Relationships with the Relative Pollination Potential and the index of 318 agricultural intensity

319 We found a strong positive correlation between our Pollination Services Index and the
320 Relative Pollination Potential of Zulian et al. (2013), (Spearman's $\rho = 0.65$, $n = 95$, $P < 0.001$,
321 Fig. 3b): both indices therefore appear to convey consistent information, and exhibit a strong
322 latitudinal gradient with larger pollination potential and pollination services in southern
323 France. In contrast, the Temporal Variation in Pollination Services and the Relative Pollination

324 Potential were not significantly related at the national scale, although there was a tendency
325 for more variable pollination services in departments with a lower Relative Pollination
326 Potential (Spearman's $\rho = -0.19$, $n = 95$, $P = 0.06$, Fig. 3c).
327 When all drivers of pollination were assessed within a single model accounting for spatial
328 autocorrelation, the Pollination Services Index was significantly correlated with the Relative
329 Pollination Potential only, but not with agricultural intensity nor with temperature (Table 2).
330 Note however that the Relative Pollination Potential encapsulates information on
331 temperatures and some components of the High Nature Value index (namely habitat
332 quality). When the Relative Pollination Potential was removed from the linear model, the
333 Pollination Services Index was significantly related negatively with agricultural intensity and
334 positively with temperature (not shown). In contrast, the Temporal Variation in Pollination
335 Services was not related with the Relative Pollination Potential, but was positively correlated
336 with the index of agricultural intensity and negatively with mean annual temperature (Table
337 2).

338

339 **4. Discussion**

340 This study is the first to our knowledge to provide spatial indices of the pollination services
341 and their temporal variation nationwide directly on the basis of crop yields and pollinator
342 dependence. Both indices exhibit strong geographical patterns, as indicated by appreciable
343 differences among departments. Below we discuss the extent to which such differences
344 among departments are indicative of true differences in the pollination services, and we
345 outline future research directions to validate further these two indices.

346

347 4.1. Two independent indices show consistent patterns in the pollination services

348 The Pollination Services Index and the Relative Pollination Potential (Zulian et al., 2013),
349 although they were obtained from fully independent datasets and methods, exhibited a
350 significant positive correlation, partly driven by a strong latitudinal gradient. The Pollination
351 Services Index developed in this study is based on the measurable and final output of
352 pollination services provided by all types of pollinators, crop yields. In contrast, the Relative
353 Pollination Potential combines literature and expert-assessment on the ecology of wild bee
354 species only. As its name indicates, it only characterizes a *potential* for one type of pollination
355 and has not been validated by data on pollinators or pollination so far. The most intuitive
356 explanation for their positive correlation is a causal one: the Relative Pollination Potential is a
357 proxy for the abundance and/or diversity of pollinator communities, which in turn controls
358 the rate of pollen delivery to crops (Garibaldi et al., 2013; Kleijn et al., 2015). With this
359 interpretation, both indices validate each other by producing consistent information from
360 independent datasets. The causal role of pollinators is further supported by the latitudinal
361 gradient in species richness observed in wild bees in Europe (Nieto et al., 2014). However,
362 cross-validation and the congruence of spatial gradients are only circumstantial evidence,
363 and a formal validation of all indices would require comparison with more direct
364 measurements of pollination services at the plant level.

365 Despite the congruence of these independent pollination services proxies, i.e. the Pollination
366 Services Index and the Relative Pollination Potential, our analysis remains correlative.

367 Therefore, we cannot exclude that the observed pattern is driven by other factors, among
368 which the latitudinal gradient in environmental conditions, without an underlying causality.

369 One important question is whether the numerous other environmental factors that have
370 recognized key impacts on crop yield (weather, soil type, farming practices including e.g. use
371 of pesticides or fertilizers, or fruit culling...) could bias the Pollination Services Index and for

372 example create a latitudinal gradient in crop yield of pollinator-dependent crops that is not
373 due to pollinators. The latitudinal gradient in the Pollination Services Index implies that
374 pollinator-dependent crops tend to have higher yields in southern vs. northern France,
375 whereas the opposite is true for pollinator-independent crops. Climate/weather, soil type or
376 farming practices can only drive such pattern if their effects on crop yield were related to
377 pollinator-dependence through mechanisms that do not involve pollination. For sake of
378 illustration, one can imagine a situation in which pollinator-dependent crops were more
379 likely to be trees than pollinator-independent crops, and in which trees in general would
380 grow better in warmer climates (two highly unlikely hypotheses). In this case, the yield of
381 pollinator-dependent crops would be higher than the national mean in warm departments
382 (southern France) and lower than the mean in northern France, which would create the
383 same signal as the one we observe. However, we cannot think of an obvious mechanism,
384 other than pollination, that would cause the effects of environmental factors on crop yield to
385 vary systematically with the pollinator dependence of crops. In summary, we detect patterns
386 of local adaptation such that pollinator-dependent crop have higher yields in southern vs.
387 northern France. The most likely explanation for this pattern remains a gradient in pollination
388 services, but we do not have the data here to make firm conclusions.

389 With these limitations in mind, the two pollination indices introduced here still show
390 patterns consistent with some of the known effects of landscape on pollinators. Analyzes
391 controlling for spatial autocorrelation patterns showed that the Relative Pollination Potential
392 was a significant correlate of the Pollination Services Index, while the index of agricultural
393 intensity, as measured by a combination of in-field practices, crop diversity and landscape
394 simplification, was not. This result suggests that the quality and diversity of landscapes may
395 prevail over agricultural practices to explain pollination of pollinator-dependent crops. This

396 absence of a relationship between pollination services and agriculture is at odds with
397 numerous studies demonstrating negative effects of intensive agriculture on pollinators,
398 particularly wild bees (Hendrickx et al., 2007; Le Féon et al., 2010; Koh et al., 2016) and the
399 service they provide (Deguines et al., 2014). This somewhat surprising result should be
400 tempered by several considerations. (1) The strong latitudinal gradient influencing all indices
401 and their environmental correlates makes it difficult to isolate individual correlations. Indeed,
402 the RPP emerges as the main correlate of the Pollination Services Index when both agricultural
403 intensification and RPP are included in the analysis, but agricultural intensification is significantly
404 negatively correlated with the Pollination Services Index when analysed in a one-way ANOVA. (2)
405 Although pollination services were not correlated with agricultural intensity on average, their
406 temporal variability increased with the index of agricultural intensity, in agreement with
407 most earlier results showing negative impacts of agriculture on pollinators and pollination.
408 (3) Drivers not included in the Relative Pollination Potential (Zulian et al., 2013) or in the High
409 Nature Value index may also influence pollinator communities. Among these drivers, other
410 pollinator groups such as flies that are not accounted for in the Relative Pollination Potential
411 could have a stronger functional role as they are known to be adapted to cooler climates
412 (Elberling and Olesen, 1999). Pesticide use could also play an important role as it has been
413 increasing steadily in France (Hossard et al., 2017), especially in northern France (“EuroStat,”
414 2011). Pesticides are known to have strong effects on pollinators, particularly on wild bees
415 (e.g. Brittain et al., 2010; Gill et al., 2012; Laycock et al., 2012) or in simplified landscapes
416 such as those encountered in northern France (Park et al., 2015). (5) Finally, both indices may
417 have been calculated at a spatial resolution too coarse to detect the local effects of within-
418 field agricultural practices (see below).

419

420 4.2. Caveats for interpretation of the index values

421 It is important to keep in mind that the Pollination Services Index does not provide an
422 absolute, but only a relative assessment of the pollination services. This limitation is not a
423 major one, but one should be careful that a positive value of the Pollination Services Index
424 does not necessarily indicate sufficient pollination, but only a better pollination than in the
425 other sampling units. With spatial variation in the pollination services, the analysis
426 introduced here will produce values of the pollination services ranging from negative values
427 that are significantly different from zero to positive values that are significantly different from
428 zero, regardless of the average effectiveness of pollination across the study area. Hence, the
429 Pollination Services Index should only be used to compare areas, not to assess pollination in
430 an absolute manner.

431 The quality of the assessment of crop pollinator dependence may also influence the two
432 indices. Here, we have used available data, which are coarse: the classes of pollinator
433 dependence can span up to 30%. In addition, within a given crop species, pollinator
434 dependence is known to vary across varieties. For example in oilseed rape, plant breeders
435 seek to develop less pollinator-dependent varieties to cope with pollinator declines
436 (Hudewenz et al., 2014). As a result, farmers may grow less pollinator dependent varieties in
437 areas with pollination deficit. This phenomenon, if it exists, should however make our
438 Pollination Services Index conservative, i.e. the standardized crop yield should decrease less
439 with increasing crop pollinator dependence than with an accurate measurement of crop
440 pollinator dependence. In any case, both indices would benefit from more precise estimates
441 of crop pollinator dependence.

442 The value of the Pollination Services Index may further be changed by our choice to work on
443 residual crop yields, thereby removing any linear temporal trend in yield. This choice was

444 made to avoid the confounding effects of genetic progress and improvement of agricultural
445 practices and is justified when the temporal trend in crop yield is positive. However, for
446 several crops, such as almonds or kiwis, the temporal trend in crop yield between 2000 and
447 2010 was negative. For pollinator-dependent crops, a decline in pollination services is one
448 likely cause of this decline in productivity. Our Pollination Services Index does not include this
449 temporal decrease in crop yield and is therefore again conservative. The index was designed
450 to detect differences in pollination services in space, but may have limited power to detect
451 temporal trends in pollination services. To address temporal changes in the pollination
452 services, we recommend calculating the index without the initial step of linear regression of
453 crop yield on years.

454 The index of Temporal Variation in Pollination Services may also be biased by standardization
455 issues although it does not require z-transformation of yield. This index is calculated as the
456 slope of the relationship between the coefficient of variation of the yield and crop pollinator
457 dependence. Since the coefficient of variation is inversely proportional to mean yield, its
458 variation may reflect variation in the mean, rather than in the variance of crop yields. In
459 other words, departments with instable pollination may in fact be departments with low
460 pollination services on average, an interpretation that is partly supported by the negative
461 relationship between the Temporal Variation in Pollination Services and the Pollination
462 Services Index. However, the alternative explanation, that departments with low services and
463 high instability are characterized by poor and variable pollinator communities, is equally
464 likely.

465

466 4.3. Perspectives

467 To go further in determining the causal link between our indices and the pollination services,

468 several perspectives could be explored. First, the two indices and the Relative Pollination
469 Potential should be compared with variables describing the structure and composition of
470 pollinator communities. Quantitative data on wild pollinators are few, especially on large
471 spatial scales and for taxonomic groups beyond bees. However, recent initiatives to monitor
472 pollinator communities via participatory science schemes may produce useful data in the
473 short term (see e.g. the French photographic survey of pollinators, Deguines et al., 2012).
474 Second, the ultimate test for these indices would be a comparison with proper estimates of
475 pollinator limitation using caging and pollen supplementation experiments (e.g. Hudewenz et
476 al., 2014). Third, a more accurate examination of the relationship between pollination
477 services indices and its potential drivers, particularly agricultural intensity may require finer
478 spatial resolutions of the indices. For example, there may be a mismatch in the departmental
479 resolution at which the indices were calculated, and the spatial resolution at which
480 agricultural practices or landscape structures influence pollinator population dynamics and
481 behavior (Steffan-Dewenter et al., 2002). However, the spatial resolution of both pollination
482 services indices depends solely on the spatial resolution of data and there is no obstacle to
483 obtaining them at much finer spatial resolution should crop yield data be available.

484

485 **5. Conclusion**

486 The Pollination Services Index and the Temporal Variation in Pollination Services are
487 correlated in a consistent way, and their correlation with the Relative Pollination Potential
488 and the index of agricultural intensity, respectively, are in line with the known influence of
489 habitat quality and agricultural practices on pollinator communities. Despite the need for
490 further work to ascertain causality, our indices pave the way to quantify and map pollination
491 services at any spatial resolution in a cost-effective way over large areas. Such maps could

492 help identifying areas suffering from deficit in pollination services and related drivers. They
493 could also contribute to evaluate agricultural and conservation practices. Last but not least,
494 they provide easy-to-grasp communication tools to raise awareness of stakeholders on
495 pollination issues.

496

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506

507 **Authors' contributions**

508 EP and CF conceived the ideas and designed methodology; GM, FA and EP collected the data;
509 GM, CF and EP analyzed the data; GM, CF, FA and EP led the writing of the manuscript. All
510 authors contributed critically to the drafts and gave final approval for publication.

511

512 **Appendix A. Supplementary data**

513 Supplementary data associated with this article can be found in the online version.

514

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686

687

688 TABLES AND FIGURES

689 Color should be used for figures 1, 2 and 3.

690

691 **Table 1** Levels of pollinator dependence and spatial coverage of 56 crops in France between
692 2000 and 2010. “Average total area” is the total annual area sown with a given type of crop,
693 averaged over the 11 years.

694

695 **Table 2** Correlations between the Pollination Services Index (PSI) or the Temporal Variation
696 in Pollination Services (TVPS) and environmental variables, as inferred from a linear mixed
697 model with administrative regions as random effect.

698

699 **Fig. 1.** Z-transformed residual crop yields as a function of crop pollinator dependence for the
700 full dataset. Each point corresponds to a crop from a department. The colors highlight data
701 from two examples of departments with extreme values of the Pollination Services Index: in
702 orange, Bouches-du-Rhône, a department where residual yields are positively related with
703 pollinator dependence (slope = 2.42 ± 0.16); in blue, Eure, a department where residual
704 yields are negatively related with pollinator dependence (slope = -1.69 ± 0.14). The grey
705 horizontal line is the regression over the full dataset (slope = 0). For sake of readability, the x-
706 coordinate of each crop has been slightly shifted such that crops within a given class of
707 pollinator dependence are not plotted on top of each other.

708

709 **Fig. 2.** Maps of the Pollination Services Index (a) and the Temporal Variation in Pollination
710 Services (b) across France, at the spatial resolution of departments. Colors indicate the slope
711 of the relationship between relative mean yield (a) or the coefficient of variation of the yield
712 (b) and the level of crop pollinator dependence. Stars indicate departments with a significant

713 relationship.

714

715 **Fig. 3.** Relationships among three pollination indices in France: (a) Pollination Services Index

716 vs. Temporal Variation of Pollination Services; (b) Pollination Services Index vs. Relative

717 Pollination Potential; (c), Temporal Variation in Pollination Services vs. Relative Pollination

718 Potential. Each point represents a department; colors indicate the latitude of the centroid of

719 the department.

720

Median level of pollinator dependence (%)	Positive impact of animal pollination on production of crops	Number of crops	Mean number of departments	Average total area per year (ha)
0	No increase	21	95.0	9,753,839
5	Little	8	92.2	57,721
25	Modest	10	93.6	1,998,652
65	Great	12	93.1	129,423
95	Essential	5	84.8	21,488

722

723 **Table 1** Levels of pollinator dependence and spatial coverage of 56 crops in France between
724 2000 and 2010. “Average total area” is the total annual area sown with a given type of crop,
725 averaged over the 11 years.

726

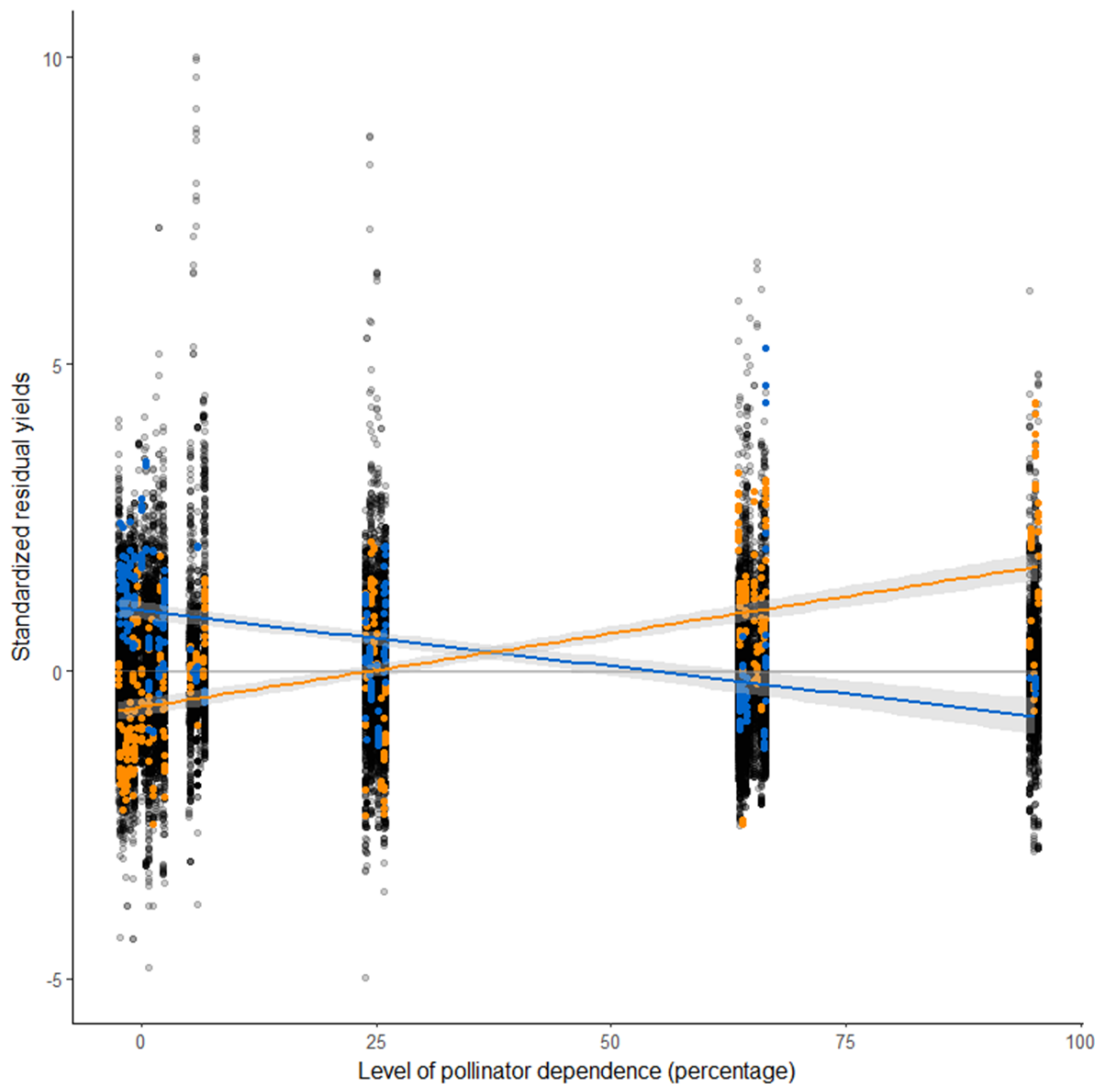
Response Variable	Independent variables	Estimate	df	Chisq	P value
PSI	Relative Pollination Potential	8.33	1,70	8.22	0.004**
	Index of agricultural intensity	-0.03	1,70	0.11	0.743
	Mean annual temperature	0.07	1,70	0.92	0.338
TVPS	Relative Pollination Potential	1.04	1,70	1.97	0.161
	Index of agricultural intensity	0.05	1,70	5.49	0.019*
	Mean annual temperature	-0.04	1,70	4.21	0.040*

727

728 **Table 2** Correlations between the Pollination Services Index (PSI) or the Temporal Variation
729 in Pollination Services (TVPS) and environmental variables, as inferred from a linear mixed
730 model with administrative regions as random effect.

731

732 **Fig. 1.** Z-transformed residual crop yields as a function of crop pollinator dependence for the
733 full dataset. Each point corresponds to a crop from a department. The colors highlight data
734 from two examples of departments with extreme values of the Pollination Services Index: in
735 orange, Bouches-du-Rhône, a department where residual yields are positively related with
736 pollinator dependence (slope = 2.39 +/- 0.16); in blue, Eure, a department where residual
737 yields are negatively related with pollinator dependence (slope = -1.78 +/- 0.19). The grey
738 horizontal line is the regression over the full dataset (slope = 0). For sake of readability, the x-
739 coordinate of each crop has been slightly shifted such that crops within a given class of
740 pollinator dependence are not plotted on top of each other.

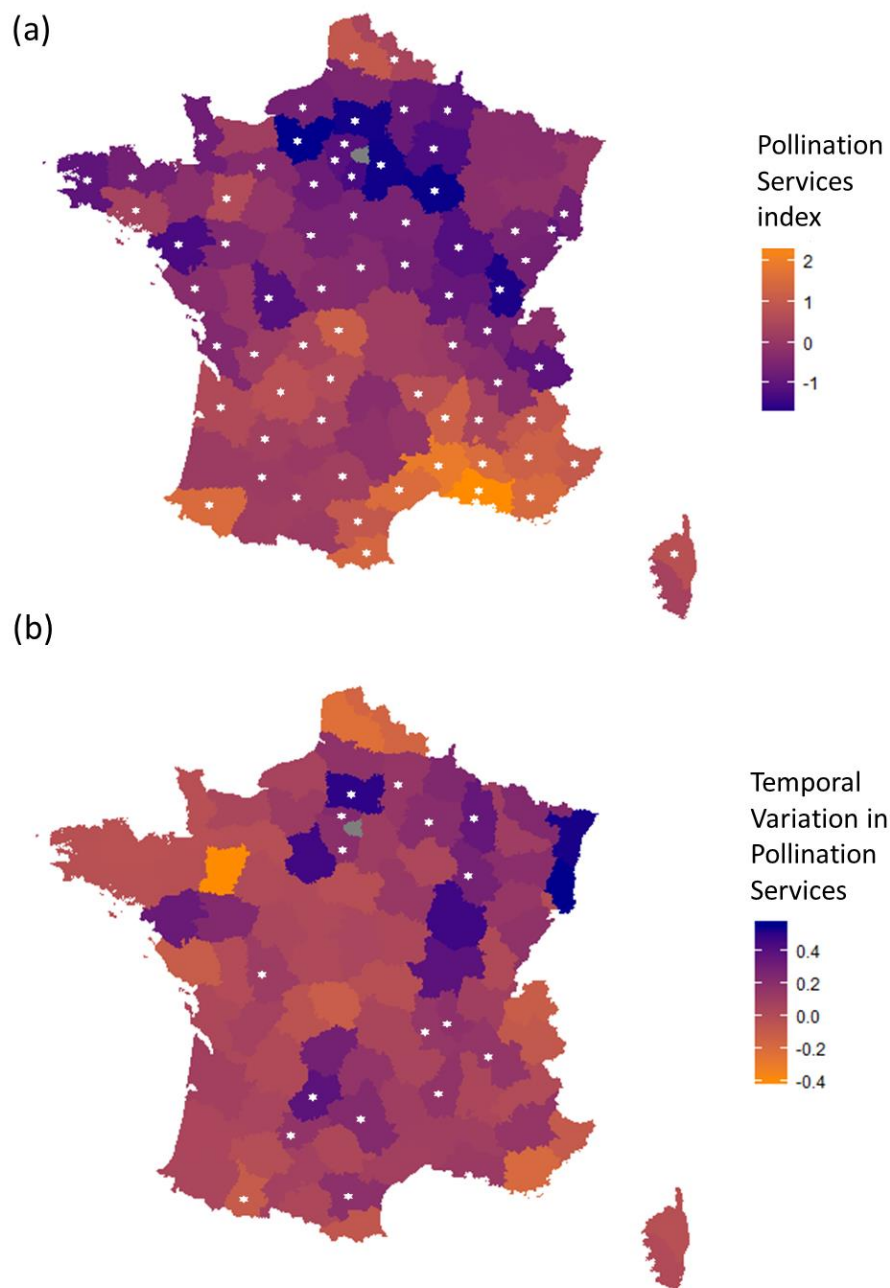


741

742

743 **Fig. 2.** Maps of the Pollination Services Index (a) and the Temporal Variation in Pollination
744 Services (b) across France, at the spatial resolution of departments. Colors indicate the slope
745 of the relationship between relative mean yield (a) or the coefficient of variation of the yield
746 (b) and the level of crop pollinator dependence. Stars indicate departments with a significant
747 relationship.

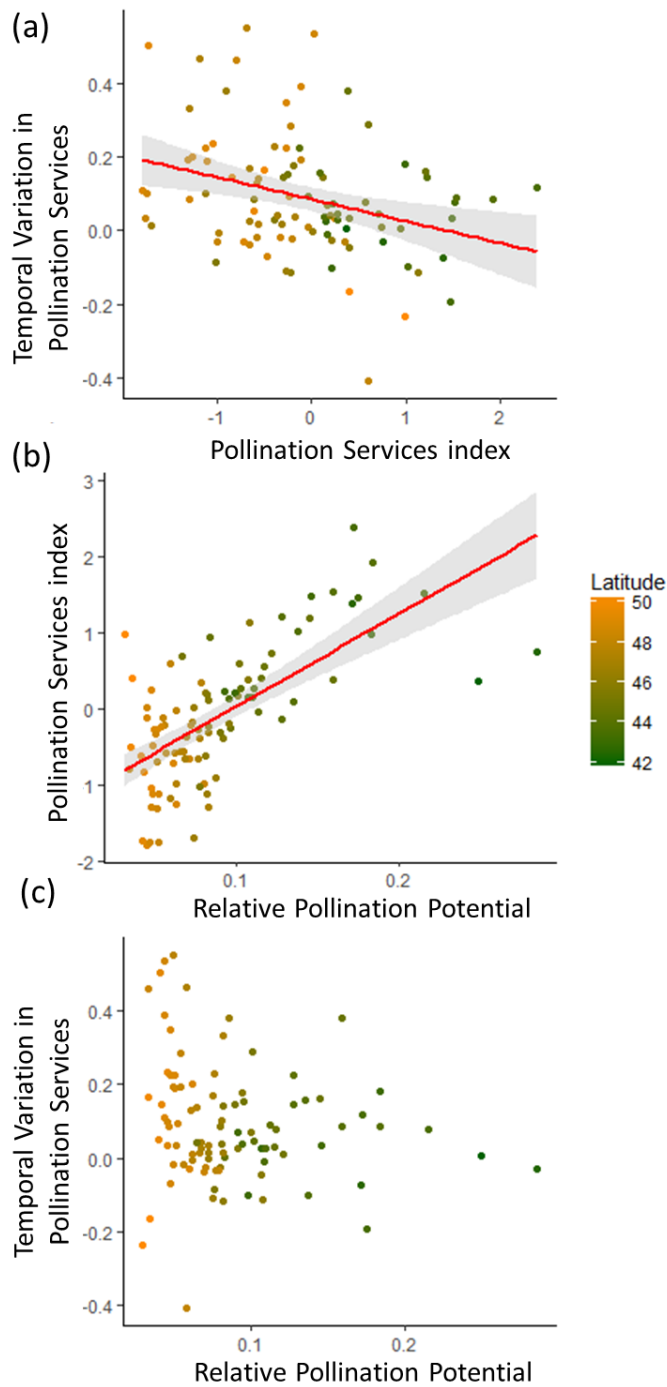
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750

751 **Fig. 3.** Relationships among three pollination indices in France: (a) Pollination Services Index
752 vs. Temporal Variation of Pollination Services; (b) Pollination Services Index vs. Relative
753 Pollination Potential; (c), Temporal Variation in Pollination Services vs. Relative Pollination
754 Potential. Each point represents a department; colors indicate the latitude of the centroid of
755 the department.



756

757 **Appendix A. Supplementary Data**

758 Color should be used for figures A1, A3, A4.

759

760 Table A1. List of the 56 crops grown in 95 departments during the 2000-2010 period.

761

762 Fig. A1. PCA on the three High Nature Value components. The ordination diagram is plotted
763 for axes 1 and 2 (a). The distribution of eigenvalues is shown in (b).

764

765 Fig. A2. Changes in standardized mean yield with increasing level of crop pollinator
766 dependence for each of the 95 departments. Dots represent crop yield and the line indicates
767 the estimate from the linear regression model described in the main text. Colors indicate the
768 sign and slope of the relationship between relative mean yield and the level of crop
769 pollinator dependence, as for Fig. 1.

770

771 Fig. A3. Changes in yield stability with increasing level of crop pollinator dependence for each
772 of the 95 departments. Dots represent crop yield and the line indicates the estimate from
773 the linear regression model described in the main text. Colors indicate the slope of the
774 relationship between the coefficient of variation of the yield and the level of crop pollinator
775 dependence, as for Fig. 1.

776

777 Table A1. List of the 56 crops grown in 95 departments during the 2000-2010 period.

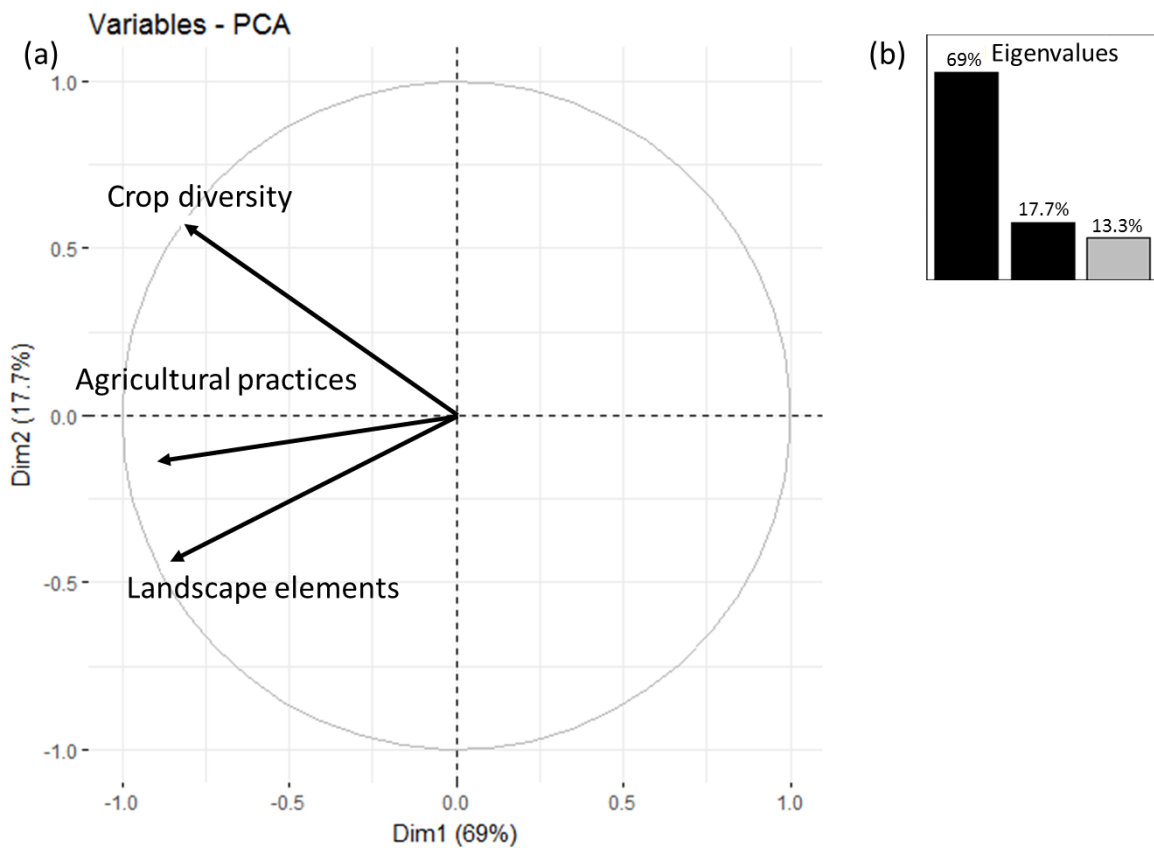
Crop name	Taxonomic group	Level of pollinator dependence	Positive impact of animal pollination on production	Number of departments growing the crop	Average total area per year (ha)	Average yield per ha (100 kg/ha)
Kiwifruits	<i>Actinidia deliciosa</i>	95	essential	42	4161	5377.18
Total oat	<i>Avena sativa</i>	0	no increase	88	100993.36	3572.45
Other rapeseeds	<i>Brassica napus</i> and <i>Brassica rapa</i> subsp. <i>oleifera</i>	25	modest	85	1239754.45	2469.55
Peppers	<i>Capsicum annuum</i>	5	little	56	520.64	14705.36
Chestnuts	<i>Castanea sativa</i>	25	modest	44	7030.09	527.73
Watermelons	<i>Citrullus lanatus</i>	95	essential	24	156.18	5269.82
Clementines and mandarins	<i>Citrus clementina</i> and <i>Citrus nobilis</i>	5	little	4	1650.91	403.09
Grapefruits	<i>Citrus paradisi</i>	5	little	4	216.27	340.45
Hazelnuts	<i>Corylus avellana</i> var. <i>grandis</i>	0	no increase	53	2919.18	722.45
Muskmelons	<i>Cucumis melo</i>	95	essential	64	12504.36	9385.27
Cucumbers	<i>Cucumis sativus</i>	65	great	80	546.73	123404.45
Gherkins	<i>Cucumis sativus</i>	65	great	47	227.73	5222.36
Zucchini	<i>Cucurbita pepo</i>	95	essential	87	2539.82	26212.09
Squashes	<i>Cucurbitaceae</i>	95	essential	86	2126.36	18566.91
Figs	<i>Ficus carica</i>	25	modest	19	415	915.45
Strawberries	<i>Fragaria x ananassa</i>	25	modest	92	3498.36	10864.36
Soybean	<i>Glycine max</i>	25	modest	68	59235.45	1411
Sunflower seeds	<i>Helianthus annuus</i>	25	modest	80	611718.55	1837.55
Total barley	<i>Hordeum vulgare</i> and <i>Hordeum hexasticon</i>	0	no increase	89	1630336.82	4870.64
Nuts	<i>Juglans regia</i>	0	no increase	69	16420.45	1044.45
Lentils	<i>Lens culinaris</i>	0	no increase	56	8195	456.45
Flaxseeds	<i>Linum usitatissimum</i>	5	little	69	10352.45	1007.82
Sweet Lupines	<i>Lupinus albus</i>	0	no increase	73	4864.36	1349.91
Tomatoes	<i>Lycopersicon esculentum</i>	5	little	88	4736.55	92174.45
Cider apples	<i>Malus domestica</i>	65	great	64	11251.36	7818.09
Table apples	<i>Malus domestica</i>	65	great	93	45964.09	28771.18
Other unmixed cereals	NA	0	no increase	61	28786.64	1407.18
Melanges of cereals (excluding meteil)	NA	0	no increase	82	49438.18	2345.91
Olives	<i>Olea europaea</i>	0	no increase	16	16535.45	187.64
Rice	<i>Oriza sativa</i>	0	no increase	3	18643.45	161.45
Avocados	<i>Persea americana</i>	65	great	2	8.45	98.27
Shelled beans	<i>Phaseolus vulgaris</i>	5	little	73	7003.09	3305.55
Dry beans	<i>Phaseolus vulgaris</i>	5	little	50	2871.18	999.36
Green beans	<i>Phaseolus vulgaris</i>	5	little	92	30369.64	8746.36
Protein peas	<i>Pisum sativum</i>	0	no increase	87	262965.64	3000.18
Green peas	<i>Pisum sativum</i> subsp. <i>sativum</i> var. <i>sativum</i>	0	no increase	86	33349.64	4817.64
Dried peas	<i>Pisum sativum</i> subsp. <i>sativum</i> var. <i>sativum</i>	0	no increase	21	1044.27	386.18
Apricots	<i>Prunus armeniaca</i>	65	great	39	14456.18	1805.64
Cherries	<i>Prunus avium</i>	65	great	79	11016.45	3231.18
Plums	<i>Prunus domestica</i>	65	great	72	18680.82	5578.64
Almonds	<i>Prunus dulcis</i>	65	great	18	1360.723	224.45
Peaches and nectarines	<i>Prunus spp</i>	65	great	60	16863.64	6599.82
Pears	<i>Pyrus communis</i>	65	great	85	8103.18	15934.09
Blackcurrants and blueberries	<i>Ribes nigrum</i> and <i>Vaccinium myrtillus</i>	25	modest	80	2642.82	2174.64
Redcurrants	<i>Ribes rubrum</i>	25	modest	74	364	2809.45
Raspberries	<i>Rubus idaeus</i>	65	great	89	943.27	3652.73
Rye	<i>Secale cereale</i>	0	no increase	87	27067.82	3856.36
Eggplants	<i>Solanum melongena</i>	25	modest	73	461	18528.73
Sorghum	<i>Sorghom bicolor</i>	0	no increase	72	51877.82	2809.18
Triticale	<i>Triticosecale</i>	0	no increase	86	276058.55	4420.09
Total bread wheat	<i>Triticum aestivum</i>	0	no increase	89	4435083.45	5404.36

Total durum wheat	<i>Triticum durum</i>	0	no increase	68	376115.09	2423
Broad beans	<i>Vicia faba</i>	25	modest	85	73532.36	2291.45
Vine	<i>Vitis vinifera</i>	0	no increase	74	896643.36	4955.45
Maize (grain and seed)	<i>Zea mays</i>	0	no increase	89	1581688.27	7234.36
Maize (sweetcorn)	<i>Zea mays</i>	0	no increase	35	24360.27	3542.27

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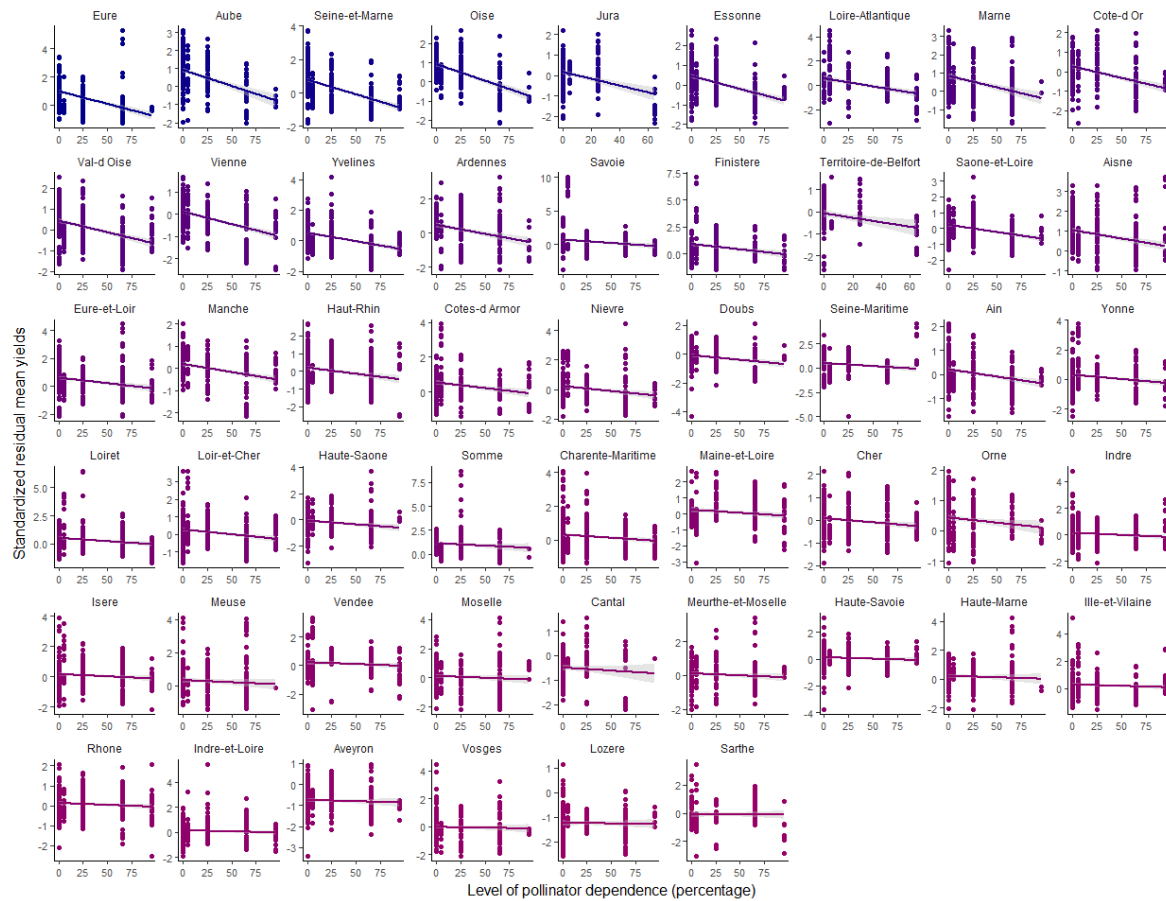
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781 for axes 1 and 2 (a). The distribution of eigenvalues is shown in (b).



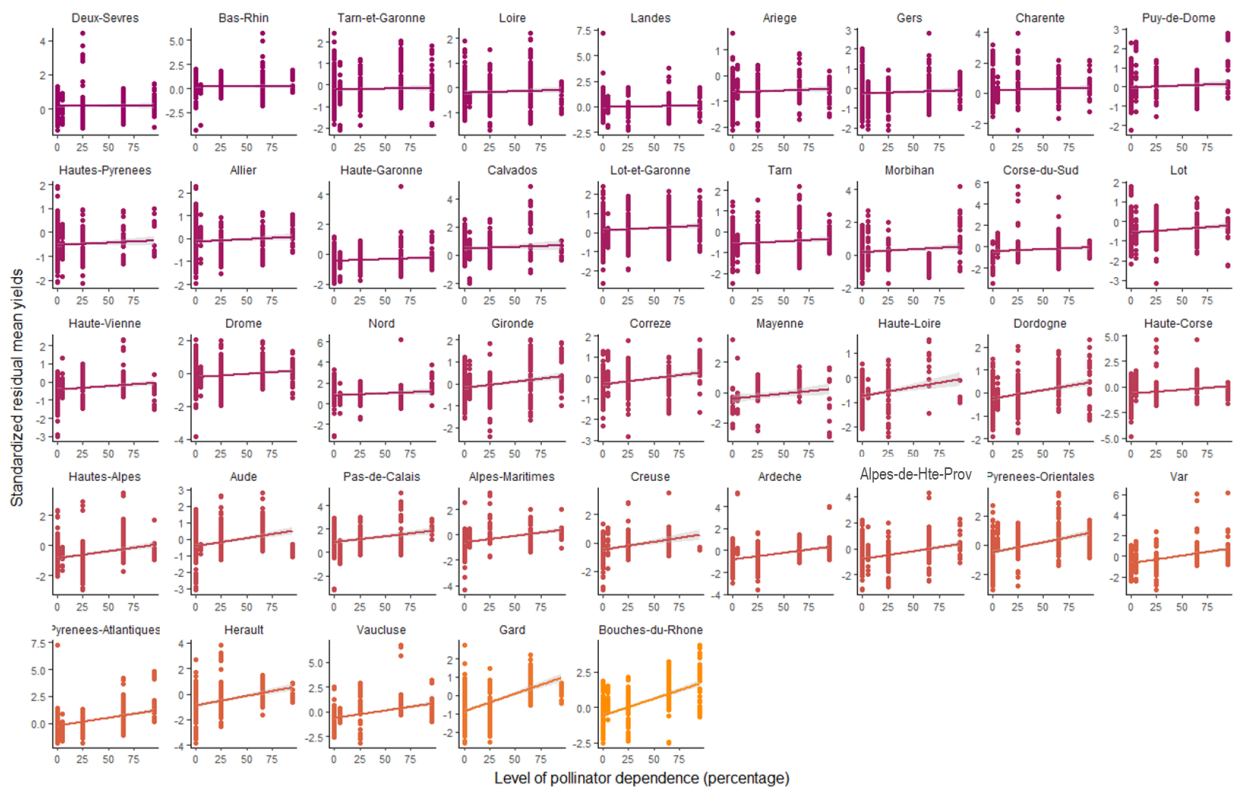
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 786 the estimate from the linear regression model described in the main text. Colors indicate the
 787 sign and slope of the relationship between relative mean yield and the level of crop
 788 pollinator dependence, as for Fig. 1.



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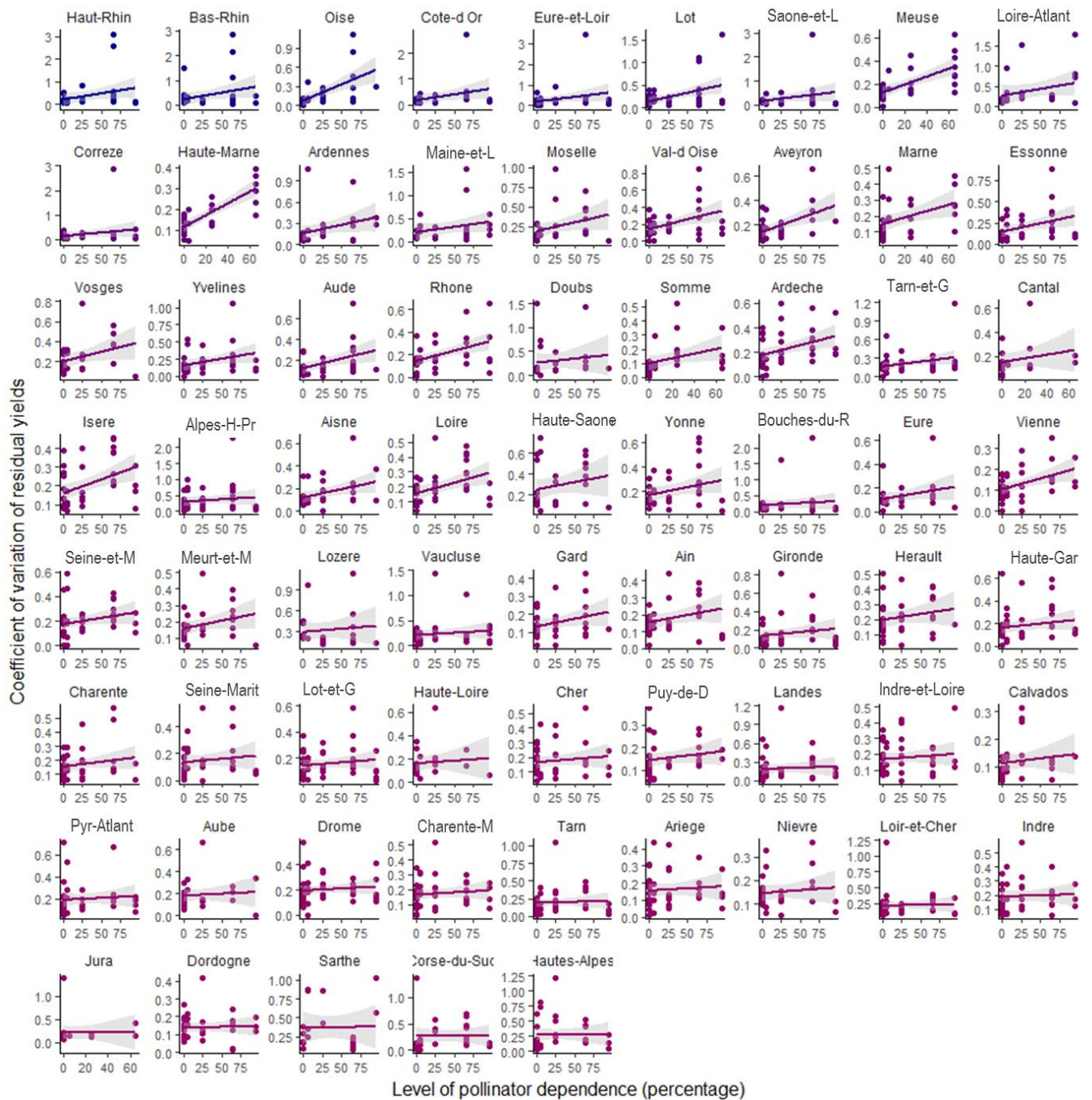
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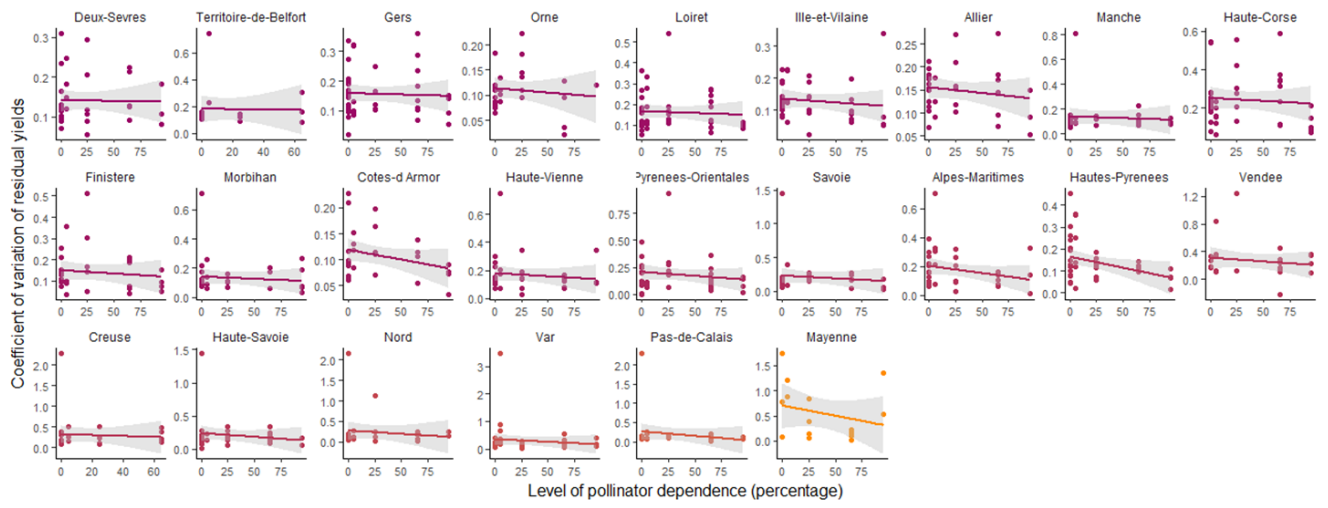
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 797 the linear regression model described in the main text. Colors indicate the slope of the
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 799 dependence, as for Fig. 1.



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