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1 **Classification:** Biological science – Ecology

2

3 **Land-use history impacts functional diversity across multiple trophic groups**

4

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35 **KEYWORDS:** agricultural ecosystems – biodiversity loss – functional diversity – grasslands –
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37 **ABSTRACT**

38 Land-use change is a major driver of biodiversity loss worldwide. Although biodiversity often
39 shows a delayed response to land-use change, previous studies have typically focused on a narrow
40 range of current landscape factors, and have largely ignored the role of land-use history in shaping
41 plant and animal communities and their functional characteristics. Here, we used a unique database
42 of 220,000 land-use records to investigate how 20-years of land-use changes have affected
43 functional diversity across multiple trophic groups (primary producers, mutualists, herbivores,
44 invertebrate predators and vertebrate predators) in 75 grassland fields with a broad range of land-
45 use histories. The effects of land-use history on multitrophic trait diversity were as strong as other
46 drivers known to impact biodiversity, e.g. grassland management and current landscape
47 composition. The diversity of animal mobility and resource-acquisition traits was lower in
48 landscapes where much of the land had been historically converted from grassland to crop. In
49 contrast, functional biodiversity was higher in landscapes containing old permanent grasslands,

50 most likely because they offer a stable and high quality habitat refuge for species with low mobility
51 and specialized feeding niches. Our study shows that grassland-to-crop conversion has lasting
52 impacts on the functional biodiversity of agricultural ecosystems. Accordingly, land-use legacy
53 effects must be considered in conservation programs aiming to protect agricultural biodiversity. In
54 particular, the retention of permanent grassland sanctuaries within intensive landscapes may offset
55 ecological debts.

56 **SIGNIFICANCE**

57 The World's agricultural landscapes have seen dramatic declines in their biodiversity. Because
58 biodiversity responses to land-use changes can be delayed, understanding how current biodiversity
59 is impacted by historical land-use changes is crucial to protect and restore agricultural biodiversity.
60 By utilizing a long-term land-use record database, we show that historical land-use changes
61 continue to shape current biodiversity. Our study expands our understanding of global biodiversity
62 change by identifying land-use history effects to be as strong as the effects of current management
63 and the amount of semi-natural land cover, often assumed to be the major drivers of biodiversity
64 change in agricultural landscapes. Accordingly, land-use legacy effects must be considered in
65 management programs that aim to protect and restore biodiversity.

66 /body

67 **INTRODUCTION**

68 Habitat destruction caused by land-use change is a major driver of global biodiversity declines (1).
69 While land-use changes often have time-delayed impacts on biodiversity (2, 3), we know very little
70 about the relationship between land-use history and present-day biodiversity. The presence of
71 remnant and alternative habitats in the landscape can buffer biodiversity loss through time, if
72 organisms are able to persist in, and disperse to these refuges (4). These meta-population processes
73 can delay or prevent species extinction for years or decades (4), meaning we may have
74 underestimated the impacts of past land-use change on biodiversity. Understanding the long-term
75 response of biodiversity to land-use change is crucial if we are to limit species extinctions and
76 biodiversity decline by implementing sound and timely conservation and restoration efforts.

77 Species can differ significantly in their responses to land-use changes (5), making it hard to
78 generalize biodiversity response as a whole, and to predict which species and taxa may suffer the
79 most from habitat destruction in the long run. A solution to this problem is the use of species traits,
80 as species sharing similar traits have been shown to respond consistently to land use change (6, 7).
81 Furthermore, in agricultural landscapes, trait diversity plays an important role in determining the
82 capacity of ecosystems to cope with future environmental changes (8) and secure the provision of
83 key ecosystem services. However the long term response of functional diversity to land-use changes
84 is unknown as previous studies investigating the effects of land-use history have focused on species
85 richness (3, 9), ignoring trait diversity. A general understanding of how the trait diversity of
86 multiple trophic groups responds to land-use changes over time may therefore improve our capacity
87 to manage agricultural biodiversity, and secure sustainable long-term agroecosystem functioning.

88 Here, we investigated how 20-years of past land-use changes affected the functional trait
89 diversity of seven taxonomic groups in grasslands (vascular plants, wild bees, hoverflies,
90 grasshoppers, carabid beetles, spiders and birds), belonging to five trophic groups (primary

91 producers, pollinators, herbivores, invertebrate and vertebrate predators) (see for details *SI*
92 *Appendix*, Table S2). We used a unique database of 220,000 land-use records in an agricultural
93 region of 430 km² dominated by crop production in western France (11,000 fields recorded annually
94 since 1994, ref. 10) to investigate the effect of multiple aspects of land-use history, operating at the
95 field and landscape level, on functional diversity (*SI Appendix*, Fig. S1 and Table S1). Historically,
96 the study region was a typical rural area composed of mixed crop-livestock systems. Fifty years
97 ago, grassland was the dominant land use, covering 60% of the study area (10). *These grasslands*
98 *were either grazed or mown for livestock production.* Since that time and up to the present day,
99 shifts from livestock to annual crop production resulted in a strong decline in grassland cover and in
100 2014, grasslands covered only 12% of the area.

101 Within the study area, we sampled 75 grasslands with a wide range of land-use histories,
102 while controlling for the effects of current landscape composition and the management of the
103 sampled grassland field. Land-use history was assessed by the age of the sampled grassland field
104 (“Field age”) and by three independent landscape metrics (*SI Appendix*, Fig. S1 and Table S1): (i)
105 the time elapsed since the first grassland-to-crop conversion for all fields within a landscape of 1-
106 km radius of the sampled grassland (“Time as cropland”). High value of time as cropland indicates
107 that most grasslands in the landscape were converted into crops long ago; (ii) the permanency of the
108 grassland cover in the landscape (“Grassland permanency”). A high value of grassland permanency
109 corresponds to landscapes with old permanent grasslands; (iii) the turnover of rotation from crop to
110 grassland in the landscape (“Crop-grassland turnover rate”). A high value of crop-grassland
111 turnover rate indicates that sown grasslands are maintained for several years. These three metrics
112 complement each other to inform on the loss, the stability and turnover of grasslands in the
113 landscape.

114 We focused on a core set of independent organismal traits that mediate species responses to
115 land-use changes (Fig. S2): body size, mobility (e.g. wing span) and resource-use traits (e.g.

116 mandible strength or beak size). Such traits can directly determine a species' ability to respond
117 rapidly to land-use intensification, e.g. frequent disturbances and resource homogenization in
118 agricultural landscape may for species with smaller size, a generalist diet, shorter generation time
119 and higher dispersal abilities (6, 11). We summarized the functional diversity of the entire trophic
120 chain using multitrophic and multi-trait diversity metrics (9). We also investigated how land use
121 affects different facets of functional trait diversity by compiling three multitrophic trait diversity
122 indices for mobility, resource-acquisition and body size traits separately. We controlled for
123 confounding effects of the local species pool (the multitrophic density and species richness,
124 following ref. 9) in our analyses, to isolate net effects of land-use changes on functional diversity
125 (see methods). We hypothesized that landscapes in which grassland was converted to crop long ago
126 would support low grassland multitrophic trait diversity by selecting generalist species and reducing
127 the diversity of body size and mobility traits. We further hypothesized that increasing grassland
128 permanency and decreasing the crop-grassland turnover rate could mitigate biodiversity loss by
129 providing stable and high quality habitat to low mobility organisms and feeding specialist species.

130

131 **RESULTS**

132 All models accounted for the influence of multitrophic species richness and density on trait
133 diversity (Fig. 1). Multitrophic trait diversity increased linearly with multitrophic species richness
134 and decreased with multitrophic density (Fig. 2), with the exception of resource-acquisition trait
135 diversity for which multitrophic density had no effect. We also found multitrophic species richness
136 to be more strongly affected by land-use history (43% of explained variance) than by current land
137 use (18% of explained variance) (*SI Appendix*, Figs. S4 and S5). On the contrary, multitrophic
138 density was mostly driven by current land use (62% vs. 38% of variance explained by land-use
139 history).

140 The best-selected model explained 70% of the variance in multi-trait diversity (Fig. 1; see
141 also *SI Appendix*, Table S5). Of this, current land use accounted for 16% of the explained variance
142 (Fig. 1), where multi-trait diversity was higher in landscapes with high grassland cover (Fig. 2).
143 Land-use history explained 12% of multi-trait diversity, through the effects of grassland field age
144 (5% of the explained variance) and grassland permanency in the landscape (accounted for 7% of the
145 explained variance) (Fig. 2). These effects were positive: multi-trait diversity was higher in fields
146 that had been grasslands for a long time and were surrounded by other permanent grasslands (Fig
147 2).

148 When considering each trait separately, we found that mobility, resource-acquisition and
149 body size trait diversity responded differently to past and current land use. Land-use history was the
150 main driver of the diversity of mobility traits (34% of explained variance) (Fig. 1). Mobility trait
151 diversity was lower in fields embedded in landscapes converted to cropland long-ago (Fig. 2). In
152 contrast, the diversity of mobility traits was higher in old grassland fields and in landscapes in
153 which grassland cover was more permanent. Past and current land use accounted for an equal
154 amount (28%) of explained variance for resource-acquisition trait diversity (Fig. 1). The diversity of
155 resource-use strategies initially increased following grassland-to-cropland conversion in the
156 landscape (during the first 10 years) but subsequently decreased (Fig. 2). Current land use could
157 either mitigate this loss, as resource-acquisition trait diversity increased with present-day grassland
158 cover, or accentuate it, as it decreased with grassland field productivity, a proxy of grassland
159 management intensity, and the amount of mass flowering crops in the landscape. Our model
160 explained less variation in body size diversity, although this did respond to current land use (16% of
161 explained variance) (*SI Appendix*, Fig. S6).

162 When considering each trophic group separately, plant trait diversity was only impacted by
163 current grassland field productivity (27% of explained variance). For animals, the importance of
164 land-use history decreased with increasing trophic level, while the importance of current landscape-

165 scale predictors increased (Figs. 3 and 4, see also *SI Appendix*, Table S6). Herbivore (i.e.
166 grasshoppers) and mutualist (i.e. wild bees and hoverflies) trait diversity was strongly affected by
167 land-use history (respectively 39% and 27% of explained variance) and was higher in old grassland
168 fields (Fig. 4). Land-use history accounted for 28% of the explained variance in invertebrate
169 predator trait diversity, which increased in landscapes dominated by permanent grasslands.
170 Vertebrate predator trait diversity was mainly driven by current landscape composition, and
171 increased in landscapes with a high cover of mass flowering crops (16% of explained variance) and
172 forest (46% of explained variance).

173

174 **DISCUSSION**

175 We investigated how land-use history affects the functional diversity of multiple trophic groups in
176 grasslands. We found that historical land use continues to play an important role in shaping the
177 present-day functional diversity across multiple trophic groups, and that it is of equal importance to
178 well established land-use drivers of biodiversity in agricultural landscapes, such as grassland
179 management intensity (7) and current landscape composition (6). Ignoring the role of land-use
180 legacies on functional diversity may therefore hinder our ability to predict how biodiversity
181 responds to land-use changes, and the functional consequences of biodiversity change on
182 ecosystems.

183 Multi-trait diversity was most strongly influenced by the species pool, *i.e. the density of*
184 *individuals and the taxonomic diversity observed within the sampled grasslands*. There was a
185 negative relationship between multi-trait diversity and density. High population densities, together
186 with low functional diversity, occur when a small number of functionally similar species benefit
187 from land-use intensification in agricultural landscapes. These few species may benefit from the
188 resources offered by particular crop monocultures and become hyper abundant, e.g. in pest
189 outbreaks (12). However, by increasing functional diversity, we may limit dominance by a few

190 species with potentially negative effects on crops, as suggested by the dilution effect hypothesis (13,
191 14). We also found that multi-trait diversity strongly increased with taxonomic diversity (Fig. 2),
192 which highlights low functional redundancy among species across all the trophic groups studied. A
193 low functional redundancy implies that species loss may be accompanied by strong declines in
194 functional diversity and uncertain outcomes in agroecosystem functioning. While agricultural
195 landscapes have the potential to host high trait diversity (15), the low functional redundancy
196 observed in our study suggests that the functional biodiversity of agroecosystems is particularly
197 vulnerable to land-use changes and species loss (16).

198 Decomposing multi-trait diversity into three independent indices (Fig. S2) allowed us to
199 investigate the mechanisms through which land-use history alters biodiversity in agricultural
200 landscapes. The multitrophic diversity of mobility and resource-acquisition traits was lower in
201 landscapes that were converted from grassland to cropland long ago (Fig. 2), highlighting that
202 habitat destruction has not only immediate, but also long-lasting negative effects on the functional
203 diversity of agroecosystems. The conversion of permanent grasslands into annual crops may have
204 particularly strong effects on low mobility organisms and species with narrow feeding niches.
205 However, our results show that maintaining permanent grasslands in the surrounding landscape
206 mitigates this loss (Fig. 2), probably by providing stable, heterogeneous and resource-rich habitats
207 in which many species can persist in and migrate between. While increasing the quantity of semi-
208 natural habitats in the landscape is often viewed as an important method to conserve biodiversity in
209 agricultural landscapes (e.g. 18), our results highlight that increasing the quality of these habitats –
210 through the conservation of old permanent grasslands in the landscape – may be equally important.
211 Finally, we observed that mobility trait diversity decreased linearly with time since landscape
212 conversion to cropland, while resource-acquisition trait diversity showed a hump-shaped response:
213 it increased during the first 10 years after grassland-to-crop conversion but then decreased (Fig. 2).
214 Spatial and temporal disturbances can create a concentration of transient species in remnant

215 habitats, thus locally increasing resource-acquisition trait diversity (18). However, resource-
216 acquisition trait diversity will decrease after some time due to the scarcity of habitats and resources
217 in the landscape (9). Quantifying the duration of this effect may be essential to slow down species
218 loss and delay extinction.

219 Resource-acquisition trait diversity was also strongly impacted by current land use. Locally,
220 we found a strong negative effect of the grassland field productivity (Fig. 3). High grassland
221 productivity is associated with high rates of fertilization, which decreases plant diversity, and in
222 turn, the availability of feeding niches (19). This has been observed in both in experiments and real-
223 world landscapes, and leads to a global homogenization of species resource-use strategies at higher
224 trophic levels (20). In addition, at the landscape scale, the proportion of mass flowering crops
225 (ranging from 0% to 44% in the study area) negatively affected resource-acquisition trait diversity.
226 Mass flowering crops offer short pulses of uniform and homogeneous resources for herbivores and
227 mutualists that may select for particular resource-acquisition traits and therefore reduce their
228 diversity (e.g. 33). As the diversity of resource-acquisition traits drives overall resource utilization
229 (22), the community level homogenization of resource-acquisition traits following land-use
230 intensification could threaten the delivery of essential agroecosystem services such as nutrient
231 recycling (23), pollination (24) and biological control (25).

232 We did not find clear response of body size to land-use changes (Fig. 1 and *SI Appendix*,
233 Fig. S6), in contrast to other studies focusing on single trophic groups (e.g. 37). Body size is an
234 integrative trait related to many aspects of animal species physiology and ecology (e.g. metabolism,
235 ref. 13; mobility and dispersal, or else stoichiometry, ref. 39) and may not have the same functional
236 significance across multiple trophic groups (28). As a result, our synthetic index of multitrophic
237 body size may not show a consistent response to land-use changes. This may explain why our
238 analyses predicted less variation in body size trait diversity, than they did for mobility or resource-
239 acquisition traits.

240 We found that past and current land use had contrasting impacts on trait diversity of
241 different trophic groups (Fig. 3). For instance, primary consumers (i.e. herbivores and mutualists)
242 responded more strongly to local history (through the age of the sampled grasslands) while
243 predators were more impacted by past and present-day landscape composition (Fig. 4 and *SI*
244 *Appendix*, Table S6). Accordingly, delayed responses to land-use changes could create temporal
245 mismatches between interacting trophic levels, if land-use changes disrupt interacting partners
246 inconsistently. This may lead to the disruption of ecological interactions and further biodiversity
247 loss (29). While plants are expected to experience time-delayed responses to habitat loss because of
248 persistence in seed banks (30), plant trait diversity was not impacted by land-use history (Fig. 3).
249 However, we found a strong effect of land-use history on plant species richness (*SI Appendix*, Fig.
250 S7), suggesting that legacy effects of land use affect plant species independently of the traits
251 investigated in this study. While the functional diversity of certain trophic groups showed divergent
252 responses to land-use changes (Figs. 4), our study shows that there is a consistent pattern in the
253 response of overall ecosystem trait diversity, thus suggesting that our integrated index of multi-trait
254 diversity provides a simple quantitative measure of the whole ecosystem biodiversity response.

255 Our results revealed that present-day functional biodiversity was impacted by land-use
256 changes that happened up to 20 years ago, thus demonstrating that land-use actions have long-
257 lasting impacts and that extinction debts (*sensu* 9) are commonplace in agricultural landscapes (3).
258 In an era of global biodiversity change, our results emphasize the need to consider land-use legacies
259 in conservation programs that aim to protect the biodiversity of agroecosystems and its associated
260 ecosystem functions and services. In particular, our results emphasize the need to preserve
261 permanent grasslands in agricultural landscapes, as it provides a shelter to low mobility organisms
262 and species with narrow feeding niches. While large-scale policy schemes encourage the retention
263 of permanent grasslands, they have largely decreased in their cover over the last years (31). Our

264 results call for immediate actions to conserve and restore permanent grasslands in order to preserve
265 the functionality of agricultural landscapes and avoid future extinction debt.

266

267 **MATERIALS AND METHODS**

268 **Study area.** The study was conducted in 2014 in the Long Term Socio-Ecological Research
269 (LTSER) “Zone atelier Plaine & Val de Sèvre” (ZAPVS) located in western France (32). The
270 LTSER covered approximately 430 km² of an intensively managed agricultural plain. Historically,
271 it was a typical rural area characterized by the presence of mixed crops-livestock systems (dairy
272 goats and cows). Grassland was the dominant land use fifty years ago covering about 60% of the
273 area (32). Since that time, shifts from grazing livestock to feeding livestock, and shifts from
274 livestock production to annual crop production have resulted in a strong decline in grassland cover.
275 In 2014, grasslands covered about 12% of the area and included artificial grasslands (i.e., alfalfa
276 with 3% of the area), temporary (sown with pure grasses or in mixtures with legume species and ≤ 5
277 year old) and permanent grasslands (> 5 year old) managed by grazing, mowing or abandoned. The
278 remaining areas were covered by crops (66% of landscape area). Soils are mostly composed of
279 karst, with calcareous rocks providing shallow calcareous soils with low water retention and pH $>$
280 7. Since 1994, land cover of the study area has been monitored on a yearly basis at the field scale,
281 by using about 30 land-use types (11,000 fields approximately, see ref. 21 for methodological
282 details on land cover monitoring), and has been stored in a Geographical Information System (GIS)
283 database, running on QGIS v 2.14.

284

285 **Grassland selection and land-use metrics.** We monitored 75 grassland fields within the study
286 area. The grassland fields were selected among hay meadows of varying ages and vegetation types
287 (pure legumes, pure or mixed grasses, legume and grass mixture, post-cultural vegetation). The
288 average age of the grassland field was 8 year-old ($sd = 6.55$). We calculated for each of the 75

289 grassland fields the current landscape composition, and landscape metrics linked to land-use
290 history, within a 1 km-radius landscape (*SI Appendix*, Fig. S1). This scale was chosen to
291 approximate the dispersal distance of different taxa (e.g. 39). For landscape composition, we
292 considered landscape elements known as favorable or resource rich habitats for the different groups
293 of taxa, i.e. the proportion of the landscape covered by grasslands, forests and mass flowering crops
294 (oilseed rape and sunflower). Landscape composition metrics varied between 0-35 % for grassland,
295 0-32 % for forests and 0-44 % for mass flowering crop covers. For land-use history metrics, we
296 calculated for all field in the 1 km-radius landscape surrounding the focal grasslands: (i) the time
297 elapsed since the first grassland-to-crop conversion (*SI Appendix*, Fig. S1); (ii) the time spent into
298 current land use since the last tillage (hereafter called “Field age”). The age of crop-field was 1 year
299 and the age of grassland field varied between 1 and 20 years (set to 20 years if it had not been
300 ploughed since 1994); and (iii) the rate of turnover from crop to grassland since the last conversion
301 of the field into cropland. This metric is linked to the lifespan of grasslands sown in crop rotation
302 and is higher when the average lifespan of sown grasslands in the landscape is longer. To account
303 for the size of the field, all these metrics were weighted by the field area. We then averaged these
304 three metrics at the landscape level (hereafter called “Time as cropland”, “Grassland permanency”
305 and “Crop-grassland turnover rate”) (*SI Appendix*, Fig. S1).

306

307 **Species richness and density.** Seven taxonomic groups were sampled on the 75 grassland fields.
308 The taxonomic groups were chosen for their association with key ecological functions: primary
309 producers (vascular plants), pollinators (wild bees and hoverflies), herbivores involved in carbon
310 and nitrogen cycling (grasshoppers), invertebrate predators that are natural enemies of pests
311 (carabid beetles and spiders) and vertebrate predators (birds) of important cultural value (see *SI*
312 *Appendix*, Table S2). Sampling was performed throughout the growing season from April to August
313 2014 in each grassland field following standardized protocols (10). Details of sampling methods are

314 provided in *SI Appendix Methods S1*. Relative abundance per plant species was calculated as the
315 sum of the species cover in the 10 quadrats divided by the total cover of all species. For animals,
316 species density was estimated as the number of individuals captured (invertebrates) or recorded
317 (birds) divided by sampling intensity (number of traps or point counts in the grassland). The number
318 of species in each grassland field was determined in the lab for all invertebrate species.

319

320 **Trait measurements and trait diversity.** Functional trait data were collected for all taxonomic
321 groups. Plant trait data came from a local database from the LSTER site (23). Bird morphological
322 traits were compiled from the literature (34). For all other taxonomic groups, all measurements were
323 performed using a stereo microscope (Leica Microsystems M50) equipped with an integrated high
324 definition microscope camera (Leica IC80 HD). Details of trait measurements are provided in *SI*
325 *Appendix, Methods S2*. In total, we collected trait data for 178 species distributed across the
326 different trophic groups (*SI Appendix, Methods S2*).

327 We calculated the community abundance-weighted variance (35) for each taxonomic group
328 separately and each trait separately. For single traits, the variance is a measure of the trait dispersion
329 within a given community weighted by the abundance of each individual species and is a measure
330 of functional trait diversity of a given community (35). We also computed a multi-trait index of
331 functional diversity based on trait dispersions for each taxonomic group separately – the Functional
332 Dispersion (FD) (36).

333

334 **Multitrophic trait diversity measurements.** We used methods developed to study ecosystem
335 multifunctionality to calculate a multi-trait diversity index considering on all traits and taxonomic
336 groups. This approach (averaging approach, see 54) consists of calculating the average standardized
337 values of multiple functional diversities. Our multi-trait functional diversity index was thus
338 calculated as the average standardized FD values across the taxonomic groups (similar to

339 multidiversity indices following 8). Using this index allows us to identify the environmental
340 conditions, which maximize functional trait diversity across multiple taxonomic groups. Note that
341 the averaged multi-trait diversity index was highly correlated with the threshold-50 multi-trait
342 diversity index (37) - calculated as the percentage of community variance values that exceeds 50%
343 of their maximum observed community variance ($r=0.87$, see *SI Appendix*, Table S3). Similarly, we
344 calculated an average index of multitrophic density – average standardized values of the total
345 density for the different animal taxonomic groups (i.e. grasshoppers, wild bees, hoverflies, carabids,
346 spiders and birds) – and an average index of multitrophic species richness, following 8. In addition,
347 to test if land-use changes have similar effects on different axes of trait variation, we also calculated
348 averaged indices for mobility trait diversity, resource-acquisition trait diversity and body size trait
349 diversity values as the average standardized community variance values of these three types of
350 traits, across the taxonomic groups. To calculate these trait indices, we excluded plant traits as the
351 three selected plant traits are associated with different functions and other axes of variation. Finally,
352 to test if the response of each trophic group to land-use changes is similar, we computed multi-trait
353 diversity, species richness and density indices for five trophic groups separately: primary producers
354 (vascular plants), mutualists (wild bees and hoverflies), herbivores (grasshoppers), invertebrate
355 predators (carabids and spiders) and vertebrate predators.

356

357 **Assessing the effects of past and current land use.** We evaluated the effects of land-use changes
358 on grassland trait diversity by using linear models. We ran separate analyses on: (i) the multi-trait
359 diversity; (ii) the mobility, resource-acquisition and body size trait diversity; (iii) on the multi-trait
360 diversity of the different trophic groups separately. We included in our models the effects of the
361 grassland field age and of the three landscape land-use history metrics as predictors of functional
362 trait diversity. We also controlled for current landscape composition (% grassland, % forest and %
363 mass flowering crop areas). We used plant productivity as a proxy measure of grassland

364 management, as it is related to fertilizer inputs. This was assessed by harvesting plant biomass each
365 month (between February and August 2014) above a cutting height of 5 cm from the soil surface,
366 within five 35 × 35 cm quadrats. Productivity was then calculated as the weight of dried-plant
367 material (oven-dried at 60°C for 72h) product per square meter per day between the initial biomass
368 measurement and peak biomass (end of May). We considered quadratic terms for grassland field
369 age, landscape land-use history metrics, current grassland field productivity and landscape
370 composition to assess potential non-linear effects of these variables. Further co-varying factors
371 accounted for the number of mowing events and soil depth were included. Our models also
372 integrated the coordinates of the centroid of each sampled grassland (latitude and longitude) to
373 correct for additional spatial effects not accounted for by the field and landscape predictors (38).
374 Finally, as the local species pool (defined by both the density and the species richness) may affect
375 functional trait diversity metrics (39), we included in the models the multitrophic density and
376 multitrophic species richness indices to isolate the net effects of land-use changes on multitrophic
377 trait diversity. We ran separate analyses on the multitrophic density and the species richness, and
378 results are presented in *SI Appendix*, Fig. S4 and Fig. S5.

379 We then performed a series of models for the multi-trait diversity, mobility trait diversity,
380 resource-acquisition trait diversity and body size trait diversity; and for the multi-trait diversity of
381 each taxonomic group separately. We first used a backward stepwise regression procedure using the
382 software JMP 11 (SAS Institute) to select, between all models, the best-fitting models with lower
383 AICc ($\Delta \text{AICc} < 2$). Second, using the best selected models, we performed a model-averaging
384 procedure based on AICc selection ($\Delta \text{AICc} < 2$) to determine parameter coefficients for the best
385 final set of predictors of our response variables. This procedure was performed using the function
386 *dredge* in the R package Multi-Model Inference (*MuMIn*) (40). Model residuals were inspected for
387 constant variance and normality. We standardized all variables (z-scored: mean-centred and divided
388 by the standard deviation) to interpret parameter estimates on a comparable scale (41). [Correlation](#)

389 among the predictors used was low (*SI Appendix*, Table S1) and did not induce multicollinearity
390 issues in our analyses (*SI Appendix*, Table S4). The inclusion of many predictors in statistical
391 models increases the chance of type I error (false positives). To account for this we used a
392 Benjamini and Hochberg procedure to control for false discovery rates and adjust P-values (42). To
393 evaluate the relative importance of the predictors as drivers of trait diversity, we expressed the
394 importance of predictors as the percentage of variance they explain, based on the comparison
395 between the absolute values of their standardized regression coefficients and the sum of all
396 standardized regression coefficients from the predictors. This method is similar to a variance
397 partitioning analysis because we previously transformed all predictors to z-scores (38, 43, 44). The
398 following identifiable variance fractions were then examined: (i) land-use history, (ii) current land
399 use, and (iii) the species pool.

400 **DATA AVAILABILITY**

401 The data that support the findings of this study will be openly available at <https://datadryad.org>.

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418

419 **AUTHOR CONTRIBUTIONS**

420 GLP, IB and NG designed research; GLP, IB, LH, MR and NG performed research; GLP, IB, LH
421 and NG analyzed data; and GLP, IB, YLBP, YC, LH, CV, VB, MR, PM and NG wrote the paper.

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- 517

518 **FIGURE LEGENDS**

519 **Fig. 1.** Importance of the drivers of multi-trait diversity, mobility trait diversity, resource-
520 acquisition trait diversity and body size trait diversity. Relative effects (% R^2), resulting from a
521 model averaging procedure, were calculated for each group of predictors (i.e. land-use history,
522 current land use and the species pool). All predictors were scaled to interpret parameter estimates on
523 a comparable scale. Note that for mobility, resource-acquisition and body size trait diversity, we
524 focused on animal traits and excluded plant traits from the analyses. Results were consistent
525 considering spatial scales ranging from 500-1500 m radii surrounding the sampled grasslands (*SI*
526 *Appendix*, Fig. S3).

527
528 **Fig. 2.** Effects of land-use history (field age, time as cropland, grassland permanency and crop-
529 grassland turnover rate), current land use (field productivity, % grassland, % mass flowering, %
530 forest) and of the species pool (multitrophic density and richness) on (A) multi-trait diversity, (B)
531 mobility trait diversity and (C) resource-acquisition trait diversity. Lines show model fits and
532 shaded areas correspond to the 95% confidence band. Model predictions were calculated using a
533 model averaging procedure. Note that for mobility trait and resource-acquisition trait diversity, we
534 focused on animal traits and excluded plant traits from the analyses. All predictors were scaled to
535 interpret parameter estimates on a comparable scale. P-values of the best selected models for each
536 model parameter are given. P-values were adjusted following (57) to control for false discovery
537 rates (see *SI Appendix*, Table S7). Gray dots (N=75) correspond to observed data.

538
539 **Fig. 3.** Importance of the drivers of multi-trait diversity within the different trophic groups (primary
540 producers, herbivores, mutualists, invertebrate predators and vertebrate predators). Relative effects
541 (% R^2), resulting from the model averaging procedure, were calculated for each group of predictors

542 (i.e. land-use history, current land use and the species pool). All predictors were scaled to interpret
543 parameter estimates on a comparable scale.

544

545 **Fig. 4.** Effects of land-use history (field age, time as cropland, grassland permanency and crop-
546 grassland turnover rate) and current land use (field productivity, % grassland, % mass flowering, %
547 forest) on the multi-trait diversity of each trophic group. Lines show model fits for primary
548 producers (green), herbivores (yellow), mutualists (orange), invertebrate predators (brown) and
549 vertebrate predators (blue). Model predictions were calculated using the model averaging
550 procedure. All predictors were scaled to interpret parameter estimates on a comparable scale. P-
551 values of the best selected models for each model parameter are given, *, *P-value* < 0.05; ** *P-*
552 *value* < 0.01; *** *P-value* < 0.001. P-values were adjusted following (58) to control for false
553 discovery rates (see *SI Appendix, Table S7*). Dots (N=75) correspond to observed data and colors
554 indicate the trophic group.