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

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1 -Article Title: New indices for rapid assessment of pollination services based on crop yield
2 data: France as a 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 effectiveness and 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 and
37 crop pollinator dependence; the Temporal Variation in Pollination Services is defined as the
38 slope of the linear regression between the inter-annual coefficient of variation of crop yield
39 and crop pollinator dependence. We calculated these two indices in France, where we show
40 extensive spatial variation in the estimated pollination services. We further show that this
41 variation in Pollination Services Index is negatively correlated with the index of Temporal
42 Variation in Pollination Services, and positively correlated with habitat quality for pollinators.
43 Looking at France with a departmental resolution, results showed that intensive farming is
44 not significantly associated with lower values of the Pollination Services Index, but it is
45 positively correlated with higher Temporal Variation in Pollination Services. Despite some
46 limitations that deserve further attention, these indices may constitute promising, cost-
47 effective tools to highlight regions of pollination deficit over large areas.

48

49 **Highlights**

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

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

52 -Pollination effectiveness correlates positively with habitat quality for pollinators.

53 -Pollination stability correlates negatively with intensive farming.

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

55

56 **Keywords:** Pollination effectiveness; Pollination stability; Relative Pollination Potential; Crop
57 yield; Ecosystem services; Intensive farming.

58

59 **1. Introduction**

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

75
76 The actual contribution of pollinators to crop yields is however known to vary through space
77 and time depending on the abundance, composition or diversity of pollinator communities
78 (Garibaldi et al., 2011b). Assessing the pollination services over large areas is crucial to
79 quantify the provision of these services, to identify general spatial patterns, temporal trends
80 and potential drivers of pollination services, as well as to inform land-management decisions
81 and to achieve conservation objectives. Moreover, the assessment of the spatial distribution
82 of the pollination services over large spatial extents has become a policy priority in the last

83 years (see e.g. “Action 5” of the EU biodiversity strategy, European Commission, 2011).

84 However, so far there is no simple means to evaluate this variation over large areas.

85 Numerous local scale studies have demonstrated a positive effect of wild pollinator

86 abundance or diversity on crop production and its temporal stability (Garibaldi et al., 2016,

87 2013, 2011b). Most of these field-scale studies use data-intensive experimental methods to

88 collect detailed information on flower-visitor richness, visitation rates, and seed or fruit set,

89 thereby providing precise estimates of the pollination services at a local scale. Although they

90 are fundamental for an accurate measure of animal pollination, these methods cannot easily

91 be used to assess the pollination services over larger areas, because they are expensive and

92 extremely time-consuming.

93 To our knowledge, a single, indirect measure of the pollination services exists at the

94 European scale: Zulian et al. (2013) introduced the Relative Pollination Potential index,

95 defined as the potential of ecosystems to support crop pollination by wild bees. The Relative

96 Pollination Potential combines literature and expert-assessed parameters on the ecology of

97 wild bee species, with spatial information on resource availability for such pollinators (i.e.,

98 food and nesting sites). The Relative Pollination Potential decreases with the distance to

99 semi-natural habitats (a proxy of the bee visitation rate) and increases with annual

100 temperature (a proxy of wild bee activity). The mapping of this index shows an increase in

101 pollination potential along a North-South gradient following the temperature gradient in

102 Europe (Zulian et al., 2013). However, the indicator only uses a-priori and expert-based

103 assumptions on wild bee ecology, it is not based on observations of pollinators or pollination,

104 and has not been validated against data. For this reason, its interpretation as an indicator of

105 the pollination service might be questionable.

106

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

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

131 and spatial resolution of crop yield data.

132

133 **2. Materials and methods**

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

137

138 2.1. Crop dataset and pollinator dependence

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

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

159

160 2.2. Calculation of the Pollination Services and the Temporal Variation in 161 Pollination Services indices

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

166

167 *Pollination Services Index*

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

179 residuals has two important implications for the interpretation of the index.

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

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

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

213

214 *Temporal Variation in Pollination Services*

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

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

228

229 2.3. Correlations with the Relative Pollination Potential, another index of
230 pollination services, and the High Nature Value index

231 We examined, using the Spearman's rank correlation coefficient, all the pairwise correlations
232 between the Pollination Services Index, the Temporal Variation in Pollination Services, and
233 the Relative Pollination Potential of Zulian et al. (2013). For each department, the Relative
234 Pollination Potential is provided at a 100m x 100m pixel resolution; we calculated the average
235 Relative Pollination Potential in agricultural areas as the mean over all farmland pixels of a
236 department.

237 Both the Relative Pollination Potential and the Pollination Services Index exhibit a strong
238 latitudinal gradient (see below). To examine the spatial patterns in both Pollination Services
239 Index and Temporal Variation in Pollination Services, as well as their environmental
240 correlates, while checking for biases due to the latitudinal gradient and particularly for a
241 strong spatial autocorrelation in the data, we then used linear mixed models (Pinheiro and
242 Bates, 2000). These models included three fixed explanatory variables that are likely to drive
243 most of the latitudinal gradient, namely the Relative Pollination Potential (habitat
244 availability), agricultural intensity and temperature (climate). We also included administrative
245 regions ($n = 22$, i.e. administrative regions group about 4-5 neighbouring administrative
246 departments) as a random variable in the model, to further account for unidentified drivers
247 of the latitudinal gradient. We then checked that the residuals of both models were spatially
248 uncorrelated using Moran's Index with inverse-distance weighting.

249 We used the High Nature Value index (Andersen et al., 2004; Pointereau et al., 2010, 2007)
250 to characterize agricultural intensity. The High Nature Value index is defined in areas where

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

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

274

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

286

287 **3. Results**

288 3.1. Latitudinal gradient in the pollination services

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

297

298 3.2. Negative correlation between the pollination services and their temporal

299 variation

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

315

316 3.3. Relationships with the Relative Pollination Potential and the index of 317 agricultural intensity

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

323 Potential were not significantly related at the national scale, although there was a tendency
324 for more variable pollination services in departments with a lower Relative Pollination
325 Potential (Spearman's $\rho = -0.19$, $n = 95$, $P = 0.06$, Fig. 3c).
326 When all drivers of pollination were assessed within a single model accounting for spatial
327 autocorrelation, the Pollination Services Index was significantly correlated with the Relative
328 Pollination Potential only, but not with agricultural intensity nor with temperature (Table 2).
329 In contrast, the Temporal Variation in Pollination Services was not related with the Relative
330 Pollination Potential, but was positively correlated with the index of agricultural intensity and
331 negatively with mean annual temperature (Table 2).

332

333 **4. Discussion**

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

340

341 4.1. Two independent indices show consistent patterns in the pollination services
342 The Pollination Services Index and the Relative Pollination Potential (Zulian et al., 2013),
343 although they were obtained from fully independent datasets and methods, exhibited a
344 significant positive correlation, partly driven by a strong latitudinal gradient. The Pollination
345 Services Index developed in this study is based on the measurable and final output of
346 pollination services provided by all types of pollinators, crop yields. In contrast, the Relative

347 Pollination Potential combines literature and expert-assessment on the ecology of wild bee
348 species only. As its name indicates, it only characterizes a *potential* for one type of pollination
349 and has not been validated by data on pollinators or pollination so far. The most intuitive
350 explanation for their positive correlation is a causal one: the Relative Pollination Potential is a
351 proxy for the abundance and/or diversity of pollinator communities, which in turn controls
352 the rate of pollen delivery to crops (Garibaldi et al., 2013; Kleijn et al., 2015). With this
353 interpretation, both indices validate each other by producing consistent information from
354 independent datasets. The causal role of pollinators is further supported by the latitudinal
355 gradient in species richness observed in wild bees in Europe (Nieto et al., 2014). However,
356 cross-validation and the congruence of spatial gradients are only circumstantial evidence,
357 and a formal validation of all indices would require comparison with direct measurements of
358 pollination effectiveness.

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

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

363 One important question is whether the numerous other environmental factors that have
364 recognized key impacts on crop yield (weather, soil type, farming practices including e.g. use
365 of pesticides or fertilizers or fruit culling...) could bias the Pollination Services Index and for
366 example create a latitudinal gradient in crop yield of pollinator-dependent crops that is not
367 due to pollinators. The latitudinal gradient in the Pollination Services Index implies that
368 pollinator-dependent crops tend to have higher yields in southern vs. northern France,
369 whereas the opposite is true for pollinator-independent crops. Climate/weather, soil type or
370 farming practices can only drive such pattern if their effects on crop yield were related to

371 pollinator-dependence through mechanisms that do not involve pollination. For sake of
372 illustration, one can imagine a situation in which pollinator-dependent crops were more
373 likely to be trees than pollinator-independent crops, and in which trees in general would
374 grow better in warmer climates (two highly unlikely hypotheses). In this case, the yield of
375 pollinator-dependent crops would be higher than the national mean in warm departments
376 (southern France) and lower than the mean in northern France, which would create the
377 same signal as the one we observe. However, we cannot think of an obvious mechanism,
378 other than pollination, that would cause the effects of environmental factors on crop yield to
379 vary systematically with the pollinator dependence of crops. In summary, we detect patterns
380 of local adaptation such that pollinator-dependent crop have higher yields in southern vs.
381 northern France. The most likely explanation for this pattern remains a gradient in pollination
382 effectiveness, but we do not have the data here to make firm conclusions.

383 With these limitations in mind, the two pollination indices introduced here still show
384 patterns consistent with some of the known effects of landscape on pollinators. Analyses
385 controlling for spatial autocorrelation patterns showed that the Relative Pollination Potential
386 was a significant correlate of the Pollination Services Index, while the index of agricultural
387 intensity, as measured by a combination of in-field practices, crop diversity and landscape
388 simplification, was not. This result suggests that the quality and diversity of landscapes may
389 prevail over agricultural practices to explain pollination of pollinator-dependent crops. This
390 absence of a relationship between pollination services and agriculture is at odds with
391 numerous studies demonstrating negative effects of intensive agriculture on pollinators,
392 particularly wild bees (Hendrickx et al., 2007; Le Féon et al., 2010; Koh et al., 2016) and the
393 service they provide (Deguines et al., 2014). This somewhat surprising result should be
394 tempered by several considerations. (1) The strong latitudinal gradient influencing all indices

395 and their environmental correlates makes it difficult to isolate individual correlations. (2)
396 Although pollination services were not correlated with agricultural intensity on average, their
397 temporal variability increased with the index of agricultural intensity, in agreement with most
398 earlier results showing negative impacts of agriculture on pollinators and pollination. (3)
399 Drivers not included in the Relative Pollination Potential (Zulian et al., 2013) or in the High
400 Nature Value index may also influence pollinator communities. Among these drivers, other
401 pollinator groups such as flies that are not accounted for in the Relative Pollination Potential
402 could have a stronger functional role as they are known to be adapted to cooler climates
403 (Elberling and Olesen, 1999). Pesticide use could also play an important role as it has been
404 increasing steadily in France (Hossard et al., 2017), especially in northern France (“EuroStat,”
405 2011). Pesticides are known to have strong effects on pollinators, particularly on wild bees
406 (e.g. Brittain et al., 2010; Gill et al., 2012; Laycock et al., 2012) or in simplified landscapes
407 such as those encountered in northern France (Park et al., 2015). (5) Finally, both indices may
408 have been calculated at a spatial resolution too coarse to detect the local effects of within-
409 field agricultural practices (see below).

410

411 4.2. Caveats for interpretation of the index values

412 It is important to keep in mind that the Pollination Services Index does not provide an
413 absolute, but only a relative assessment of the pollination services. This limitation is not a
414 major one, but one should be careful that a positive value of the Pollination Services Index
415 does not necessarily indicate sufficient pollination, but only a better pollination than in the
416 other sampling units. With spatial variation in the pollination services, the analysis
417 introduced here will produce values of the pollination services ranging from negative values
418 that are significantly different from zero to positive values that are significantly different from

419 zero, regardless of the average effectiveness of pollination across the study area. Hence, the
420 Pollination Services Index should only be used to compare areas, not to assess pollination in
421 an absolute manner.

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

433 The value of the Pollination Services Index may further be changed by our choice to work on
434 residual crop yields, thereby removing any linear temporal trend in yield. This choice was
435 made to avoid the confounding effects of genetic progress and improvement of agricultural
436 practices and is justified when the temporal trend in crop yield is positive. However, for
437 several crops, such as almonds or kiwis, the temporal trend in crop yield between 2000 and
438 2010 was negative. For pollinator-dependent crops, a decline in pollination effectiveness is
439 one likely cause of this decline in productivity. Our Pollination Services Index does not include
440 this temporal decrease in crop yield and is therefore again conservative. The index was
441 designed to detect differences in pollination effectiveness in space, but may have limited
442 power to detect temporal trends in pollination effectiveness. To address temporal changes in

443 the pollination services, we recommend calculating the index without the initial step of linear
444 regression of crop yield on years.

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

456

457 4.3. Perspectives

458 To go further in determining the causal link between our indices and the pollination services,
459 several perspectives could be explored. First, the two indices and the Relative Pollination
460 Potential should be compared with variables describing the structure and composition of
461 pollinator communities. Quantitative data on wild pollinators are few, especially on large
462 spatial scales and for taxonomic groups beyond bees. However, recent initiatives to monitor
463 pollinator communities via participatory science schemes may produce useful data in the
464 short term (see e.g. the French photographic survey of pollinators, Deguines et al., 2012).

465 Second, the ultimate test for these indices would be a comparison with proper estimates of
466 pollinator limitation using caging and pollen supplementation experiments (e.g. Hudewenz et

467 al., 2014). Third, a more accurate examination of the relationship between pollination
468 services indices and its potential drivers, particularly agricultural intensity may require finer
469 spatial resolutions of the indices. For example, there may be a mismatch in the departmental
470 resolution at which the indices were calculated, and the spatial resolution at which
471 agricultural practices or landscape structures influence pollinator population dynamics and
472 behaviour (Steffan-Dewenter et al., 2002). However, the spatial resolution of both pollination
473 services indices depends solely on the spatial resolution of data and there is no obstacle to
474 obtaining them at much finer spatial resolution should crop yield data be available.

475

476 **5. Conclusion**

477 The Pollination Services Index and the Temporal Variation in Pollination Services are
478 correlated in a consistent way, and their correlation with the Relative Pollination Potential
479 and the index of agricultural intensity, respectively, are in line with the known influence of
480 habitat quality and agricultural practices on pollinator communities. Despite the need for
481 further work to ascertain causality, our indices pave the way to quantify and map pollination
482 services at any spatial resolution in a cost-effective way over large areas. Such maps could
483 help identifying areas suffering from deficit in pollination services and related drivers. They
484 could also contribute to evaluate agricultural and conservation practices. Last but not least,
485 they provide easy-to-grasp communication tools to raise awareness of stakeholders on
486 pollination issues.

487

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497

498 **Authors’ contributions**

499 EP and CF conceived the ideas and designed methodology; GM, FA and EP collected the data;
500 GM, CF and EP analysed the data; GM, CF, FA and EP led the writing of the manuscript. All
501 authors contributed critically to the drafts and gave final approval for publication.

502

503 **Appendix A. Supplementary data**

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

505

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676

677

678 TABLES AND FIGURES

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

680

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

684

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

688

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

698

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

703 relationship.

704

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

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

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

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

709 the department.

710

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

714 **Table 1** Levels of pollinator dependence and spatial coverage of 56 major crops in France

715 between 2000 and 2010. “Average total area” is the total annual area sown with a given type

716 of crop, averaged over the 11 years.

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*

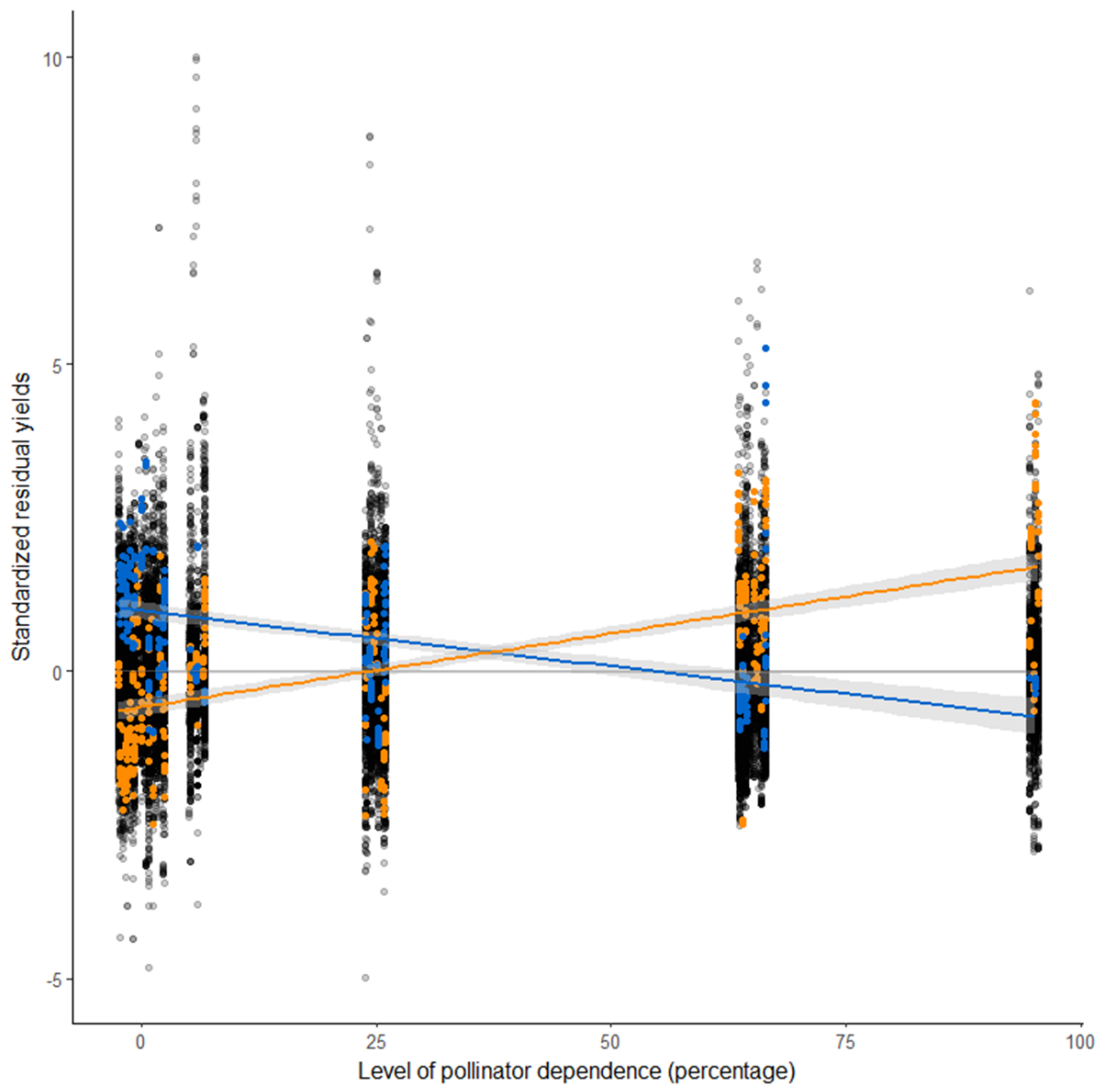
719

720 **Table 2** Correlations between the Pollination Services Index (PSI) or the Temporal Variation

721 in Pollination Services (TVPS) and environmental variables, as inferred from a linear mixed

722 model with administrative regions as random effect.

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

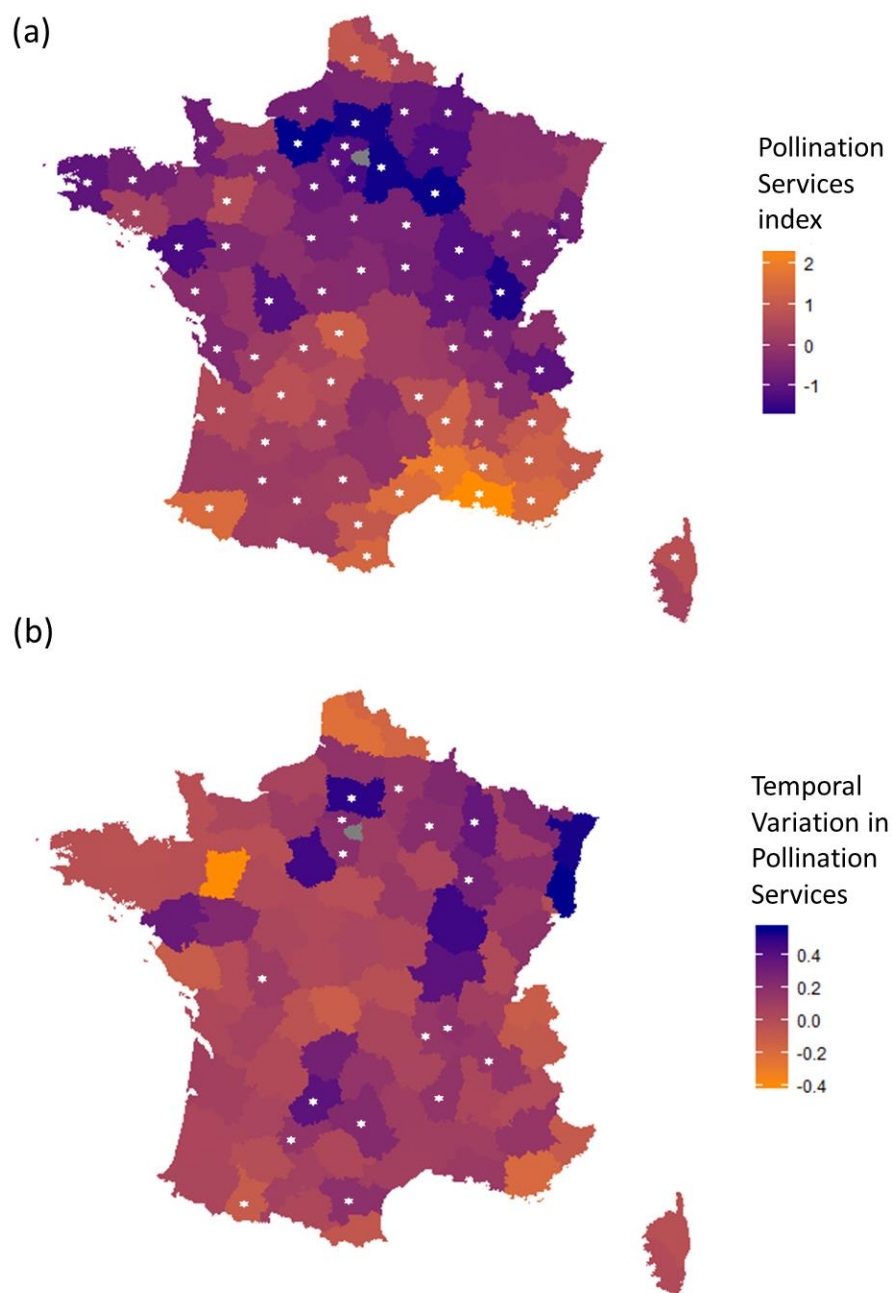


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733

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

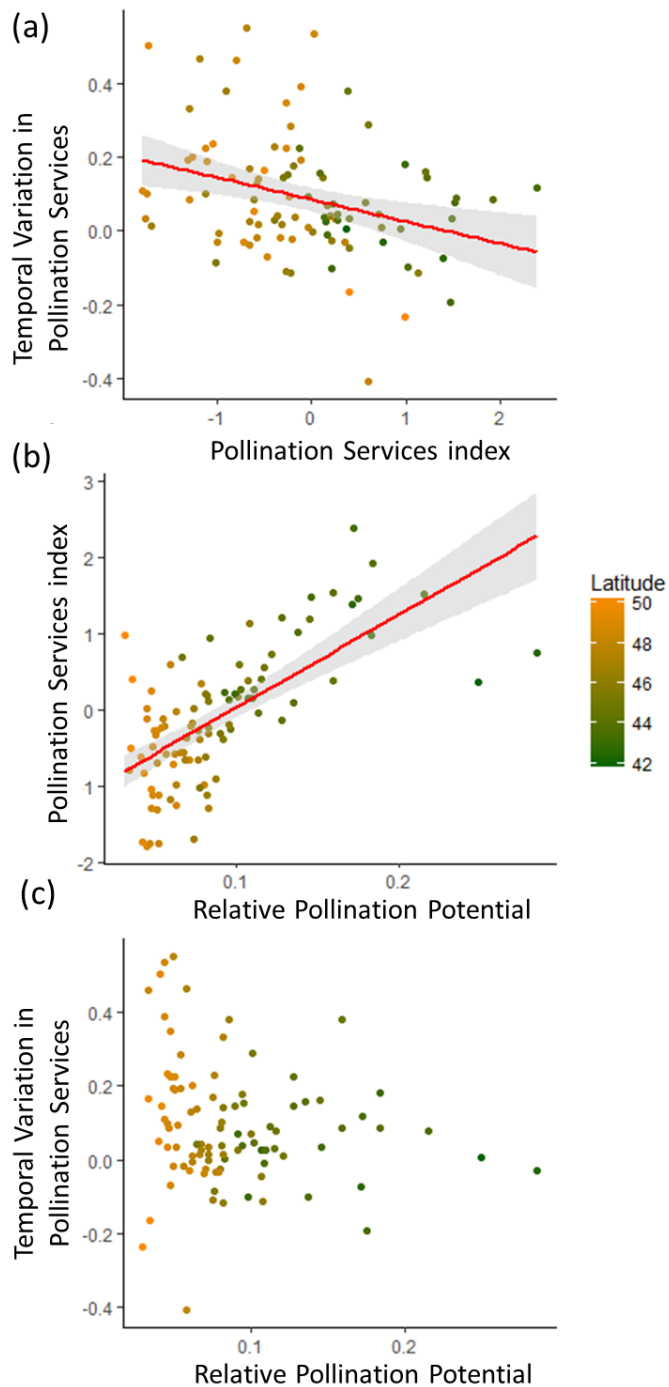
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742 **Fig. 3.** Relationships among three pollination indices in France: (a) Pollination Services Index
743 vs. Temporal Variation of Pollination Services; (b) Pollination Services Index vs. Relative
744 Pollination Potential; (c), Temporal Variation in Pollination Services vs. Relative Pollination
745 Potential. Each point represents a department; colors indicate the latitude of the centroid of
746 the department.



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748

749 **Appendix A. Supplementary Data**

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

751

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

753

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

756

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

762

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

768

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

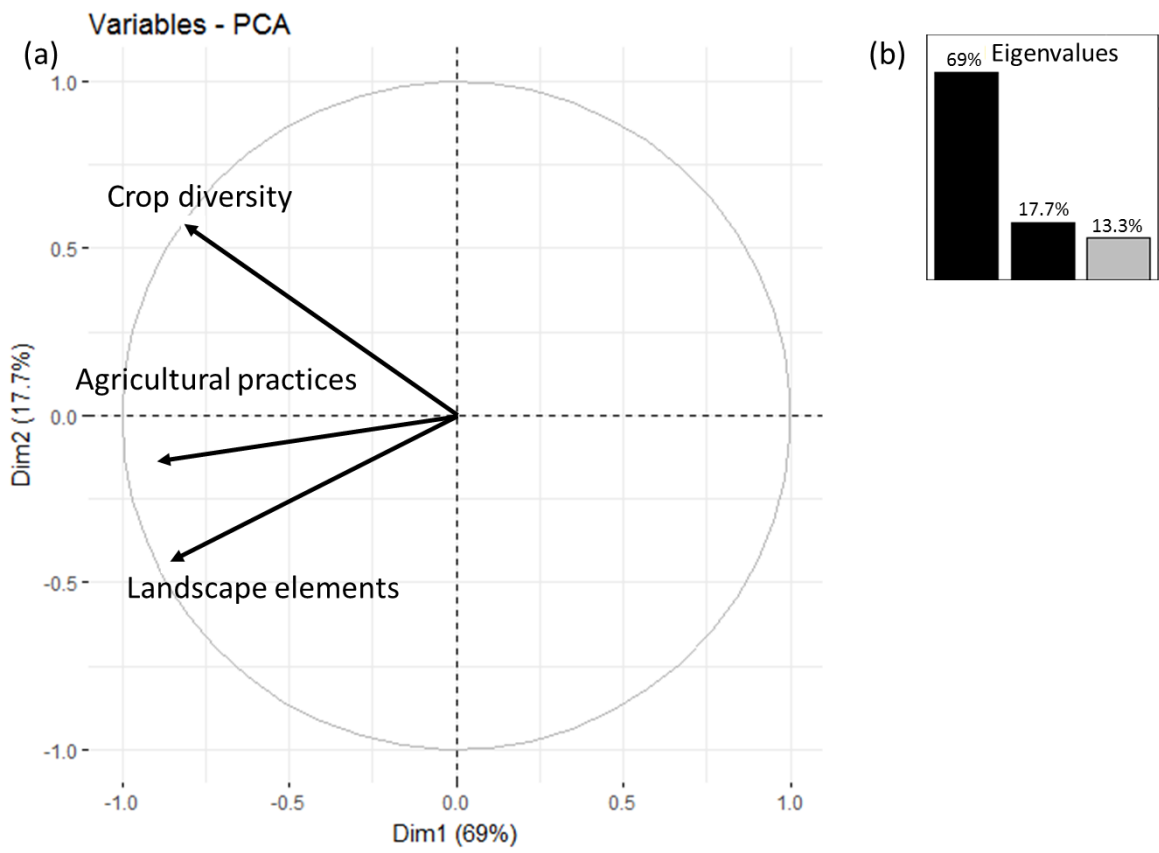
Crop name	Taxonomic group	Level of pollinator dependence	Positive impact of animal pollination on production	Number of departments growing the crop	Average total area per year (ha)	Average yield per ha (100 kg/ha)
Kiwifruits	<i>Actinidia deliciosa</i>	95	essential	42	4161	5377.18
Total oat	<i>Avena sativa</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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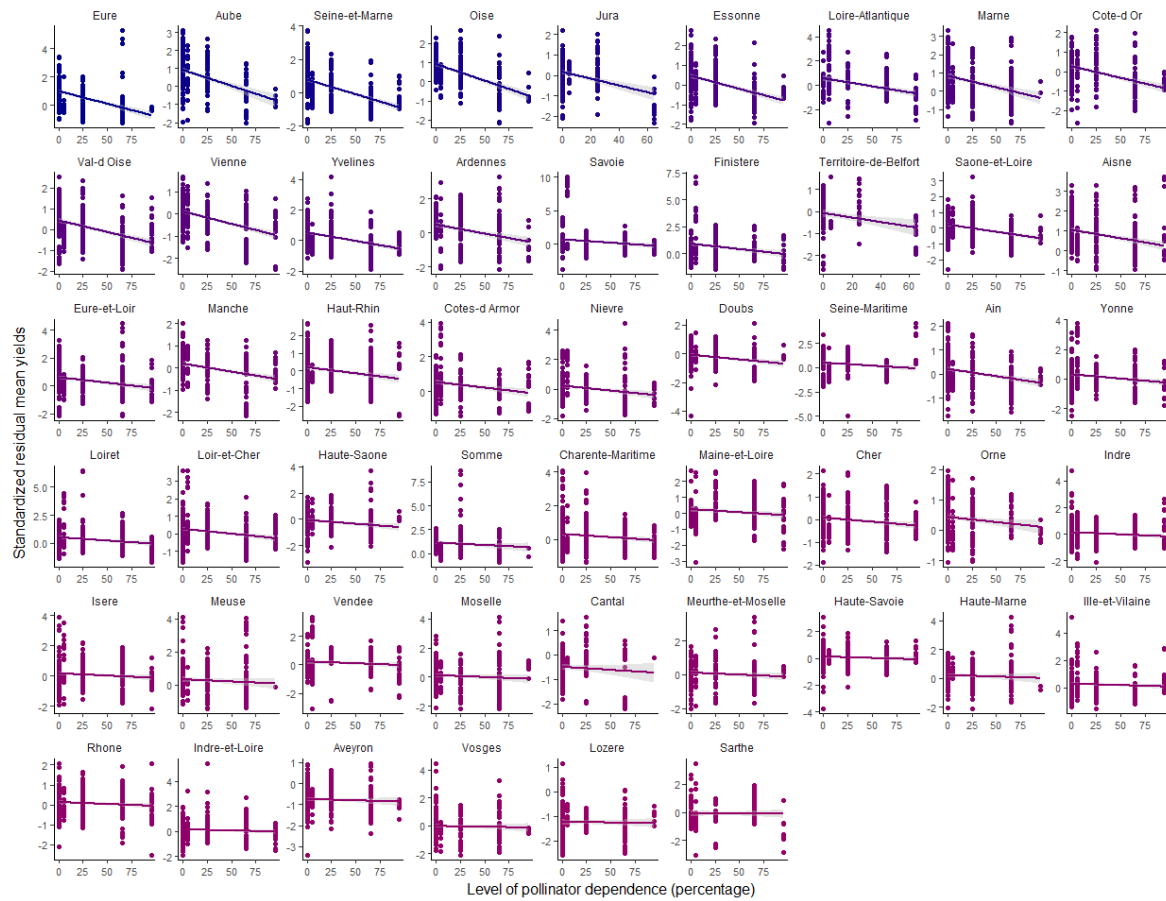
772 Fig. A1. PCA on the three High Nature Value components. The ordination diagram is plotted
773 for axes 1 and 2 (a). The distribution of eigenvalues is shown in (b).



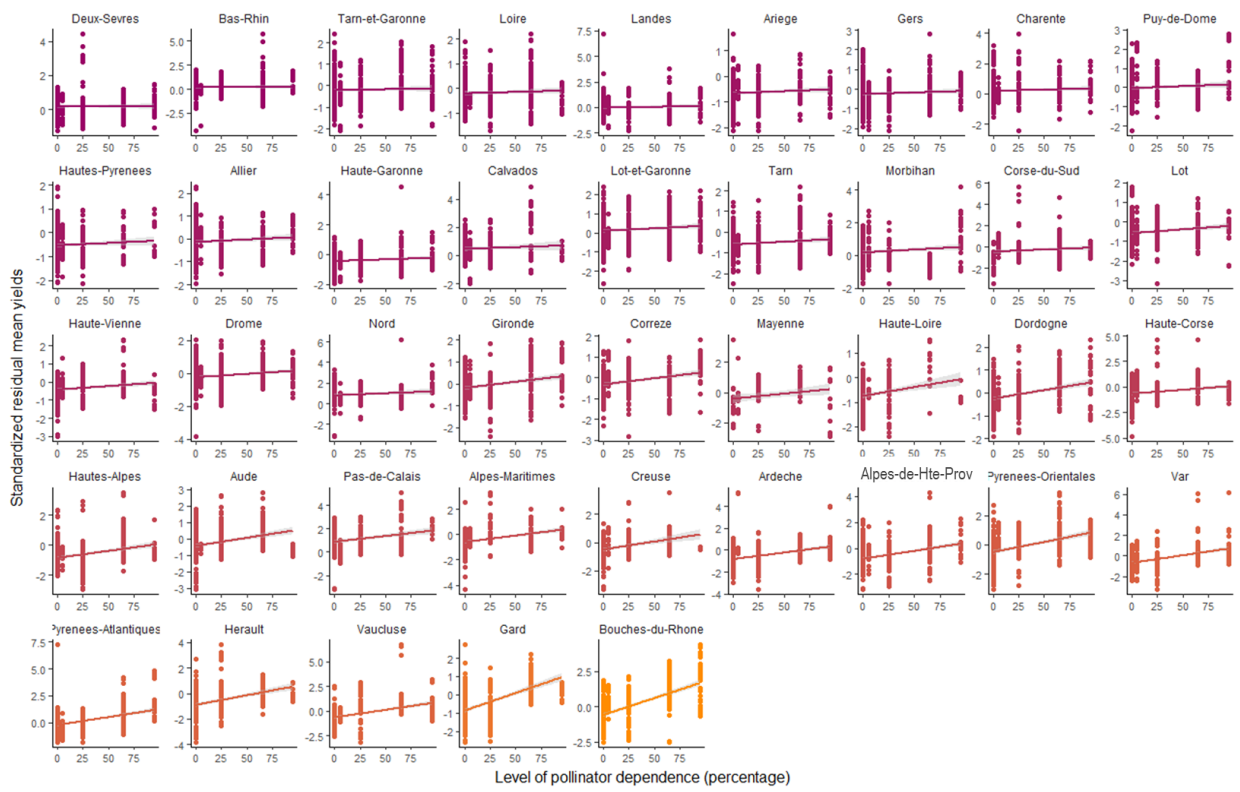
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775

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



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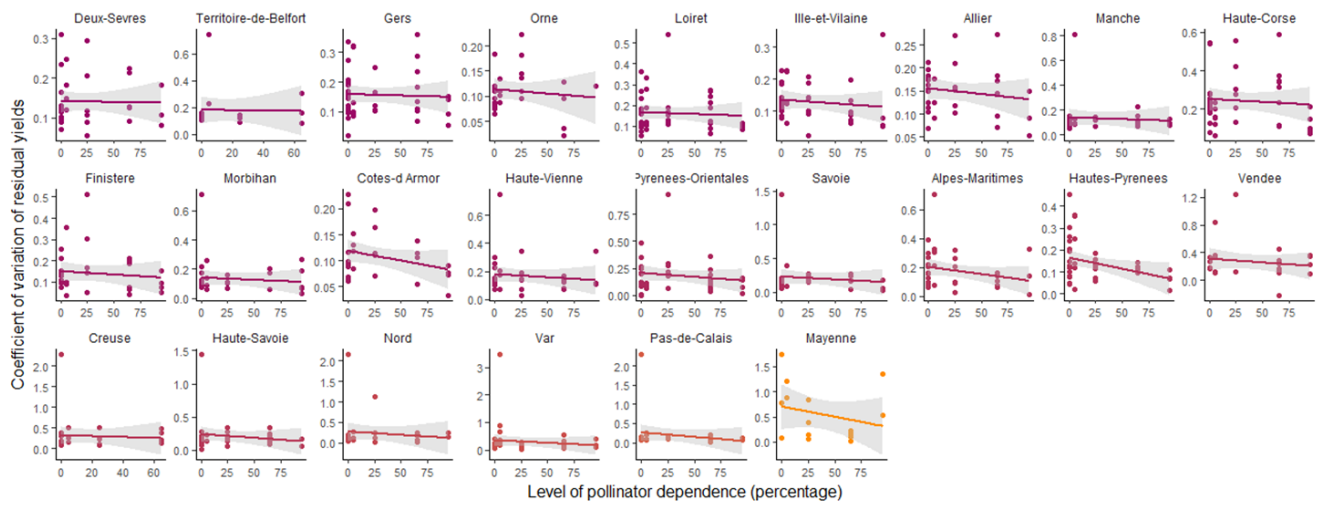
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786

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



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