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1 **Conservation agriculture affects multitrophic interactions driving the efficacy of weed**
2 **biological control**

3 B. Carbonne^{1,2,3}, L. Muneret¹, E. Laurent¹, E. Felten¹, C. Ducourtieux¹, N. Henon¹, A.
4 Matejicek¹, B. Chauvel¹, S. Petit¹

5
6 ¹ Agroécologie, INRAE, Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-
7 21000 Dijon, France

8 ² Univ Rennes, CNRS, ECOBIO [(Ecosystèmes, biodiversité, évolution)] - UMR 6553, F-35000
9 Rennes, France

10 ³ IGEPP, INRAE, Institut Agro, Univ Rennes, 49045 Angers, France

11 **Abstract**

- 12 1. Biological control is a key ecosystem service in arable lands, but its effectiveness varies
13 according to environmental and biotic contexts. Cascading interactions between
14 several trophic levels can affect natural enemies and their efficacy.
- 15 2. Here, we analysed how multitrophic interactions drive weed seed control under
16 contrasting farming systems and landscapes. In particular, we analyse how the
17 presence of higher-order predators and alternative prey affects the weed seed
18 consumption by seed predators. We monitored 30 cereal fields organised into 15 pairs,
19 each comprising one conventional and one conservation agriculture field, sampled
20 along a gradient of proportion of conservation agriculture in the landscape.
- 21 3. We found that local and landscape management under conservation agriculture
22 favours the presence of seed predators like carabids and rodents, higher-order
23 predators like shrews and alternative animal prey. Weed seed predation is promoted
24 by conservation agriculture through an increase in the number of seed predators.
25 However, alternative animal prey reduces the efficacy of carabids to consume seeds,
26 probably due to a prey switching behaviour. Similarly, shrews negatively affect the
27 activity-density of carabids, resulting in an indirect negative effect on seed predation.
- 28 4. Synthesis and applications: Our study highlights that the implementation of
29 conservation agriculture can improve the provision of biological control but the
30 resulting effect may be partially limited by the increased complexity of trophic

31 interactions. The different trophic levels respond to local management and/or the
32 surrounding landscape with cascading effects on the delivery of weed control. Our
33 study highlights the importance of considering not only the direct effects of seed
34 predators, but also the indirect effects of higher-order predators and alternative prey
35 when predicting the level of weed biological control.

36 **Keywords:** conservation agriculture; carabids; rodents; alternative resources; higher-
37 order predators; weed control; landscape composition; agroecology.

- 39 1. Les régulations biologiques constituent un service écosystémique clé dans les parcelles
40 agricoles, mais leur efficacité peut varier en fonction des contextes environnementaux
41 et biotiques. En effet, des interactions en cascade entre plusieurs niveaux trophiques
42 peuvent affecter les ennemis naturels et leur efficacité.
- 43 2. Dans cet article, nous avons étudié comment les interactions multi trophiques
44 déterminent les niveaux de prédation des graines d'adventices dans des systèmes
45 agricoles et des paysages contrastés. En particulier, nous avons analysé comment la
46 présence de prédateurs d'ordre supérieur et de proies alternatives affecte la
47 consommation de graines d'adventices par les prédateurs de graines. Nous avons suivi
48 30 parcelles de céréales échantillonnées le long d'un gradient de proportion
49 d'agriculture de conservation des sols dans le paysage. Les parcelles étaient organisées
50 en 15 paires comprenant chacune une parcelle conduite en agriculture
51 conventionnelle et une autre en agriculture de conservation des sols.
- 52 3. Nos résultats indiquent qu'une gestion en agriculture de conservation des sols,
53 localement et dans le paysage, favorise la présence de prédateurs de graines
54 d'adventices tels que les carabes et les rongeurs, et celle de prédateurs d'ordre
55 supérieur tels que les musaraignes et de proies animales alternatives. La prédation des
56 graines d'adventices est favorisée par l'agriculture de conservation des sols grâce à
57 l'augmentation du nombre de prédateurs de graines. Cependant, les proies animales
58 alternatives réduisent l'efficacité des carabes à consommer des graines, probablement
59 en raison d'un comportement de changement de proie. De même, les musaraignes
60 affectent négativement l'activité-densité des carabes, ce qui a un effet négatif indirect
61 sur la prédation des graines.
- 62 4. Synthèse et applications : Notre étude souligne que l'agriculture de conservation des
63 sols peut favoriser le contrôle biologique des adventices, mais cet effet peut être
64 partiellement limité par la complexité des interactions trophiques. Les différents
65 niveaux trophiques réagissent à la gestion locale et/ou au paysage environnant avec
66 des effets en cascade sur la régulation des adventices. Notre étude montre
67 l'importance de prendre en compte non seulement les effets directs des prédateurs
68 de graines, mais aussi les effets indirects des prédateurs d'ordre supérieur et des

69 proies alternatives lorsqu'il s'agit de prédire le niveau de contrôle biologique des
70 adventices.

71 **Mots-clés** : agriculture de conservation des sols ; carabes ; rongeurs ; ressources
72 alternatives ; prédateurs d'ordre supérieur ; régulation biologique des adventices ;
73 composition du paysage ; agroécologie.

75 Biological control is an essential ecosystem service to prevent crop losses, reducing both pests
76 and weeds in agroecosystems. This could contribute to the reduction of pesticide applications
77 (Shields et al., 2019). However, biological control remains underused by farmers, possibly
78 because its effectiveness varies over time and space, and is highly context-dependent.
79 Agroecosystems are simultaneously visited by different functional groups influencing each
80 other through interactions (Letourneau et al., 2009). Specifically, the efficacy of key natural
81 enemies providing biological control may be inhibited by trophic interactions such as
82 intraguild or higher-order predations (Finke & Denno, 2005; Martin et al., 2013) or by their
83 consumption of prey other than the targeted pest (Prasad & Snyder, 2006). The efficacy of
84 biological control thus results from complex trophic interactions, making the prediction of
85 service provision difficult (Eisenhauer et al., 2019). Therefore, we need studies accounting for
86 multitrophic levels that may have direct or indirect effects on the efficacy of biological control.

87 Among the wide array of biotic threats to crops, weeds usually have the greatest impact
88 (Oerke, 2006). Weed biological control is mainly the result of top-down regulatory forces
89 exerted by seed predators, thus reducing seed bank regeneration (Carbonne et al., 2020) and
90 weed emergence (Blubaugh & Kaplan, 2016). In temperate climates, carabids and rodents are
91 abundant weed seed predators (Kulkarni et al., 2015). However, the relationship between
92 seed predator abundance and weed seed loss seems context-dependent (Saska et al., 2008).
93 An important cause of this variation may be related to the different trophic interactions in
94 which seed predators are involved that may affect their community (Carbonne et al., 2022b)
95 and their foraging and feeding behaviours (de Heij & Willenborg, 2020). For example, carabids
96 can be predated by higher-order predators, like birds or small mammals, but also by intraguild
97 predators, with negative repercussions on biological control (Birthisel et al., 2014).
98 Additionally, a significant proportion of carabid seed predators are generalist consumers
99 which can feed on a plenty of prey (Frei et al., 2019). The presence of alternative prey (e.g.
100 collembola, earthworms or aphids), which can substitute for the consumption of weed seeds,
101 can affect carabid efficacy through prey switching (Carbonne et al., 2020; Gray et al., 2021).
102 When alternative prey is much abundant or preferred, carabids may switch from seeds to
103 other prey, indirectly dampening the biological control of weeds. The complexity of such

104 interactions that influence the efficacy of weed control requires substantial research. We need
105 studies unravelling top-down vs. bottom-up effects to harness pest control services over time.

106 In agroecosystems, the species composition and the resulting interaction network are
107 influenced by the intensity of field management with consequences on the provision of
108 services (MacFadyen et al., 2009). For example, conservation agriculture, which is
109 characterised by no-tillage and cover crops, improve the functional diversity of soil organisms,
110 including seed predators, their predators and alternative prey (Henneron et al., 2015; Petit et
111 al., 2017). At a landscape scale, the deployment of these systems could also play a major role
112 in the composition of mobile species, but its role is poorly documented (Petit et al., 2020). By
113 promoting in-field biodiversity, agroecological systems implemented locally or at landscape
114 scales can complicate trophic cascades with potential indirect negative effects on service
115 provision (Tschumi et al., 2018). Deciphering such complex relationships is necessary to
116 understand why the implementation of agroecological practices does not always guarantee
117 the promotion of biological control. This will contribute to guide the agroecological transition
118 at large scales (Haan et al., 2020).

119 Here, we evaluated how trophic interactions drive the biological control of weed seeds in
120 arable crops under conventional and conservation systems. The fields were positioned along
121 a gradient of proportion of conservation agriculture in the landscape. Specifically, using
122 structural equation modelling, we evaluated how local and landscape field management
123 interact to explain the abundance of seed predators and their efficacy to consume seeds. We
124 hypothesised that seed predators and seed consumption are promoted by local and landscape
125 management in conservation agriculture. In addition, we also hypothesised that conservation
126 agriculture promotes higher-order predators and alternative prey, which may reduce the
127 efficacy of weed seed predators.

128 **2. Materials and methods**

129 ***a. Experimental design.***

130 A field survey was conducted in 15 pairs of cereal fields (25 fields with winter wheat) within a
131 66 km radius around Dijon in France (47° 19' 19.369" N 5° 2' 29.328" E, Fig. S1). This area is
132 dominated by arable land with significant forest cover and some grasslands. All field sizes
133 ranged from 1.94 to 38.7 ha, with the exception of two experimental fields (Table S1). The

134 mean distance between two nearest sampled field pairs was 9.6 km. Within each pair,
135 biological measures were conducted in two adjoining fields with an average distance between
136 the two sampled zones of 123.6 m (SD=121.1). Within each field, measures were carried out
137 at three sample points spaced 15 m apart and located 20-50 m from the field margins (Fig. S2)
138 except for the two experimental fields. This distance allows sampling in the field core and
139 reduces the influence of field edges. Two field sampling sessions were conducted in May and
140 June 2021. Given the measurements taken in the field, our study did not require any special
141 permission or ethical approval.

142 ***b. Local and landscape management.***

143 Fields were selected to cover a gradient of proportion of conservation agricultural (“%CSA”)
144 lands in the landscape. The landscape was documented using the French Graphic Parcel
145 Register, superimposed on the CORINE Land Cover map 2000 in ArcMap 10.8. The land use
146 and the management system of the parcels were recorded through field and farmer surveys
147 within a circle of 1 km radius around focal fields. It is a relevant scale for detecting the
148 responses of seed predators to the landscape (Veres et al., 2013). The %CSA ranged from 3.1
149 to 37.5% and was not correlated with other landscape descriptors (Table S2) ensuring no
150 confounding effects.

151 Each pair consists of one field managed with conventional agriculture (“CVA”) and another
152 with CSA. CSA fields are characterised by no tillage nor superficial soil management for at least
153 4 years and by the introduction of a cover crop during the period between crops. Conventional
154 fields are tilled during the intercropping period with a rare use of a mouldboard plough. In the
155 two systems, weed management is based on rational use of chemical weed control during the
156 crop and intercropping period (Table S1). Fungicides and insecticides are used following locally
157 developed integrated management practices.

158 ***c. Seed-predators: carabids and rodents.***

159 Carabids (Coleoptera: Carabidae) were sampled using three pitfall traps per field. Each trap
160 was composed of a plastic beaker (10 cm height, 8 cm diameter), filled with 150ml of a
161 preservative solution of salt-saturated water and a few drops of odourless soap. A plastic
162 cover was placed above each trap to avoid rain flooding. The traps were exposed for seven
163 days between 3-12 May and 2-9 June 2021. Carabids were identified at the species level

164 (Coulon et al., 2011). Carabids collected in the three traps in each field were pooled to give a
165 field total per sampling session. For the analyses, we considered the carabid activity-density
166 for granivorous and omnivorous species only following Homburg et al. (2014). We caught 1204
167 (May) and 632 (June) omnivores dominated by *Poecilus cupreus* and 1370 (May) and 1217
168 (June) granivores dominated by species of the genera *Harpalus* (Table S4).

169 Rodents were captured using “INRA traps” (16 cm long, 5 cm height, 5 cm width - BTTM
170 company, Fig. S3) connected to 500 ml boxes containing hay, a gel water ball and a food pellet
171 (beef-based cat food and peanut butter) to meet the needs of the captured small mammals.
172 The traps were placed in two lines of 25 traps spaced at 3 m intervals. The two lines were
173 placed near a tractor wheel path and separated by 20 - 30 m. The traps were exposed for three
174 consecutive days and the presence of captures was checked every 24 hours. Rodent sampling
175 on all fields was conducted over a single period between 26 May and 10 June 2021. Captured
176 individuals were carefully identified, marked, and released directly into the field with minimal
177 handling; therefore, our study did not require ethical approval. All captures for the three days
178 were pooled to obtain a total abundance per field. We captured a total of 123 rodents (Table
179 S5).

180 ***d. Higher-order predators of carabids: shrews and spiders.***

181 We included shrews (Soricidae: Sorex) in higher-order predators as they are insectivores that
182 frequently consume beetles, e.g., about 60% of the spring diet consists of beetles for *Sorex*
183 *araneus* (Rudge, 1968). We captured 18 shrews using the same protocol used for rodents.

184 Moreover, we included a selection of spider taxa that are likely to consume carabids according
185 to expert opinion. Spiders were collected using the same protocol used for carabids. Spiders
186 were identified at the species level and pooled to obtain a total abundance per field. We
187 captured 587 (May) and 411 (June) spiders (Table S6).

188 ***e. Invertebrate animal resources: collembola, aphids and earthworms.***

189 Animal resource availability was described using collembola, aphids and earthworms that are
190 consumed by carabids in arable land (Frei et al., 2019).

191 Collembola and aphids were collected using suction sampling between the June 2 and June 4.
192 Suction sampling was performed using a ‘Vortis’ insect suction sampler (Burkard

193 Manufacturing Co Ltd) on windless and rainless days when the temperature was above 15°C.
194 Due to bad weather conditions, the May sampling session could not be completed. ‘Vortis’
195 samples were taken at each of the three sampling points, for each of which two suctions were
196 performed. The vortis is set at maximum speed starting from the top of the vegetation and
197 gradually descending to the soil surface, where the vacuum is maintained for 10 seconds. All
198 captures were pooled to obtain the total abundances of collembola and aphids per field. We
199 captured a total of 21047 collembola and 2376 aphids in June (Table S7).

200 To estimate the abundance of earthworms, we collected a soil volume of 18 L with a shovel
201 (15 cm height, 35 cm length, 35 cm width) in April 2021 for each field in the same area as the
202 other records. Soil samples were sorted and all earthworms were counted and classified into
203 four functional groups: endogeneous, epigeneous, strict-anecic and epi-anecic. We selected
204 epigeneous, strict-anecic and epi-anecic earthworms because they are more available on the
205 ground surface and susceptible to be consumed by carabids (Jelaska & Symondson, 2016).
206 These three groups were pooled to obtain a total abundance per field. We counted a total of
207 270 earthworms (Table S7).

208 ***f. Plant resources.***

209 Plant resources were described using the availability of weed seeds and the weed flora. Weed
210 seeds were collected and counted using the same suction sampling as those used to capture
211 collembola and aphids. All weed seeds were pooled to obtain a total abundance per field. We
212 collected a total of 321 seeds in June (Table S7).

213 Weed communities were surveyed between 7-9 June in a 50 × 40 m (2000 m²) area located
214 near the three sampling points. All plants were recorded following a W-shaped walking path
215 and identified at the species level (Jauzein, 1995). The abundance of each species was
216 estimated using a gradual scale of abundance: [0.1] found once, [0.75-1.25] less than 1; [1.75-
217 2.25] 1–2; [2.75-3.25] 3–20; [3.75-4.25] 21–50 and [4.75-5.25] more than 50 individuals per
218 m². Only plants in the flowering and fructification stages were retained as these are the ones
219 that have or will rapidly provide resources for seed predators. All abundance indices of all
220 weeds were summed to obtain a total index per field (Table S7).

221 ***g. Weed seed predation.***

222 Weed seed predation cards (Westerman et al., 2003) were used to estimate seed predation
223 rates. We selected three seeds covering different sizes, shapes and oil contents (Gaba et al.,
224 2019): *Alopecurus myosuroides* and *Galium aparine* that can lead to significant losses in cereal
225 yield production, and *Viola arvensis*, which is a model seed that is often used to measure
226 predation rates. We glued 20 seeds of each weed species on separate cards (95 × 40 mm card
227 of sandpaper) using SADER® WOOD PRO D3 diluted with two-thirds of water. At each sample
228 point, and for each seed species we exposed one card with a vertebrate enclosure cage (1 cm²
229 wire mesh) to measure predation by invertebrates and another card without cage to measure
230 total (invertebrate + vertebrate) weed seed predation. A total of 18 cards per field were
231 exposed over seven days simultaneously with the pitfall traps. The seed predation rate was
232 estimated using the number of seeds removed from the seed cards. We pooled the records
233 obtained for the three weed species to calculate the invertebrate and total predation rate per
234 field and session (Table S3).

235 ***h. Statistical analysis.***

236 We developed two piecewise structural equation models (SEM). The first SEM aimed at
237 explaining invertebrate weed seed predation by quantifying the indirect effect of local
238 management (CVA vs. CSA) and the %CSA in landscape through trophic interactions involving
239 higher-order predators, carabid seed-predators and resources (animal and plant) (Fig. 1 A). In
240 the second SEM we aimed to explain total weed seed predation using the same conceptual
241 diagram in addition to which we added the rodent seed-predators (Fig. 1 B). Separate SEMs
242 were performed for the May and June sampling sessions. As the data for the May session are
243 not complete (no plant and animal index), the corresponding SEM is provided as additional
244 material (Fig. S4 and Table S8). The small mammal survey is common to both sessions, as their
245 sampling covered both months.

246 As different methods have been used to quantify trophic resources and since some are much
247 more abundant than others, we have performed a Min-Max normalisation in order to give
248 each resource the same weight by bounding them between 0 and 1. The animal resource index
249 used was the sum of the abundances of collembola, aphids and earthworms after log-
250 transformation and Min-Max normalisation. The plant resource index was the sum of the
251 abundances of weed seed and weed plants after log-transformation and Min-Max
252 normalisation.

253 To reduce SEM complexity, the explanatory variables for each individual model in the SEMs
254 were selected in several steps. First, we applied a model selection based on the AIC and we
255 kept all selected variables in the best models ($\Delta AIC < 2$). For complex models that explain
256 predation rates, separate selections were made sequentially. In the second step, we improved
257 the fit of individual models by performing a step-by-step backward simplification. The
258 resulting SEMs were further simplified by removing non-significant relationships in cases
259 where this improved the overall AIC of the SEMs. These sequential simplifications resulted in
260 the elimination of some variables initially included (Fig. 1).

261 We used generalised linear mixed effects models within piecewise SEMs with the binomial
262 family (link = "logit") for predation rates and the poisson family (link = "log") for counts. We
263 used linear mixed-effects models for the analysis of animal and plant resource indexes. The
264 random structure of all models included the pair identity (1:15) to take account of the
265 dependence of the paired fields. We also included in some models a field observation-level
266 random effect (1:30) to correct overdispersion. The model residuals were visually checked for
267 normality and homoscedasticity using DHARMA (Hartig, 2022). Collinearity in the models was
268 low (variance inflation factor for non-interaction effects < 3). The overall fit of our piecewise
269 SEM was assessed with D-separation tests on Fisher's C statistic (Lefcheck, 2016) and AIC. For
270 the SEM explaining total seed predation in June, a significant missing path was detected and
271 added. The P-values and model parameters were recovered from the 'summary.psem' '
272 procedure (package 'PiecewiseSEM'). The stability of model parameters and the absence of
273 overfitting of the SEMs was checked by simplifying the SEMs by removing variables not
274 involved in direct/indirect effects on seed predation (Fig. S5 and Table S9). In addition, we
275 checked the stability of the linear models alone and included in the SEM.

276 All analyses and figures were conducted in R version 4.2.1 (R Core Team, 2022) and we used
277 packages lme4 (procedures 'glmer' and 'lmer'); MuMIn ('dredge'; Bartoń, 2022),
278 PiecewiseSEM ('psem'; Lefcheck, 2016) and ggeffect for the figures.

279 **3. Results**

280 ***a. Invertebrate weed seed predation***

281 The SEM for invertebrate seed predation in June represented our data well, with no significant
282 missing paths detected (Fig. 2.A; Fisher's C = 16.56, P = 0.867). Variation in invertebrate seed
283 predation rates was well-explained ($R^2m = 27\%$; $R^2c = 98\%$).

284 Local management significantly affected the granivore carabid activity-density ($p=0.017$; Table
285 1) and animal resources ($p=0.014$; Table 1). CSA fields had higher animal resources and
286 granivore carabids compared to conventionally managed fields (Fig. 3.A and B, respectively).
287 Seed predation rates were affected by an interaction effect between granivore carabids and
288 animal resources (p -value = 0.002; Table 1). We detected a positive relationship between seed
289 predation rates and granivore carabids that decreased in intensity as animal resources
290 increased (Fig. 4.A). In contrast to the June session, in May we detect a positive relationship
291 between invertebrate seed predation rates and omnivorous carabids, which are much more
292 abundant at this period (Fig. S4 and Table S8).

293 The abundance of shrews was significantly affected by %CSA in the landscape in interaction
294 with the local management ($p=0.026$; Table 1; Fig. 3.D). In CSA fields, increasing the %CSA in
295 landscape has a positive effect on shrew abundance, while no relationship was detected for
296 conventional fields. In addition, the increase in shrew abundance has a negative effect on
297 granivorous carabids ($p=0.018$; Table 1; Fig. 3.E). Spider abundance was positively correlated
298 with %CSA (Table 1).

299 Consequently, local field management and %CSA in the landscape indirectly affected
300 invertebrate weed seed predation rates through positive and negative cascading effects. CSA
301 fields favoured granivore carabids that were, in turn, positively associated with weed seed
302 predation. However, local field management and the deployment of CSA in the landscape
303 favoured animal resources and shrew abundance, respectively, which in turn reduced the
304 efficacy and the activity-density of carabids.

305 ***b. Total weed seed predation rates***

306 The SEM for total weed seed predation in June represented our data well (Fig. 3.B; Fisher's C
307 = 29.28, P = 0.503). SEM very well explained the variation in the seed predation rates ($R^2m =$
308 59% ; $R^2c = 98\%$).

309 The local management directly affected the total seed predation rates ($p<0.001$; Table 1; Fig.
310 4.B) with higher predation in CSA fields than in conventional fields. Moreover, local

311 management indirectly affected seed predation through animal resources and rodent
312 abundances. Animal resources, which were significantly higher in CSA than in conventional
313 fields, were negatively correlated to total seed predation rates ($p < 0.001$; Table 1; Fig. 4.C). The
314 abundance of rodents was significantly affected by the %CSA in the landscape in interaction
315 with local management ($p = 0.001$; Table 1; Fig. 3.C). In fields managed with conventional
316 agriculture, increasing the %CSA in the landscape has a positive effect on rodent abundance,
317 while no relationship was detected for CSA fields. The increased abundance of rodents has a
318 positive effect on the total seed predation rate ($p = 0.007$; Table 1; Fig. 4.D). Contrary to the
319 June session, in May we only detect a positive trend effect of omnivore carabids on total
320 predation rates (Fig. S4 and Table S8).

321 Consequently, local management and %CSA in the landscape directly affected total weed seed
322 predation rates, but also indirectly through two cascading effects: a negative one mediated
323 by animal resources and a positive one mediated by rodent abundance.

324 **4. Discussion**

325 Our results reveal that the implementation of conservation agriculture – both at the local and
326 landscape scales - can improve the weed control service by promoting the presence of seed
327 predators. This increase in seed predation appears to be partially limited by the complexity of
328 the multitrophic interactions including seed predators, higher-order predators and alternative
329 prey. These different trophic levels all respond to local management and/or the surrounding
330 landscape with cascading effects on the delivery of weed control. Compared to conventional
331 agriculture, we found that conservation agriculture favours the density of carabids and
332 rodents that consume weed seeds but also promotes the presence of higher-order predators
333 and alternative animal prey that reduce carabid efficacy to consume seeds.

334 ***a. Multitrophic interactions drive weed seed predation:***

335 Our results indicate that the contribution of granivore carabids to the predation of weed seeds
336 could be affected by trophic interactions involving higher-order predators and alternative prey
337 like animal resources. Invertebrate seed predation was positively affected by omnivorous and
338 granivorous carabids, respectively, in May and June. This difference may result from
339 omnivores being twice as abundant in May as in June. The increase in shrew abundance has a
340 negative effect on granivorous carabids for both periods, resulting in an indirect negative

341 effect on weed seed consumption in June. This negative effect was expected given the
342 insectivorous diet of shrews and their important consumption of large invertebrates (6-10
343 mm) encompassing many carabid species (Rudge, 1968). Predation by insectivorous
344 vertebrates, in particular shrews or birds, can negatively influence coleopteran insect
345 populations (Mooney et al., 2010). This negative effect can indirectly lead to a reduction in the
346 effectiveness of biological control (Grass et al., 2017; Martin et al., 2013) including weed seed
347 predation by carabids (Birthisel et al., 2014). Moreover, insectivorous predators can also affect
348 the foraging activity of carabids, and thus their efficacy to consume seeds (de Heij &
349 Willenborg, 2020). For example, Blubaugh et al. (2017) showed that exposure to mouse cues
350 reduced the activity-density of a seed-eating carabid, *Harpalus pensylvanicus*, but increased
351 its seed consumption, which is not observed in our study. Charalabidis et al. (2019) also
352 observed an increase in seed consumption by *H. affinis* when exposed to chemical cues from
353 *Pterostichus melanarius*, a potential intraguild predatory carabid. Therefore, the effectiveness
354 of weed seed biological control is modulated by the presence of higher-order and intraguild
355 predators that can simultaneously affect the populations and behaviour of seed-eating
356 carabids, making the prediction of service provision complex.

357 Our SEM analyses showed that the weed seed predation by carabids was reduced by the
358 availability of animal prey. This negative effect was already observed for collembola and aphid
359 prey (Carbonne et al., 2020) and could be related to carabid prey switching behaviour (Frank
360 et al., 2011). Animal prey, indeed, can be consumed by a large number of carabid species,
361 including species classified as granivorous such as *Pseudoophonus rufipes* (Frei et al., 2019).
362 The preferential consumption of one type of prey by the predator may indirectly and positively
363 affect another type of prey that will be less targeted by the predator. This pattern of indirect
364 positive interactions between prey can be termed "apparent commensalism or mutualism"
365 (Chailleux et al., 2014). Consumption of animal prey could be more attractive to some species
366 of carabids and lead to a satiation of individuals that will consume fewer seeds. Furthermore,
367 the high availability of animal prey may reduce the encounter rate between seeds and
368 carabids through a dilution effect (Evans, 2008). Consequently, the presence of animal prey
369 may indirectly preserve seeds by reducing their consumption by carabids. This observation
370 seems to be confirmed by the clear negative effect of animal resources on total seed predation
371 (without cage). However, this effect is not detected through an interaction with carabids,

372 probably because their contribution was masked by that of rodents, whose consumption on
373 seed cards is often important (Westerman et al., 2003).

374 Although seeds and animal prey appear to be concurrent prey in late spring, it is possible that
375 earlier in the growing season, animal prey may play a major role in the maintenance and
376 development of carabid populations in fields (Lundgren, 2009). The presence of alternative
377 prey may satisfy the dietary requirements of certain carabid species and permit their rapid
378 field colonisation and temporal persistence in fields (Symondson et al., 2002). Therefore, the
379 trophic interactions identified in our study can vary over the course of the cropping season,
380 depending on the dynamics of the different trophic levels. Due to incomplete data in May, we
381 could not assess the role of alternative prey during this period. However, the preharvest
382 period sampled in June corresponds to a key period for seed predation, as seed predators are
383 particularly active and weed seed rain is quite intense. Future research should extend this
384 analysis over several time replications over the cropping season and over several years to
385 verify the evolution of the trophic cascades described. Furthermore, given the high complexity
386 of interactions tested in trophic ecology SEMs (Redlich et al., 2021), ours included, we
387 recommend that future research increases the number of field replications performed.

388 ***b. Local and landscape management modulate multitrophic interactions:***

389 The conservation system favoured granivorous carabids in May and June, but also animal
390 resources compared to conventionally managed fields. These results are in accordance with
391 the previous observations of Henneron et al. (2015) showing that long-term CSA increased the
392 number of many organisms including earthworms, herbivores and granivore arthropods. The
393 absence of tillage is particularly favourable to earthworms, but also to certain carabid species,
394 whose larvae are present in the soil and are particularly sensitive to autumn tillage (Müller et
395 al., 2022). Tillage affects carabids directly by physical killing, but also indirectly by influencing
396 food resources and soil physical properties such as soil structure, water balance, and plant
397 residues (Müller et al., 2022). Moreover, the presence of cover crops in CSA could favour
398 arthropods, including carabids, by providing a favourable microhabitat and greater food
399 resources (Kulkarni et al., 2015).

400 At the landscape scale, we found that the %CSA in the landscape, in interaction with local
401 management, favoured shrew and rodent abundances. Small mammals have a high dispersal

402 capacity that allows them to colonise and move between arable fields. CSA fields may
403 represent a relatively more stable and suitable habitat for small mammals than conventional
404 fields (Ruscoe et al., 2022), and can therefore be source habitats for neighbouring fields. The
405 positive effect of %CSA on rodents was stronger in fields locally managed with conventional
406 than CSA. Rodent populations in low-disturbed fields, like those in CSA, could become
407 established over the long term, and therefore their abundance could be less dependent on
408 source habitats in the surrounding landscape. In contrast, rodent populations in highly
409 disturbed conventional fields may not be able to establish, and observed abundances could
410 mainly depend on the colonisation from surrounding source habitats (Ruscoe et al., 2022),
411 such as CSA fields for example. The increased abundance of rodents has a positive effect on
412 total seed predation in June but not in May, possibly because animal resources were not
413 included in May, which may have affected the final model. Moreover, rodents are also a
414 concern for farmers in CSA because they may generate crop damage (Ruscoe et al. 2022)
415 particularly *Microtus sp.* (voles) which are dominant in our surveys and damage the crop at
416 the time of sowing, germination or crop establishment. However, *Apodemus* species can also
417 cause damage by entering the field during the pre-harvest period and feeding on the seeds on
418 the ground or on the ears.

419 5. Conclusion

420 The simultaneous consideration of multitrophic groups, especially alternative prey and higher-
421 order predators in addition to seed predators, appears essential to understand the intensity
422 of weed seed control. Our study shows that CSA and its deployment in the landscape support
423 carabids and rodents and thus indirectly promotes the predation of weed seeds. However,
424 this increase in seed predation is partially limited by promoting insectivorous predators, such
425 as shrews, which can consume and negatively affect carabid populations and their seed
426 consumption. The presence of alternative prey, moreover, can lead to prey-switching
427 behaviour of carabids, which may shift from seeds to other food resources. Therefore,
428 conservation practices may improve overall weed biocontrol, but the resulting effect may be
429 partially attenuated by the associated increased complexity of multitrophic interactions.

430 **Data accessibility.** Data available via the Data INRAE repository

431 <https://doi.org/10.57745/51CZ5X> (Carbonne et al., 2022a).

432 **Authors' contributions.** Benjamin Carbonne participated in the design of the study, carried
433 out the statistical analyses and drafted the manuscript; Sandrine Petit and Lucile Muneret
434 conceived and coordinated the study, participated in data analysis and helped draft the
435 manuscript; Benjamin Carbonne, Lucile Muneret, Emilien Laurent, Emeline Felten, Chantal
436 Ducourtieux, Nicolas Henon, Annick Matejcek and Bruno Chauvel collected field data. Emilien
437 Laurent, Emeline Felten and Benjamin Carbonne carried out GIS analyses. All authors gave
438 their final approval for publication and agreed to be held accountable for the work performed
439 therein.

440 **Competing interests.** We declare we have no competing interests.

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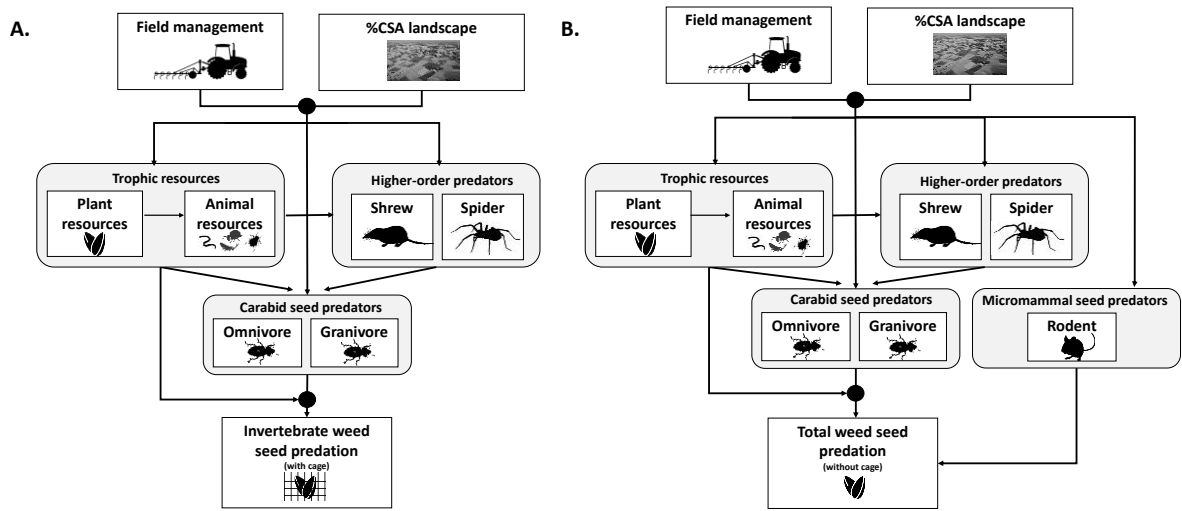
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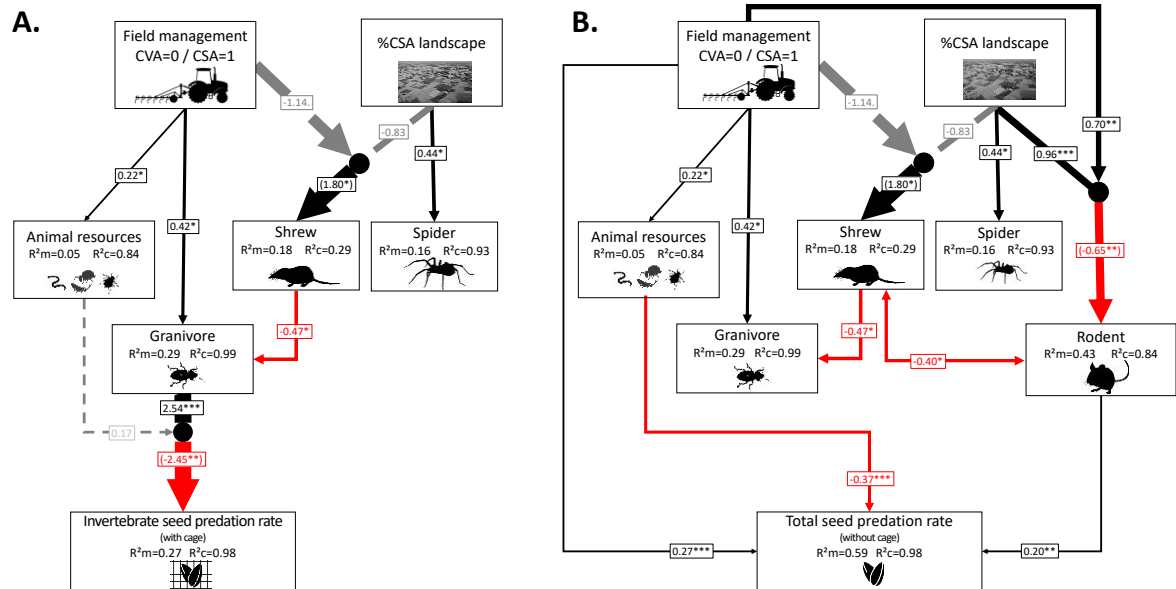
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609

610 **Figure 1:** Conceptual casual diagram for SEM explaining A. invertebrate weed seed
 611 predation and B. total weed seed predation. The diagram shows all initial tested
 612 relationships. The black circles (●) show tested two-way interactions.

613



614

615 **Figure 2:** SEMs for the June sampling session including cascading effects of ‘Field
 616 management’ (CVA: conventional and CSA: conservation agriculture) in interaction with
 617 the ‘%CSA landscape’ (the proportion of conservation agriculture in the landscape) on (A)
 618 invertebrate and (B) total weed seed predation. The indirect cascading effects considered
 619 seeds predators: ‘granivore’ carabid activity-density (for A and B) and ‘rodent’ abundance
 620 (for B); ‘shrew’ abundance as potential higher-order predators and ‘animal resources’ as
 621 alternative prey. The black and red arrows denote significant positive and negative
 622 effects, respectively. The grey dotted arrows indicate non-significant effects.
 623 Bidirectional arrows show causal correlations between variables. Standardised
 624 coefficients are shown for each path. The black circles (●) show interactions and the
 625 numbers in parentheses show interaction coefficients. The numbers of asterisks indicate
 626 the level of significance ($p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

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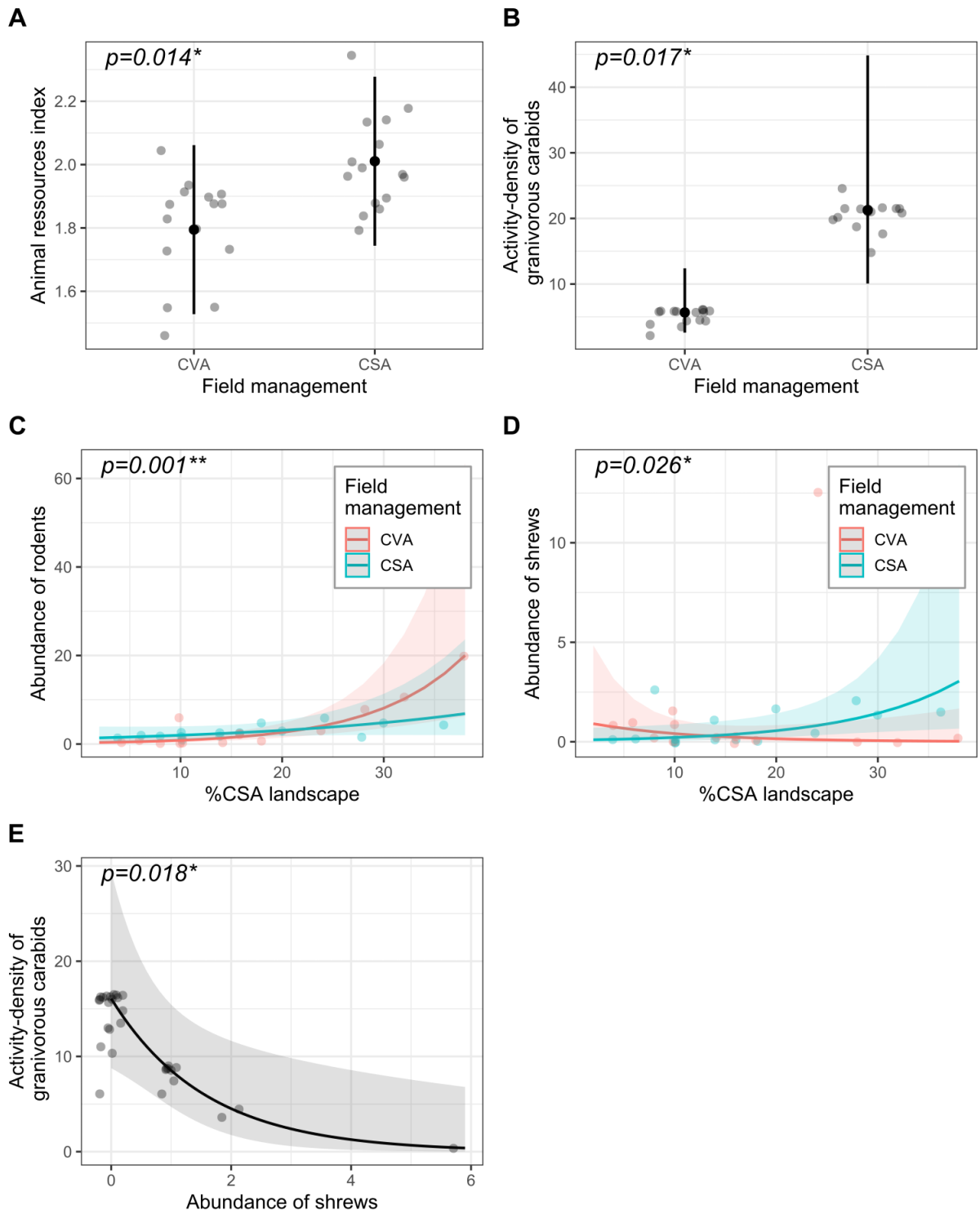
628 **Table 1:** Parameter estimates from SEMs for the June session. The response variables
629 were distinguished according to whether they were present in both SEMs or only one of
630 the two SEMs. For each response variable we reported marginal (R^2_m) and conditional
631 (R^2_c) r-squared. For each predictor with reported unscaled estimate, standard error (SE),
632 degrees of freedom (DF), critical ratio value (Crit. Value), P-value (p) and scaled estimate.
633 Highlighted are predictors with $p \leq 0.05$.

634

SEM	Response	R^2_m	R^2_c	Predictor	Unscale est.	SE	DF	Crit. Value	p	Scaled est.	
Common to both SEMs	Animal resources	0.05	0.84	Field management	0.22	0.08	14	7.98	0.014	0.22	*
				Field management	-2.57	1.40	30	-1.84	0.065	-1.14	.
	Shrews	0.18	0.29	CSA%	-0.10	0.08	30	-1.30	0.194	-0.83	
				Field management x %CSA landscape	0.19	0.09	30	2.22	0.026	1.80	*
	Granivorous carabids	0.29	0.99	Field management	1.32	0.55	30	2.40	0.017	0.42	*
				Shrews	-0.64	0.27	30	-2.36	0.018	-0.47	*
Spiders	0.16	0.93	%CSA landscape	0.04	0.02	30	2.28	0.023	0.44	*	
SEM A: Invertebrate seed predation (with cage)	Invertebrate seed predation	0.27	0.98	Granivorous carabids	0.07	0.02	30	3.30	0.001	2.54	***
				Animal resources	0.71	0.44	30	1.61	0.108	0.17	
				Granivorous carabids x Animal resources	-0.03	0.01	30	-3.17	0.002	-2.45	**
SEM B: Total seed predation (without cage)	Rodents	0.43	0.84	Field management	1.54	0.53	30	2.89	0.004	0.70	**
				%CSA landscape	0.11	0.03	30	4.12	<0.001	0.96	***
				Field management x %CSA landscape	-0.07	0.02	30	-3.20	0.001	-0.65	**
	Total seed predation	0.59	0.98	Management	1.17	0.27	30	4.39	<0.001	0.27	***
				Animal resources	-1.60	0.34	30	-4.68	<0.001	-0.37	***
				Rodent	0.08	0.03	30	2.68	0.007	0.20	**
~Shrew			~Rodent	-0.40	-	30	-2.26	0.016	-0.40	*	

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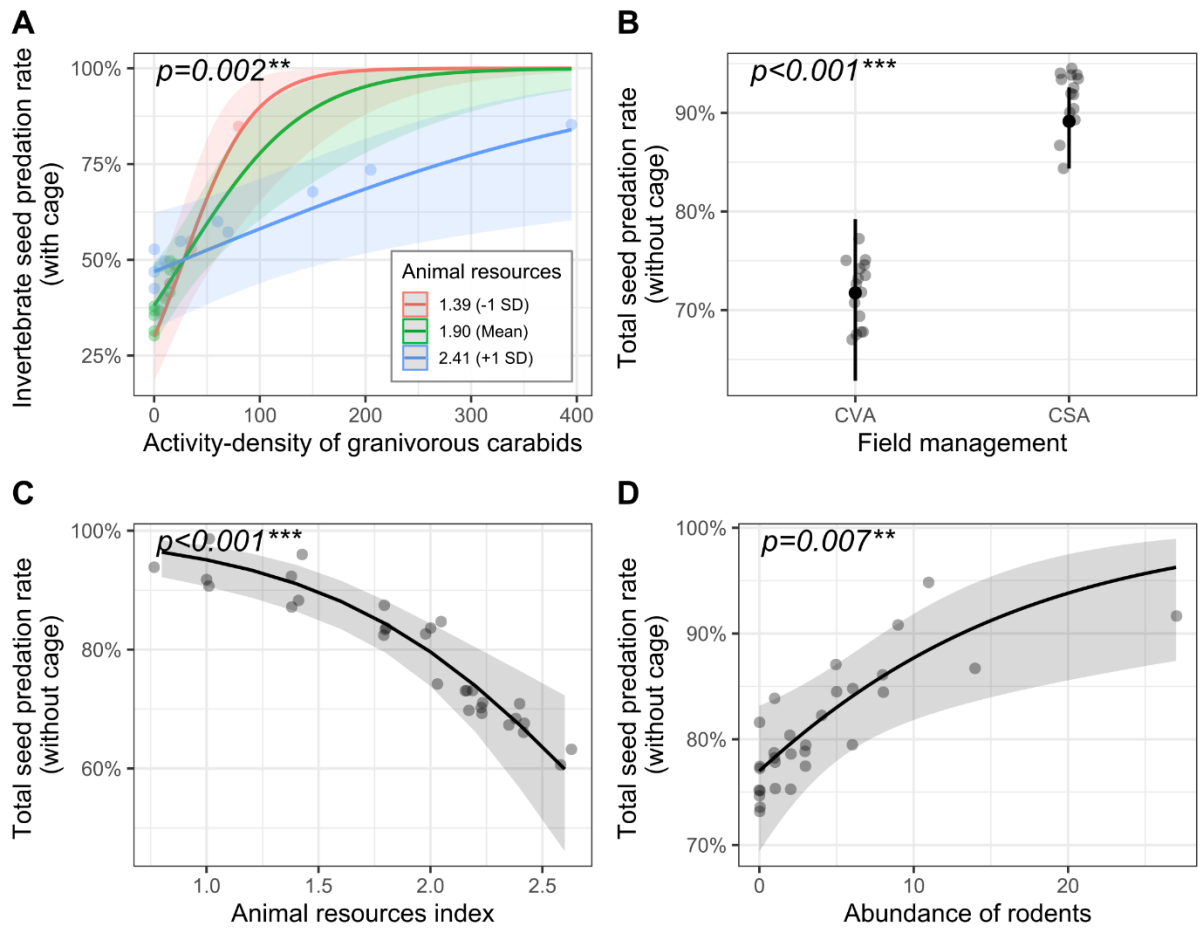
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Figure 3: Fixed-effect predictions, with the associated 95% confidence intervals and partial residual points, for the relationships between: the local management (CVA: conventional and CSA: conservation agriculture) and (A) the animal resources index and (B) the activity-density of granivore carabids; the interaction effect between the local field management and the percentage of conservation agriculture in landscape (%CSA

643 landscape) and (C) the rodent abundance and (D) the shrew abundance; (E) the granivore
644 carabids and the shrew abundance. For each of these relationships, we have reported
645 the corresponding p-value.

646



647

648

649 **Figure 4:** Fixed-effect predictions, with the associated 95% confidence intervals and
 650 partial residual points, for the relationships between: (A) the invertebrate seed predation
 651 rates and the interaction between granivorous carabids and animal resources; the total
 652 seed predation rates and: (B) the local management, (C) the animal resources and (D) the
 653 rodent abundance. “p” corresponds to p-value.

654

655