

1 **Biodiversity and yield trade-offs for organic farming**

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21 SG, JAH, TT, YL and YZ conceived the idea. SG, JAH and YZ undertook the
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23

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27

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29

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40 **Abstract**

41 Organic farming supports higher biodiversity than conventional farming, but at the
42 cost of lower yields. We conducted a meta-analysis quantifying the trade-off between
43 biodiversity and yield, comparing conventional and organic farming. We developed a
44 compatibility index to assess whether biodiversity gains from organic farming exceed
45 yield losses, and a substitution index to assess whether organic farming would
46 increase biodiversity in an area if maintaining total production under organic farming
47 would require cultivating more land at the expense of nature. Overall, organic farming
48 had 23% gain in biodiversity with a similar cost of yield decline. Biodiversity gain is
49 negatively correlated to yield loss for microbes and plants, but no correlation was
50 found for other taxa. The biodiversity and yield trade-off varies under different
51 contexts of organic farming. The overall compatibility index value was close to zero,
52 with negative values for cereal crops, positive for non-cereal crops, and varies across
53 taxa. Our results indicate that, on average, the proportion of biodiversity gain is
54 similar to the proportion of yield loss for paired field studies. For some taxa in non-
55 cereal crops, switching to organic farming can lead to a biodiversity gain without
56 yield loss. We calculated the overall value of substitution index and further discussed
57 the application of this index to evaluate when the biodiversity of less intensified
58 farming system is advantageous.

59

60 **1. Introduction**

61 In order to meet the demands of a growing world population (FAO 2019), agriculture
62 must provide sufficient food and raw materials. Agriculture occupies about 38% of the
63 land surface of the Earth (FAO 2019). However, the conversion of land from nature to
64 agriculture has caused and is still causing major biodiversity losses (Robinson &
65 Sutherland 2002; Godfray *et al.* 2010; Tilman *et al.* 2011; Newbold *et al.* 2015).
66 Ensuring sufficient food supply in a sustainable way is a challenge (Godfray *et al.* 2010;
67 Tilman *et al.* 2011; Newbold *et al.* 2015; Ramankutty *et al.* 2018; Seppelt *et al.* 2020).
68 As there is a pressing need to make agriculture less damaging to biodiversity,
69 conservation measures in agricultural landscapes need to be re-considered in a Global
70 Biodiversity Framework (Wanger *et al.* 2020). Shifting from conventional to organic
71 farming has been considered as an option for enhancing agricultural biodiversity (Tuck
72 *et al.* 2014).

73

74 Conventional farming with intensive management (e.g. routine application of synthetic
75 pesticides and fertilizers in large crop monocultures) achieves high production, but with
76 serious negative consequences for farmland biodiversity and its associated ecosystem
77 services (Reganold & Wachter 2016; Meemken & Qaim 2018; Ramankutty *et al.* 2018;
78 Beckmann *et al.* 2019). Organic farming, which uses no or only natural pesticides and
79 organic fertilizer, is seen as a more environmentally friendly option (Bengtsson *et al.*
80 2005; Albrecht *et al.* 2007; Clough *et al.* 2007; Lori *et al.* 2017). Organic farming, has
81 been rapidly increasing worldwide, in many different crops over the last decades
82 (IFOAM 2021). In general, organic farming harbors higher biodiversity but lower yield
83 than conventional farming (Batáry *et al.* 2011; Seufert *et al.* 2012; Tuck *et al.* 2014).
84 Since organic farming has a lower yield per unit area than conventional farming, more

85 land is required for producing the same amount of food (Phalan *et al.* 2011a; Balmford
86 *et al.* 2018; Meemken & Qaim 2018). Thus, additional land from non-crop such as
87 natural and semi-natural habitats need to be converted to organic farmland if the same
88 production is required. As farmland, including organically farmed land, usually harbors
89 lower biodiversity than natural habitats, such conversion likely increases the negative
90 impact of farming on biodiversity (Phalan *et al.* 2011a; Grass *et al.* 2021). Therefore,
91 due to its lower yield, organic farming could reduce and even cancel out the positive
92 effect on biodiversity gain when transferring from conventional farming by reducing
93 natural land. Whether it is worthwhile to switch from conventional to organic farming
94 in terms of the biodiversity gain and yield loss is under debate (Hodgson *et al.* 2010;
95 Phalan *et al.* 2011b; Tschardtke *et al.* 2012; Balmford *et al.* 2018).

96

97 While individual studies comparing conventional and organic farming inform us about
98 specific trade-offs between biodiversity gain and yield loss (e.g. Solomou & Sfougaris
99 2011; Gabriel *et al.* 2013), a meta-analysis that helps us to have a global synthetic
100 understanding of this topic is essential (Gurevitch *et al.* 2018). There are different,
101 stand-alone meta-analyses, which compare either yield (Seufert *et al.* 2012), or
102 biodiversity (Tuck *et al.* 2014) between organic and conventional farming, and showed
103 that results varies among taxa and crop types. Tuck *et al.* (2014) reported that species
104 richness in organic farming is about one-third higher than in conventional farming, but
105 this effect varies among taxa and crop types. For example, plants benefited more from
106 organic farming than birds, arthropods or microbes, whereas cereals exhibited larger
107 differences in biodiversity than non-cereal crops. Seufert *et al.* (2012) found yield in
108 organic farming to be about one-fourth lower than in conventional farming, but it also
109 varies among crop types, with a much larger yield gap in cereal than non-cereal crops.

110 However, it is still not known whether high yield loss always implies high biodiversity
111 gain, and how such effect differs among different crop types and taxonomic groups. To
112 evaluate whether it is worthwhile to switch from conventional to organic farming we
113 need studies that quantify the effects of organic and conventional farming on both
114 biodiversity and yield. To our knowledge, no such synthesis has been conducted.

115

116 Here, we synthesized studies that evaluated both biodiversity and yield for conventional
117 vs. organic farming, to quantify the strengths of trade-offs between biodiversity and
118 yield, to better inform agricultural management decisions. First, we aim to determine
119 whether high yield loss always means high biodiversity gain across studies and how it
120 varies between crop types and taxonomic groups. To achieve this aim, we i) examine
121 the relation of biodiversity gain to yield loss across all studies in our meta-analysis; ii)
122 define a ‘compatibility index’ to evaluate the overall difference comparing
123 conventional and organic farming based on the relative amount of biodiversity gain and
124 yield loss, and (iii) analyze whether these indices differ between crop types and
125 taxonomic groups, as well as factors that might affect the organic treatments such as
126 agricultural management intensification, climatic zonation, nation and landscape
127 context.

128

129 Second, we propose that the biodiversity gain versus yield loss relationship can provide
130 a good basis for deciding whether it is worthwhile to switch from conventional to
131 organic farming including the fact that organic farming may require the conversion of
132 more non-crop habitat to cultivated land. We developed a substitution index, which can
133 be used to infer whether transferring from conventional to organic farming would be
134 more advantageous for biodiversity conservation. We identify the overall value of this

135 substitution index, and test whether it varies between crop types and taxonomic groups.

136

137 **2. Material and Methods**

138 2.1 Literature search and screening protocol

139 We focused on studies that measured both biodiversity and yield, within a paired
140 fields/farms setting that compared organic management and conventional management.

141 Within management pairs within each study, biodiversity and yield should always have
142 been measured using the same methods and the same spatial sampling unit, so that
143 proportional increases/decrease comparisons are meaningful. We searched articles in
144 the Web of Science Core Collection database. Search terms used were Topic: (organic*
145 OR agri-environment* OR biodynamic OR agroecolog* OR "ecological agri*" OR
146 ecoagri* OR eco-agri*) AND Topic: (inorganic OR convention* OR "chemical
147 fertilizer*" OR "integrated pest management" OR pesticide* OR insecticide* OR
148 herbicide* OR fungicide*) AND Topic: (yield* OR production* OR productivit*)
149 AND Topic: (biodiver* OR richness OR diversit*) (see Appendix S1 in Supporting
150 Information for details of refinement options). We included all articles published
151 between 1990 and 2021, which resulted in 1396 studies.

152

153 In some biodiversity studies, the yield data is only included as background information
154 and not included in the topic field of Web of Science (title + keyword + abstract), hence
155 we missed these studies. The meta-analysis conducted by Tuck *et al.* (2014) focused on
156 the biodiversity comparison between organic and conventional farming, we therefore
157 conducted a full text filtering for all studies used by Tuck *et al.* (2014), which is up to
158 2011 (Fig. S1), and we subsequently used the same search terms to collect articles from
159 2011 to 2021. We classified treatments as conventional or organic according to the

160 classification within the study. For studies that did not mention organic farming, we
161 included farming management without chemical pesticide and synthetic fertilizer as the
162 organic treatment. Other managements included in organic are biological pest control
163 (e.g. micro-organisms for insects), physical control (e.g. using hand or grass cutter for
164 weed), organic manure (e.g. dairy manure and green manure) and cover crops
165 (Bengtsson *et al.* 2005; Seufert *et al.* 2012; Tuck *et al.* 2014).

166

167 We screened titles and abstracts for performing the first selection, excluding studies
168 that lacked a mean or sample size information for species richness or crop yield, which
169 resulted in a total of 359 articles for full-text assessing. Finally, a total of 75 studies met
170 selection criteria and were used in the analysis (see PRISMA diagram in Fig. S1; see
171 bibliography of the 75 studies in Appendix S2). Locations of these studies were showed
172 in Fig. S2. Detailed reasons of exclusion for the 284 studies are provided in Appendix
173 S3.

174

175 2.2 Data extraction and validation

176 Biodiversity was usually reported as the species richness (i.e. number of species)
177 observed in a temporally and/or spatially defined sample. For studies that only reported
178 biodiversity indices (e.g. Shannon entropy), the values were back-transformed to
179 species richness (see Jost *et al.* 2006). Yield could be reported as grain dry weight per
180 area or per plant. We divided crops into cereals (wheat, oat, barley, rice and maize) and
181 non-cereals (fruits, vegetables, coffee, legumes, forage grass, oil crops, tea, sunflower
182 and cocoa). Studies that only measured the overall yield with a mixture of cereal and
183 non-cereal crops were classified as mixed crops. We classified organisms into five
184 broad taxonomic groups: birds, mammals, invertebrates, microbes and plants. Studies

185 may contain multiple taxonomic groups, crop types, multiple regions or multiple
186 treatments. In the 75 selected studies, we calculated 177 biodiversity comparisons and
187 175 yield comparisons. Some studies recorded biodiversity for more than one
188 taxonomic group but only one crop type of yield, and vice versa; therefore, 205 paired
189 biodiversity and yield comparisons could be constructed from the 177 biodiversity
190 comparisons and 175 yield comparisons.

191

192 We extracted species richness and yield means, standard deviations, and sample sizes
193 either directly from the text and tables or from figures using Getdata 2.26 (Peng *et al.*
194 2019). Sixteen studies with 55 cases had no standard deviation for biodiversity, and 13
195 studies with 22 cases had no standard deviation for yield. As the scale of biodiversity,
196 yield and their standard deviation varied between studies, directly imputing missing
197 standard deviation from all dataset would generate inappropriately large values. We
198 therefore first calculated the effect size and the related variances for the studies with
199 variance information, based on which we then imputed the missing variances (van
200 Buuren & Groothuis-Oudshoorn 2011). The missing variances was computed as the
201 average value from 100 imputation chains (Kabacoff 2011).

202

203 Considering that organic treatment is poorly defined and context dependent (Seufert *et al.*
204 2017), we further divided selected studies according to different management
205 practices, climatic zones and locations. Management practices include different
206 intensification levels according to the fertilization and pesticide application following
207 Beckmann *et al.* (2019). Accordingly, two intensification levels, low and medium, were
208 identified for fertilization application and pesticide use (see Appendix S4 for details).
209 We followed Peel *et al.* (2007)'s guidelines and divided our studies into different

210 climatic zones based on their locations. As organic treatment might depend on national
211 regulations (Seufert *et al.* 2017), we divided all studies by nation, categorizing European
212 Union countries as EU. It needs to be noted that due to the lack of sufficient studies,
213 meaningful comparisons might not be possible for all categories. The number of studies
214 for each category was provided in Table S1.

215

216 Furthermore, we extracted information on the proportion of arable land at the radius of
217 1km as a proxy for landscape complexity (Tuck *et al.* 2014) for respective studies. If
218 the information was not recorded but detailed locations of study sites were available,
219 the proportions of arable land was estimated based on the most recent digital maps from
220 Google Earth. As all of these studies were published after 2005 and were mostly in
221 Europe, where temporal changes in the proportion of arable land at the landscape level
222 are likely minor.

223

224 2.3 Effect size

225 We used log response ratios to compare biodiversity and yield in organic and
226 conventional farming. As effect size for the relative biodiversity in organic and
227 conventional farming (E_b), we used the logarithm of the ratio (R_b) of species richness
228 in the organic (B_o) and conventional (B_c) treatment in each study,

$$229 \quad E_b = \ln(R_b) = \ln\left(\frac{B_o}{B_c}\right)$$

230 Similarly, as effect size for the relative yield (E_y) in the organic and conventional
231 treatment, we used the logarithm of the ratio (R_y) of yield in the organic (Y_o) and
232 conventional (Y_c) fields,

$$233 \quad E_y = \ln(R_y) = \ln\left(\frac{Y_o}{Y_c}\right)$$

234

235 The corresponding variances, $\sigma^2(E_b)$ and $\sigma^2(E_y)$ are:

236
$$\sigma^2(E_b) = \frac{\sigma_{B_o}^2}{n_{B_o} * B_o^2} + \frac{\sigma_{B_c}^2}{n_{B_c} * B_c^2}$$

237
$$\sigma^2(E_y) = \frac{\sigma_{Y_o}^2}{n_{Y_o} * Y_o^2} + \frac{\sigma_{Y_c}^2}{n_{Y_c} * Y_c^2}$$

238 where $\sigma_{B_o}^2$ and $\sigma_{B_c}^2$ are the variances of B_o and B_c , respectively, and n_{B_o} and n_{B_c} are the

239 corresponding numbers of replicate measurements ; $\sigma_{Y_o}^2$ and $\sigma_{Y_c}^2$ are the variances of Y_o

240 and Y_c , and n_{Y_o} and n_{Y_c} are the corresponding numbers of replicate measurements.

241

242 2.4 Compatibility index and substitution index

243 We propose two indices (illustrated in Fig. 2) to summarize the strength of the trade-

244 off observed between biodiversity and yield when comparing organic management to

245 conventional management. The compatibility index simply contrasts the proportional

246 increase in biodiversity with the proportional decrease of yield – it is high when

247 increasing biodiversity is highly compatible with maintaining yield (and in pure win-

248 win scenarios, see Fig. 2A and Appendix S5 for the inference). The substitution index

249 aims to quantify how comparatively biodiversity-rich a third, unfarmed landcover

250 would have to be, to favor a strategy of conventional farming combined with sparing

251 such unfarmed land. When the substitution index is high, the organic farming is likely

252 to lead to higher overall species-abundance, under certain assumptions (see Fig. 2B).

253 Our compatibility index, C_{c-o} , is defined as

254
$$C_{c-o} = \ln(R_b * R_y) = E_b + E_y$$

255 It is a heuristic measure which is higher when the biodiversity gain is large compared

256 to the yield penalty when comparing the organic management to the conventional.

257 The variance of C_{c-o} is:

258
$$\sigma^2(C_{c-o}) = \sigma^2(E_b) + \sigma^2(E_y)$$

259

260 Intuitively, a positive or high value of C_{c-o} suggests that the organic farming is effective,
261 demonstrating compatibility of yield with biodiversity on the same land (see Fig. 2A)–
262 but mathematically it does not give a condition for whether this management is the
263 optimal choice for biodiversity (see Fig. 2C).

264

265 To clarify the overall losses/gains involved in switching management, we should
266 include the potential biodiversity decrease caused by maintaining overall agricultural
267 yield in any option where yield-per-area is lower. Conversely, it may sometimes be
268 beneficial to conventional farming if this “spares” some land with a high biodiversity
269 value.

270

271 Consider an area divided in a proportion conventionally managed agricultural land p
272 and a proportion uncropped land $(1-p)$ (Fig. 1; although N and B are illustrated as blocks,
273 we don't make any assumption about the spatial configuration of these landcovers).

274 Assuming biodiversity in the whole of the area is a weighted average of the biodiversity
275 of its component areas, the total biodiversity would be $p * B_c + (1 - p) * N$ where N
276 is the biodiversity in the natural area. In an area with the same production output from
277 organic farming, the area proportion for agriculture would be $\frac{p}{R_y}$. The biodiversity in

278 this situation would be $\frac{p}{R_y} * B_o + \left(1 - \frac{p}{R_y}\right) * N$.

279

280 From the viewpoint of biodiversity maximization, organic farming would be the better

281 solution if:

$$282 \quad \frac{p}{R_y} B_o + \left(1 - \frac{p}{R_y}\right) N > p B_c + (1 - p) N$$

283

284 which can be simplified to either:

$$285 \quad \frac{R_b - R_y}{1 - R_y} > \frac{N}{B_c}$$

286 in the expected case where the organic farming has lower yield ($R_y < 1$), or the

287 opposite inequality

$$288 \quad \frac{R_b - R_y}{1 - R_y} < \frac{N}{B_c}$$

289 in the unexpected case if ever the organic farming has higher yield ($R_y > 1$).

290

291 We can furthermore consider the following scenarios where no trade-off actually

292 exists:

293

294 1) When $R_y \geq 1$ & $R_b > 1$, i.e. no yield loss but biodiversity gain when comparing
295 conventional to organic farming, then organic farming is always preferred, which can
296 also be considered as a win-win scenario (blue hatched area in Fig. 2B).

297

298 2) When $R_y < 1$ & $R_b \leq 1$, i.e. no biodiversity gain but only yield loss, then organic
299 farming cannot be preferred, which can also be considered a lose-lose scenario (red
300 hatched area in Fig. 2B).

301

302 Usefully, without knowing N , we set up a substitution index (S_{c-o}) as:

303
$$S_{c-o} = \frac{R_b - R_y}{1 - R_y}$$

304

305 The substitution index measures a threshold for the biodiversity of low-intensive
306 organic farming, to evaluate whether converting to organic farming is worthwhile as
307 extra land would be needed when reaching the same total production. In other words, if
308 the S_{c-o} is larger than the ratio in biodiversity in non-farmed areas to conventional land,
309 (i.e. N/B_c), then organic farming is preferred. Otherwise, it is not preferred.

310

311 The variance of S_{c-o} is (see Appendix S6 for derivation):

312
$$\sigma^2(S_{c-o}) = \left(\frac{\sigma^2(R_b)}{(R_b - 1)^2} + \frac{\sigma^2(R_y)}{(1 - R_y)^2} \right) * \left(\frac{R_b - 1}{1 - R_y} \right)^2$$

313

314 2.5 Data analysis

315 We first conducted a meta-regression to determine linear relationships between the
316 mean effect size of yield ($E_y = \ln(R_y)$) and biodiversity ($E_b = \ln(R_b)$) based on the
317 mixed-effects model with the restricted maximum likelihood (REML) and weighted
318 considering the sampling variances (Gurevitch *et al.* 2001; Zuur *et al.* 2009), of which
319 E_b is the independent variable. Because some studies contain multiple cases, we created
320 a hierarchical dependence structure in the model by including study identity and species
321 taxa as a random factor (Peng *et al.* 2019; Wan *et al.* 2020). Analysis was first
322 conducted for the overall dataset, subsequently separate for each taxon group.

323

324 Next, we used mixed-effects model with REML in a hierarchical structure to estimate
325 the grand mean biodiversity effect size (E_b), yield (E_y) and compatibility index (C_{c-o})
326 as well. Mean effect sizes for the different taxa in each crop type were first estimated

327 separately, and then estimated for crop types by merging all taxa, and finally the overall
328 effect size. Birds in the non-cereal crop type only had one study which did not allow us
329 to calculate the between-study variance, thus birds in non-cereal crop were not included
330 in the hierarchical model structure (Chen & Peace 2013). Furthermore, we compared
331 the organic-conventional ratio of biodiversity (R_b), yield (R_y) and the compatibility
332 index (C_{c-o}) for different management intensities, climatic zones and study nations.
333 Comparisons were separated by crop types and taxa, while groups ≤ 3 studies were not
334 compared. Accordingly, meaningful comparisons were possible for low and medium
335 fertilizer intensities for microbes and plants in non-cereal crop species. We further
336 analyzed the correlation between the effect size of biodiversity (E_b), yield (E_y),
337 compatibility index and the proportion of arable land. Correlations were analyzed by
338 meta-regression for each taxon group and overall dataset, again based on the mixed-
339 effects model with REML and weighted according to their variances.

340

341 We calculated the value of S_{c-o} based on the mean of E_b and E_y , for the taxa in each crop
342 types, and then the overall value. Some sub-groups were not used for the S_{c-o} calculation
343 because they were in the ‘win-win’ or ‘lose-lose’ quadrants (Fig 2B) (only cases with
344 $R_b > 1$ and $0 < R_y < 1$ were analyzed).

345

346 Finally, we assessed potential publication bias with funnel plots and a trim-and-fill
347 assessment (Duval & Tweedie 2000). Heterogeneity was assessed with the Q test. Bias
348 corrected equations were used to recalculate all the effect sizes (Appendix S7).

349

350 All analyses were conducted in R (version 4.0.3; R Core Team 2020). Package “metafor”
351 (version 2.4-0; Viechtbauer 2010) was used for conducting all meta-analysis models.

352 The missing variance resulted from missing standard deviation was imputed by package
353 “mice” (version 3.13.0; van Buuren & Groothuis-Oudshoorn 2011). All data were
354 included in Appendix S4.

355

356 **3. Results**

357 **3.1 Biodiversity and yield relationships**

358 Looking at biodiversity gain and yield loss when moving from conventional to organic
359 farming, we found that the majority (111 out of 205 cases) had trade-offs with positive
360 biodiversity gain (i.e. higher biodiversity and lower yield in organic than conventional)
361 and a minority had trade-offs with negative biodiversity gain (15 cases). We found 47
362 cases of win-win, while 32 cases were lose-lose situation (Fig. 3).

363

364 When combining all studies, we found no significant linear relationship between the
365 overall effect sizes (log ratios of organic to conventional farming) for biodiversity and
366 yield ($\beta = -0.03$, $SE = 0.03$, $P = 0.253$, Fig. 3). Examining the different taxa, there were
367 significant negative linear relationship for microbes ($\beta = -0.26$, $SE = 0.12$, $P = 0.028$)
368 and plants ($\beta = -0.15$, $SE = 0.05$, $P = 0.002$), but not for any of the other taxa (Fig. 3).

369

370 **3.2 Compatibility and substitution index**

371 Overall, the compatibility index (C_{c-o}) was very close to 0 (0.05, 95% CI = -0.05~0.14)
372 (Fig. 4A), while the average response ratios for organic-conventional ratio of
373 biodiversity (R_b) and yield (R_y) were 1.23 and 0.83 (Fig. 4B). The compatibility index
374 of non-cereal crops was positive (0.18, 0.04~0.33), while that of cereal crops was not
375 significantly different from zero (-0.09, -0.19~0.01) (Fig. 4A).

376

377 Comparing the different taxa, birds had significantly negative C_{c-o} values in both cereal
378 and non-cereal crops (Fig. 4A). In contrast, plants had a significant positive mean C_{c-o}
379 value cereal crops, but no significance for non-cereal crops (Fig. 4A). The ratio of
380 overall biodiversity in non-cereal crops was significantly larger than 1, while the yield
381 was not significantly different from 1 (Fig. 4B). The same trend was observed for
382 microbes and plants in non-cereal crops (Fig. 4B), indicating that a biodiversity gain is
383 compatible with little or no yield loss for those taxa under organic farming.

384

385 Comparing different intensities of fertilization application, the organic-conventional
386 ratio of biodiversity (R_b) was higher at medium than low intensity level for non-cereal
387 microbes (Fig. S3). No significant difference for other variables and plants (Fig. S3).

388 There was no significant difference for C_{c-o} values between different climatic zones for
389 all taxa when looking cereal and non-cereal crops separately, although variation for the
390 ratio of biodiversity and yield observed for certain taxa (Fig. S4). While limited
391 comparisons were available, differences in R_b , R_y and C_{c-o} were observed among
392 different nations for invertebrates in both cereal and non-cereal crops (Fig. S5). The
393 proportion of arable land negatively correlated with the log ratio of yield (E_y) for
394 microbial studies, and positively correlated with the log ratio of biodiversity (E_b) and
395 the compatibility index (C_{c-o}) for bird studies (Fig. S6). No significant correlation was
396 observed for the overall trend and other taxa (Fig. S6).

397

398 The overall mean effect size of the substitution index S_{c-o} was 2.40 (Table 1).
399 Comparing crop types, the grand mean effect size of S_{c-o} in cereal crops was 1.98. For
400 non-cereal crops overall, biodiversity increased and there was no yield loss, thus
401 organic farming is preferred for biodiversity conservation in general.

402

403 The S_{c-o} showed high variance between the different taxa and crop species (Table 1).
404 The mean effect size of S_{c-o} for birds in cereal crops was 1.18, whereas there was no
405 biodiversity gain in non-cereal crops, and thus organic farming was not preferred for
406 bird biodiversity. The value of the S_{c-o} for microbes in cereal crops was 1.38, whereas
407 there was no yield loss with biodiversity gain in non-cereal crops. The S_{c-o} for the
408 invertebrates was much lower for cereal crops (1.83) than for non-cereal crops (4.18),
409 while for plants this value was much similar between cereal (3.90) and non-cereal (4.88).

410

411 3.3 Publication bias and heterogeneity analysis

412 The funnel plot and trim-and-fill assessment estimated that there was no sign of bias
413 for C_{c-o} of each grand mean and group (Fig. S7, S8), except a positive bias for plants
414 in cereal crops (6 estimated missing cases on the left side of the funnel plots) (Fig.
415 S8). The Q test indicated heterogeneity among all study groups, except for birds in
416 non-cereal crops (Table S2).

417

418 4. Discussion

419 *Biodiversity gain and yield loss*

420 Our study quantified the trade-off between biodiversity and yield in conventional and
421 organic farming. Previously, meta-analyses compared the conventional and organic (or
422 low intensity) farming independently for either yield or biodiversity (Seufert *et al.* 2012;
423 Tuck *et al.* 2014; Beckmann *et al.* 2019) and hence did not analysis the trade-offs
424 between biodiversity and yield. Here we compared yield and biodiversity differences
425 within paired fields setting to understand whether the strength of the trade-off was
426 consistent, or under what circumstances the trade-off became more extreme.

427

428 By examining the relation between biodiversity gain and yield loss across studies, we
429 did not find a significant linear relationship between the effect size of yield and that of
430 biodiversity for switching from conventional to organic farming. Although negative
431 linear relationships between the log response ratios for biodiversity of microbes and
432 plants and yield in organic and conventional farming were observed, there was only a
433 shallow decrease of yield with increasing biodiversity in the organic farming examples.
434 This result indicates that a higher biodiversity gain does not necessarily mean a much
435 greater yield loss. The result is not surprising as both biodiversity loss and yield gain in
436 different studies are influenced by differences in environmental factors such as climatic
437 conditions, surrounding landscapes, study taxa and management strategies (Gomiero *et*
438 *al.* 2011; Tuck *et al.* 2014; Tschardtke *et al.* 2021). In fact, it is also possible that
439 biodiversity enhances yield through the provision of ecosystem services and hence
440 enables the potential of ecological intensification for food security (Bommarco *et al.*,
441 2013).

442

443 The compatibility index that we developed provides a picture of the overall relative size
444 of the biodiversity gain and yield loss. By synthesizing all studies, we found that the
445 index is positive, but close to zero, indicating that the biodiversity gain in organic
446 farming is almost equivalent to the yield loss. This positive effect is mainly driven by
447 the non-cereal crops, where there is no yield loss, while the biodiversity gain is similar
448 for both cereal and non-cereal crops. Organic farming with no yield loss combined with
449 a biodiversity gain supports the organic movement, but this mainly occurs in non-cereal
450 crops (see Fig. 3) to achieve a win-win situation in biodiversity and yield. We found an
451 overall ratio of 1.23 in biodiversity gain comparing organic and conventional farming,

452 which is similar to the 1.34 that Tuck *et al.* (2014) found. Our overall organic to
453 conventional yield ratio (0.83) is similar to that from Seufert *et al.* (2012) (0.75),
454 although Seufert *et al.* (2012) used a much more elaborated sorting of crop types. In
455 other words, our results show that, on average, organic farming has a one-fourth (23%,
456 compared to conventional) gain in biodiversity with a similar cost (20%, compared to
457 organic) in terms of yield decline.

458

459 The sub-group analysis showed that biodiversity gain for different taxa in different
460 crops were mostly similar, but with a higher value for plants and a lower value for
461 birds in cereal crops. Higher biodiversity for plants as compared to animals and
462 microbes in organic versus conventional farms has also been reported in other meta-
463 analyses (Bengtsson *et al.* 2005; Batáry *et al.* 2011), which is likely because the effect
464 of herbicides on weeds is larger than the effect of other pesticides and chemical
465 fertilizer on animals and microbes. In addition, the growing crops themselves can be a
466 food resource for animals, whereas crops suppress weeds. The low compatibility
467 value for birds is caused by the low biodiversity gain (not significantly larger than 0)
468 and high yield loss (almost 50% loss in cereal crops, see Fig. 4B), but it needs to be
469 noted that there was only one study of birds. Overall, our results suggest that, when
470 focusing on microbes and plants in non-cereal crops, switching from conventional to
471 organic farming is viable, because the biodiversity gain comes at a cost of little, or no,
472 yield loss.

473

474 While more studies are needed, our results suggest that biodiversity and yield trade-off
475 is context-dependent due to the variation of organic treatment. Intermediate intensity of
476 fertilization application in the organic farming may enhance both yield and biodiversity

477 for studies on microbes in non-cereal crops. Although differences were observed in the
478 ratio of biodiversity and yield between organic and conventional farming for certain
479 taxa across climatic zones, no significant difference was found in the compatibility
480 index indicating an overall compromise trade-off for yield and biodiversity. We
481 observed a negative correlation between the proportion of arable land and the log ratio
482 of yield for microbial studies and a positive correlation with the log ratio of biodiversity
483 for birds. Considering the unexpected cases for these taxa, i.e. yield in organic is higher
484 than in conventional farming for microbe studies, while biodiversity in organic is lower
485 than in conventional for birds, results suggest that these extreme cases are likely to
486 occur in landscapes where the proportion of arable land is low. Our results again
487 highlighted the importance of landscape factors in driving the biodiversity-yield trade-
488 off (Tuck *et al.* 2014; Smith *et al.* 2020; Tscharntke *et al.* 2021).

489

490 ***The substitution index and its application***

491 The substitution index (S_{c-o}) that we developed in this study provides an initial view if
492 it is worthwhile to switch from conventional to organic farming in a landscape when
493 the objective is to restore biodiversity while maintaining productivity. The overall mean
494 S_{c-o} value is about 2.4, which indicates that, on average, organic-farming would be a
495 more effective strategy if the unfarmed lands are less than 2.4-times as biodiverse as
496 conventional farms. This overall value, however, needs to be interpreted with caution,
497 particularly because there are such marked differences between cereal and non-cereal
498 crops.

499

500 The mean S_{c-o} value is about 2.0 for the cereals, which indicates that organic farming is
501 better if non-crop land has a biodiversity less than 2.0 times that of conventional farms.

502 However, though there are rather few studies that have made this biodiversity
503 comparison, semi-natural areas often exceed this biodiversity threshold, and even
504 uncropped field margins may do so (Hodgson *et al.* 2010; Phalan *et al.* 2011b). Looking
505 at the taxonomic breakdown for cereal crops, birds, microbes and invertebrates showed
506 a low substitution index, indicating that it is easier for non-crop areas to exceed the
507 threshold, whereas plants show a high substitution index.

508

509 For non-cereal crops, there is almost no yield loss combined with a biodiversity gain,
510 thus organic farming is the preferred option. However, this conclusion is very sensitive
511 to the large uncertainty in the yield ratio. Whenever we are confident that $R_y > 1$ (i.e.
512 yield of organic farms is higher than that of conventional one), organic farming is a
513 reasonable option. When R_y is close to, but less than 1, there is a possibility that
514 conventional farming can be an effective strategy. Sub-group analysis showed large
515 variances of the S_{c-o} for non-cereal crops, and little conformity across taxa. Birds were,
516 even in non-cereal crops, likely favored by conventional farming, while microbes were
517 likely favored by organic farming. Invertebrates and plants showed a high and uncertain
518 threshold for conventional farming (i.e. non-crop areas only beneficial if up to 20-times
519 as biodiverse as conventional farms).

520

521 The high variance of the S_{c-o} value that we calculated in this meta-analysis presents a
522 difficulty to directly use the S_{c-o} to guide management and policy-making, because it is
523 always context-dependent. However, by including biodiversity observation from
524 natural habitats, the index provides a window that allows policy-makers and
525 stakeholders to make decisions to choose organic or conventional farming at a local
526 scale. Nonetheless, values might be different for different taxa. For example, in

527 Mbalmayo Forest Reserve in Cameroon, the ratios of arthropod and bird biodiversity
528 between primary forest and conventional farm are about 1.7 and 4.5 (Lawton *et al.*
529 1998). Thus, if the S_{c-o} value for arthropods is larger than 1.7, organic farming strategy
530 could be acceptable, but the value should reach at least 4.5 for bird conservation. The
531 required value might be higher for other locations, for example in the Lore Lindu
532 National Park in Indonesia, where arthropod and bird diversity differences between
533 primary forest to conventional land are about 2.5 and 5 (Schulze *et al.* 2004). In total,
534 the S_{c-o} provides a tool to evaluate biodiversity and yield trade-off, and can indicate the
535 threshold when the biodiversity of organic-farming is advantageous, despite the extra
536 area it takes up. We fully acknowledge that the value of the S_{c-o} varies between locations
537 and taxa. Also it is rarely obvious which land -if any- is encroached upon by organic
538 management. Nonetheless, if similar S_{c-o} values among different regions were observed,
539 then organic farming is more likely preferred for regions with lower species-richness in
540 the remaining non-crop habitats.

541

542 When looking at larger scales, the substitution index can be used to address the
543 biodiversity conservation and land-use intensification debates (e.g. Beckmann *et al.*,
544 2019, i.e. to help the decision makers to address whether a less intensive farming system
545 is more beneficial than an intensive one in terms of yield production and biodiversity
546 conservation (Seppelt *et al.*, 2020). The Biodiversity conservation and land-use
547 intensification trade-off is also related to the “land sparing” vs. “land sharing” debate
548 (Hodgson *et al.* 2010; Godfray & Garnett 2014; Phalan *et al.* 2016; Balmford *et al.*
549 2018). In the “land sparing” strategy, the agricultural land is intensively used for high
550 yielding agriculture to leave as much land as possible for conserving high biodiversity
551 in natural lands (Green *et al.* 2005; Phalan *et al.* 2011a; Ramankutty *et al.* 2018). In the

552 “land sharing” strategy, the agricultural land is managed extensively and biodiversity-
553 friendly, however, more land is required for achieving the same total production as in
554 intensive agriculture (Fischer *et al.* 2008; Phalan *et al.* 2011a; Kremen 2015). Thus, the
555 substitution index can be interpreted as the minimum threshold for the biodiversity of
556 any spared land (as a multiple of the biodiversity of conventional farmland), which
557 would be needed to render a land-sparing strategy optimal. Therefore, when the
558 substitution index is high it is probably difficult to find spared land rich enough in
559 biodiversity, and so the lower intensity agriculture is likelier to maximize biodiversity.
560 When the substitution index is low, it arguably should be easy to find uncultivated land
561 rich enough in biodiversity, that could be combined with the conventional farming to
562 form a “winning” land-sparing strategy.

563

564 ***Future directions and conclusion***

565 Here we only used species richness and crop yield to evaluate the trade-off for
566 conventional-organic conversion. Species richness could be affected by the observation
567 scales (e.g. sampling effort, Belmaker & Jetz 2011) and should be considered in further
568 study. To investigate other metrics, such as species composition, species abundance and
569 farmer income are also encouraged to provide a more comprehensive understanding of
570 this topic (Baudron *et al.* 2021). Further studies are also needed to examine species
571 according to ecological function or their relationship with humans (e.g. synanthropic or
572 not), and divide crops into more specific crop types. In addition, here we assume a linear
573 species-area relationship, a non-linear relationship may also need to be considered,
574 particularly when extending our substitution to a larger scale (Egan & Mortensen 2012).
575 Furthermore, organic farming is not the only way for farmland biodiversity
576 conservation. Studies are also encouraged to investigate trade-offs between the cost and

577 biodiversity gain of other management in agriculture, such as small and diversified
578 fields for biodiversity-friendly landscapes (Tscharntke *et al.* 2021).

579

580 Overall, this study provides (1) a compatibility index to evaluate trade-offs between
581 biodiversity gain and yield loss when switching from conventional to organic farming,
582 and (2) a substitution index to indicate the preferred strategy of conventional to organic
583 farming for maintaining both biodiversity and productivity while considering the
584 impacts of the land claim of agriculture on overall biodiversity. Our results do show the
585 possibility of high biodiversity gain at the cost of little, or no, yield loss when
586 converting from conventional to organic farming in non-cereal crops, indicating that
587 organic farming can be the preferred option to maximize biodiversity. Although the
588 high variance indicates the context-dependency when considering conventional or
589 organic farming, we provided a tool to help local decision makers to address whether a
590 less intensive farming system is beneficial for yield production and biodiversity
591 conservation.

592

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602 **References**

- 603 Albrecht, M., Duelli, P., Müller, C., Kleijn, D. & Schmid, B. (2007). The Swiss agri-
604 environment scheme enhances pollinator diversity and plant reproductive
605 success in nearby intensively managed farmland. *Journal of Applied Ecology*,
606 44, 813-822.
- 607 Balmford, A., Amano, T., Bartlett, H., Chadwick, D., Collins, A., Edwards, D. *et al.*
608 (2018). The environmental costs and benefits of high-yield farming. *Nature*
609 *Sustainability*, 1, 477–485.
- 610 Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011). Landscape-moderated
611 biodiversity effects of agri-environmental management: a meta-analysis.
612 *Proceeding of the Royal Society B*, 278, 1894–1902.
- 613 Baudron, F., Govaerts, B., Verhulst, N., McDonald, A. & Gérard, B. (2021). Sparing
614 or sharing land? Views from agricultural scientists. *Biological Conservation*,
615 259, 109167.
- 616 Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceașu, S., Kambach, S., Kinlock, N.L.
617 *et al.* (2019). Conventional land-use intensification reduces species richness and
618 increases production: A global meta-analysis. *Global Change Biology*, 25,
619 1941–1956.
- 620 Bengtsson, J., Ahnström, J. & Weibull, A.-C. (2005). The effects of organic agriculture
621 on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology*,
622 42, 261–269.
- 623 Belmaker, J. & Jetz, W. (2011). Cross-scale variation in species richness–environment
624 associations. *Global Ecology and Biogeography*, 20, 464-474.
- 625 Bommarco, R., Kleijn, D., & Potts, S.G. (2013). Ecological intensification: harnessing
626 ecosystem services for food security. *Trends in Ecology & Evolution*, 28, 230-

627 238.

628 Chen, D.G. & Peace, K.E. (2013). *Applied Meta-Analysis with R*. CRC Press.

629 Clough, Y., Kruess, A. & Tschardtke, T. (2007). Local and landscape factors in
630 differently managed arable fields affect the insect herbivore community of a
631 non-crop plant species. *Journal of Applied Ecology*, 44, 22–28.

632 Duval, S. & Tweedie, R. (2000). Trim and fill a simple funnel-plot-based method.
633 *Biometrics*, 56, 455–463.

634 Egan, J.F. & Mortensen, D.A. (2012). A comparison of land-sharing and land-sparing
635 strategies for plant richness conservation in agricultural landscapes. *Ecological*
636 *Applications*, 22, 459-471.

637 FAO (2019). FAOSTAT. Available at: <http://faostat3.fao.org> Last accessed 1 June
638 2021.

639 Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J. *et al.*
640 (2008). Should agricultural policies encourage land sparing or wildlife-friendly
641 farming? *Frontiers in Ecology and the Environment*, 6, 380–385.

642 Gabriel, D., Sait, S.M., Kunin, W.E. & Benton, T.G. (2013). Food production vs.
643 biodiversity: comparing organic and conventional agriculture. *Journal of*
644 *Applied Ecology*, 50, 355–364.

645 Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F. *et*
646 *al.* (2010). Food security the challenge of feeding 9 billion people. *Science*, 327,
647 812-818.

648 Godfray, H.C.J. & Garnett, T. (2014). Food security and sustainable intensification.
649 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369,
650 20120273.

651 Gomiero, T., Pimentel, D. & Paoletti, M.G. (2011). Environmental Impact of Different

652 Agricultural Management Practices: Conventional vs. Organic Agriculture.
653 *Critical Reviews in Plant Sciences*, 30, 95-124.

654 Grass, I., Batáry, P. & Tschardtke, T. (2021). Combining land-sparing and land-sharing
655 in European landscapes. *Advances in Ecological Research*, 64, 251-303.

656 Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. (2005). Farming and
657 the Fate of Wild Nature. *Science*, 307, 550–555.

658 Gurevitch, J., Curtis, P.S. & Jones, M.H. (2001). Meta-analysis in ecology. *Advances*
659 *in Ecological Research*, 32, 199-247.

660 Gurevitch, J., Koricheva, J., Nakagawa, S. & Stewart, G. (2018). Meta-analysis and the
661 science of research synthesis. *Nature*, 555, 175–182.

662 Hodgson, J.A., Kunin, W.E., Thomas, C.D., Benton, T.G. & Gabriel, D. (2010).
663 Comparing organic farming and land sparing: optimizing yield and butterfly
664 populations at a landscape scale. *Ecology Letters*, 13, 1358–1367.

665 IFOAM (2021). Available at: <https://www.ifoam.bio/> Last accessed 1 June 2021.

666 Jost, L., Baños, Tungurahua & Ecuador (2006). Entropy and diversity. *OIKOS*, 113, 2.

667 Kabacoff, R.I. (2011). *R in action. Chapter 15 Advanced methods for missing data.*
668 Manning Publications Co., United States of America.

669 Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity
670 conservation. *Annals of the New York Academy of Sciences*, 1355, 52–76.

671 Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M.
672 *et al.* (1998). Biodiversity inventories, indicator taxa and effects of habitat
673 modification in tropical forest. *Nature*, 391, 72–76.

674 Lori, M., Symnaczyk, S., Mäder, P., De Deyn, G. & Gattinger, A. (2017). Organic
675 farming enhances soil microbial abundance and activity—A meta-analysis and
676 meta-regression. *PLOS ONE*, 12, e0180442.

677 Meemken, E.-M. & Qaim, M. (2018). Organic agriculture, food security, and the
678 environment. *Annual Review of Resource Economics*, 10, 4.1–4.25.

679 Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A. *et al.* (2015).
680 Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45-50.

681 Peel, M.C., Finlayson, B.L. & McMahon, T.A. (2007). Updated world map of the
682 Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.*, 11, 1633-1644.

683 Peng, S., Kinlock, N.L., Gurevitch, J. & Peng, S. (2019). Correlation of native and
684 exotic species richness a global meta-analysis finds no invasion paradox across
685 scales. *Ecology*, 100, e02552.

686 Phalan, B., Balmford, A., Green, R.E. & Scharlemann, J.P.W. (2011a). Minimising the
687 harm to biodiversity of producing more food globally. *Food Policy*, 36, S62-
688 S71.

689 Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011b). Reconciling food
690 production and biodiversity conservation land sharing and land sparing
691 compared. *Science*, 333, 1289-1291.

692 Phalan, B., Green, R.E., Dicks, L.V., Dotta, G., Feniuk, C., Lamb, A. *et al.* (2016). How
693 can higher-yield farming help to spare nature? *Science*, 351, 450-451.

694 R Core Team (2020). *R: a language and environment for statistical computing*. R
695 *Foundation for Statistical Computing, Vienna, Austria*. www.r-project.org.

696 Ramankutty, N., Mehrabi, Z., Waha, K., Jarvis, L., Kremen, C., Herrero, M. *et al.*
697 (2018). Trends in global agricultural land use: implications for environmental
698 health and food security. *Annual Review of Plant Biology*, 69, 789-815.

699 Reganold, J.P. & Wachter, J.M. (2016). Organic agriculture in the twenty-first century.
700 *Nature Plants*, 2, 15221.

701 Robinson, R.A. & Sutherland, W.J. (2002). British Ecological Society Blackwell

702 Science Ltd Post-war changes in arable farming and biodiversity in Great
703 Britain. *Journal of Applied Ecology* 39, 157–176.

704 Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D. *et*
705 *al.* (2004). Biodiversity indicator groups of tropical land-use systems comparing
706 plants, birds, and insects. *Ecological Applications*, 14, 1321–1333.

707 Seppelt, R., Arndt, C., Beckmann, M., Martin, E.A. & Hertel, T.W. (2020). Deciphering
708 the Biodiversity–Production Mutualism in the Global Food Security Debate.
709 *Trends in Ecology & Evolution*, 35, 1011-1020.

710 Seufert, V., Ramankutty, N. & Foley, J.A. (2012). Comparing the yields of organic and
711 conventional agriculture. *Nature*, 485, 229–232.

712 Seufert, V., Ramankutty, N. & Mayerhofer, T. (2017). What is this thing called organic?
713 – How organic farming is codified in regulations. *Food Policy*, 68, 10-20.

714 Smith, O.M., Cohen, A.L., Reganold, J.P., Jones, M.S., Orpet, R.J., Taylor, J.M. *et al.*
715 (2020). Landscape context affects the sustainability of organic farming systems.
716 *Proc Natl Acad Sci USA*, 117, 2870-2878.

717 Solomou, A. & Sfougaris, A. (2011). Comparing conventional and organic olive groves
718 in central Greece: plant and bird diversity and abundance. *Renewable*
719 *Agriculture and Food Systems*, 26, 297–316.

720 Tilman, D., Balzer, C., Hill, J. & Befort, B.L. (2011). Global food demand and the
721 sustainable intensification of agriculture. *Proc Natl Acad Sci USA*, 108, 20260-
722 20264.

723 Tschardtke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I. *et al.*
724 (2012). Global food security, biodiversity conservation and the future of
725 agricultural intensification. *Biological Conservation*, 151, 53-59.

726 Tschardtke, T., Grass, I., Wanger, T.C., Westphal, C. & Batáry, P. (2021). Beyond

727 organic farming – harnessing biodiversity-friendly landscapes. *Trends in*
728 *Ecology & Evolution*, 36, 919-930.

729 Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A. & Bengtsson, J. (2014).
730 Land-use intensity and the effects of organic farming on biodiversity: a
731 hierarchical meta-analysis. *Journal of Applied Ecology*, 51, 746–755.

732 van Buuren, S. & Groothuis-Oudshoorn, K. (2011). mice: Multivariate imputation by
733 chained equations in R. *Journal of Statistical Software*, 45, 1-67.

734 Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor Package.
735 *Journal of Statistical Software*, 36, 1–48.

736 Wan, N.F., Zheng, X.-R., Fu, L.-W., Pødenphant Kiær, L., Zhang, Z., Chaplin-Kramer,
737 R. *et al.* (2020). Global synthesis of effects of plant species diversity on trophic
738 groups and interactions. *Nature Plants*, 6, 503–510.

739 Wanger, T.C., DeClerck, F., Garibaldi, L.A., Ghazoul, J., Kleijn, D., Klein, A.-M. *et*
740 *al.* (2020). Integrating agroecological production in a robust post-2020 Global
741 Biodiversity Framework. *Nature Ecology & Evolution*, 4, 1150–1152.

742 Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009). *Mixed*
743 *effects models and extensions in ecology with R*. Springer Science & Business
744 Media, Stanford.

745

746 **Table 1. Taxon-and crop-specific substitution index (S_{c-o}) weighted means with 95%**
747 **confidence intervals in brackets, only calculated for sub-groups where there**
748 **appears to be the expected trade-off (higher biodiversity and lower yield in lower**
749 **intensity agriculture). Higher values of the substitution index mean that organic**
750 **farming is likelier to maximise biodiversity despite the extra land it takes up.**

	Cereal	Non-cereal
Bird	1.18 (0.57~1.80)	'lose' $R_b \leq 1$
Invertebrate	1.83 (1.13~2.51)	4.18 (0.51~7.85)
Microbe	1.38 (0.97~1.78)	'win' $R_y \geq 1$
Plant	3.90 (2.71~5.09)	4.88 (-9.87~19.63)
Grand mean	1.98 (1.53~2.43)	'win' $R_y \geq 1$
Overall	2.40 (1.62~3.18)	

751

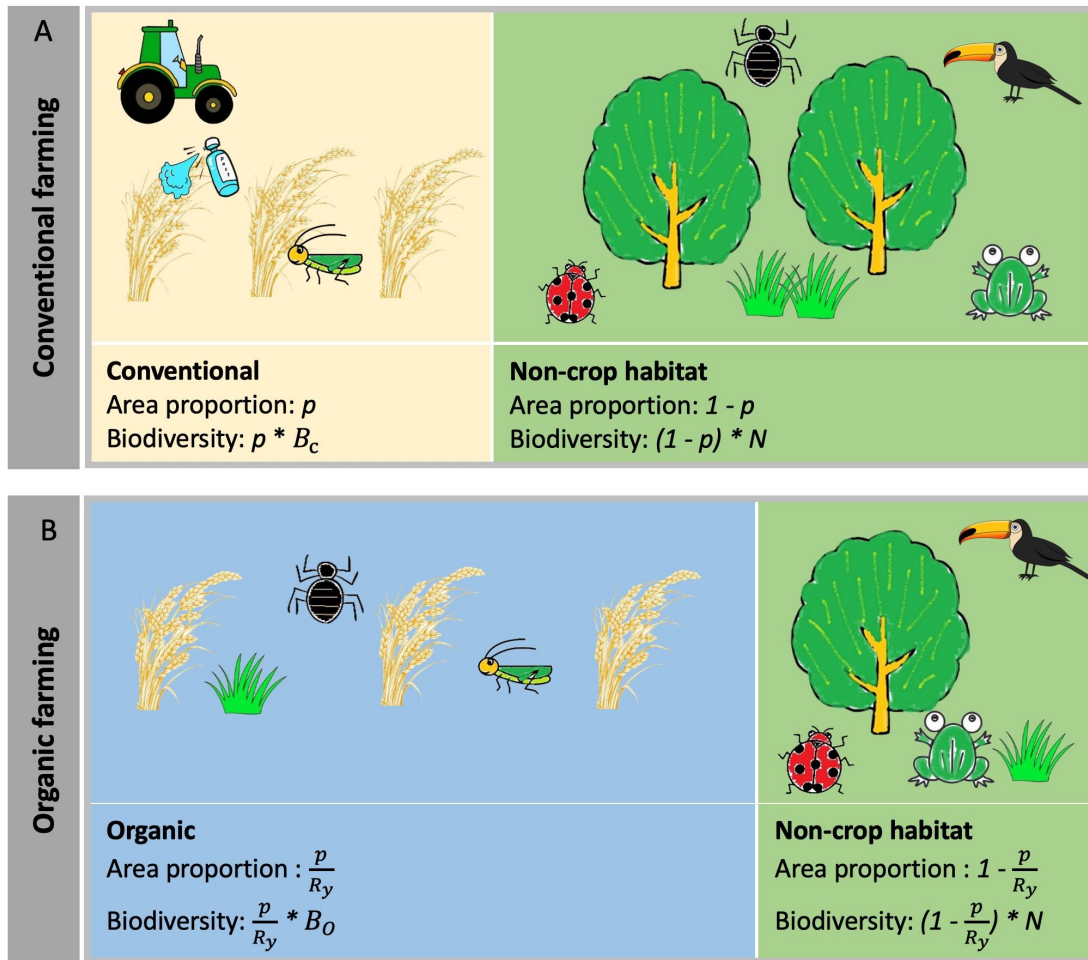


Figure 1. Diagram showing the conventional (A) and organic (B) farming strategies that could reach the same total food production. If land management is to be changed, a factor $1/R_y$ more land is required for the organic farming, or conversely, a fraction of land could be released if the farming is conventional. These uncultivated areas could be in any spatial configuration; we make no assumption about whether they are distributed around the fields/farms themselves, or somewhere separate. Given simplifying assumptions, the formulas for the area and biodiversity of each land component help us to evaluate which strategy results in the highest total biodiversity-abundance.

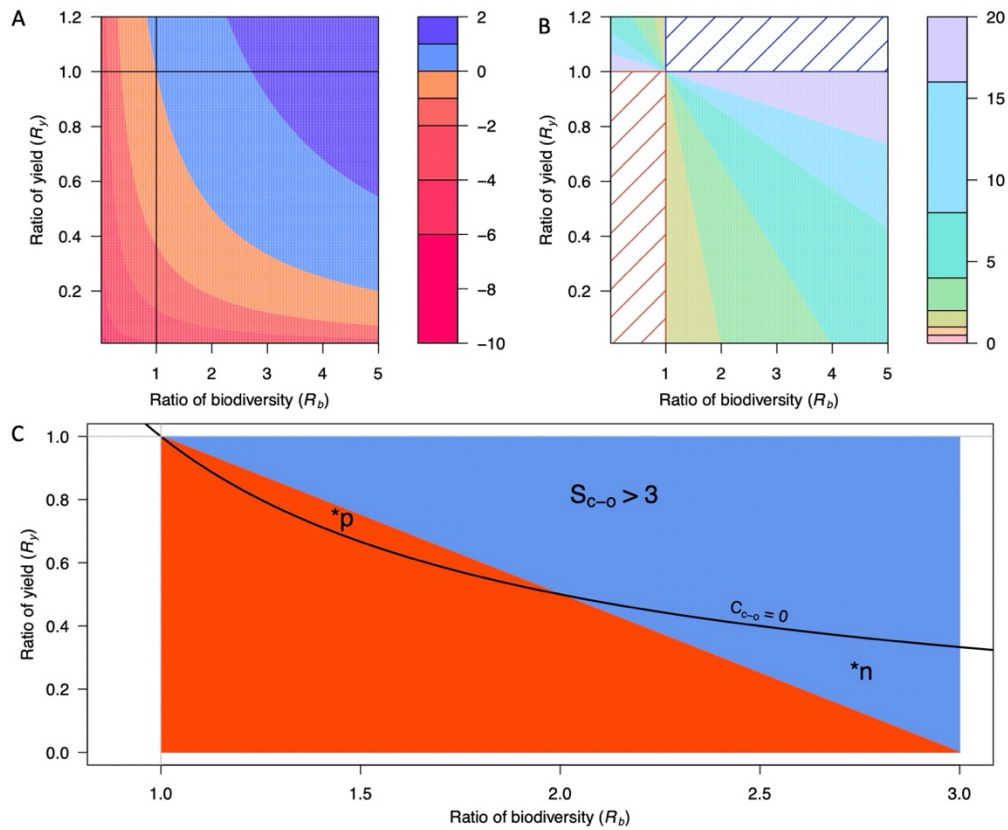


Figure 2. Illustrative diagrams of our two proposed indices which depend on the ratios of biodiversity (R_b) and of yield (R_y) between organic and conventional farming. (A) The compatibility index (C_{c-o}), which is the log ratio of biodiversity and yield (i.e. $E_b + E_y$) when shown by colour zones (truncated at -10 and 2); (B) The substitution index (S_{c-o}) index shown by colour zones (truncated at 1 and 20); the shaded areas in blue and red refer to win-win and lose-lose situations respectively for both biodiversity and yield under organic farming; (C) An example to show how a positive compatibility index ($E_b + E_y > 0$) doesn't necessarily indicate that organic farming is the most efficient conservation strategy. The black curve, where compatibility index = 0, intersects with an example threshold value of $S_{c-o} = 3$ (background blue where $S_{c-o} > 3$). Areas labelled *p shows where compatibility index is positive, but conventional farming is preferred; *n shows where compatibility index is negative but organic farming is preferred.

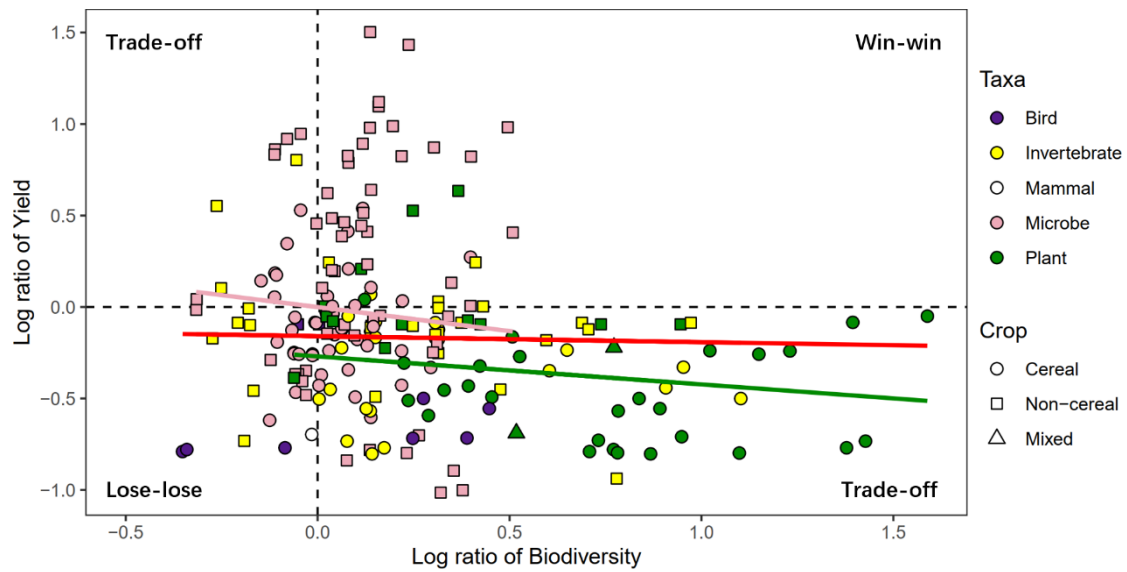


Figure 3. Scatter plot of log yield ratio vs log biodiversity ratio in organic vs conventional farming. Effect sizes were calculated from treatment pairs within studies. The red line shows the overall linear regression (n=205); the pink line refers to the linear regression for microbes (n=100) and the green one for plants (n=43).

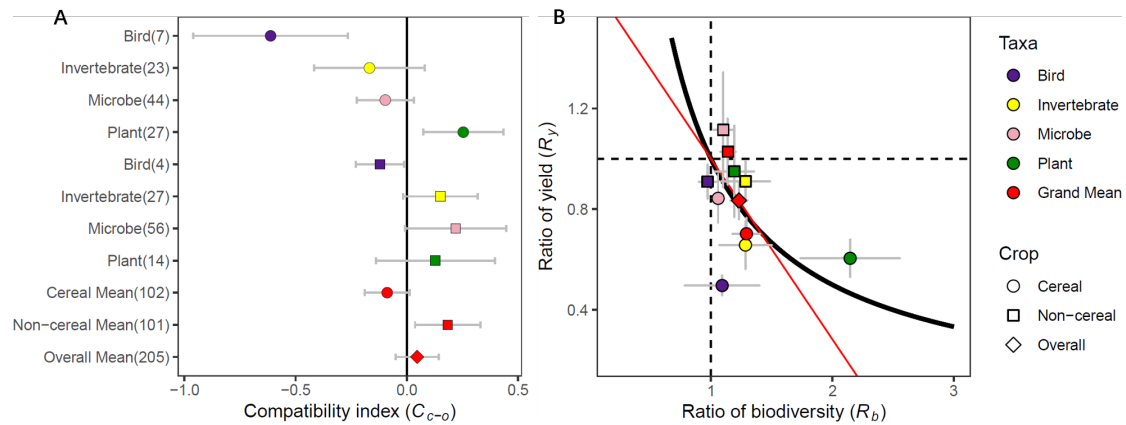


Figure 4. (A) The mean compatibility index (i.e. the contrast in log biodiversity gain and yield loss, C_{c-o}) for all studies and sub-groups; error bars represent 95% confidence intervals; numbers in brackets refer to number of cases. (B) The ratio in yield (R_y) and biodiversity (R_b) between organic and conventional fields for different taxa in different crop types, and for all studies. Dots and error bars show the mean value and 95% CI. The black curve shows where compatibility index $C_{c-o}=0$; the red line shows where substitution index S_{c-o} equals its overall mean of 2.4 (see Table 1).