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1 Title : A multi-site experiment to test biocontrol effects of wildflower strips in
2 different French climate zones

3

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28 **Abstract**

29 Sowing of wildflower strips has been integrated in agri-environment schemes of several
30 European countries. Their beneficial effects on natural enemies of pest insects are well
31 documented but (1) the desired spill-over into crop fields has not always been demonstrated,
32 and (2) the need to adapt sown mixtures to regional climatic differences has been rarely
33 addressed.

34 We set up a multi-site experiment in different French climatic regions to compare effects of a
35 wildflower strip with a grass mixture and spontaneous vegetation. The design included five
36 regions, three to five fields per region and the three strip treatments being repeated in each
37 field. We tested strip treatment effects on vegetation (plant species richness, plant and flower
38 cover) and on natural enemies (hoverflies, ladybirds, aphid predation). In a subset, we further
39 analysed the spill-over into winter wheat fields including natural enemies and pest insects
40 (cereal aphids, leaf beetles).

41 The wildflower strip mixture developed well in all regions and increased plant species
42 richness and flower cover compared with grass strips and spontaneous vegetation. We found
43 a corresponding higher hoverfly abundance and aphid predation in wildflower strips that
44 were consistent in all regions, whereas ladybird abundance was not affected. A significantly
45 higher hoverfly abundance, aphid predation and aphid parasitism in wheat fields close to
46 wildflower strips indicated a spill-over. No corresponding margin treatment effects were
47 observed for aphid and leaf beetle abundance in the field. A multivariate analysis comparing
48 the influence of climate and vegetation parameters showed that floral cover better explained
49 variation in natural enemy abundance and predation than climate. Our results demonstrated
50 that similar mixtures of native plants can be used over large climatic gradients to improve
51 biocontrol. Further research is, however, needed to increase the spill-over into crop fields and
52 to obtain consistently strong effects in different climate zones.

53

54 KEYWORDS: Conservation biological control, ecosystem services, field margin, natural
55 enemies, natural regulation, semi-natural habitat

56

57 **Introduction**

58

59 In many European regions, there is an ongoing loss of semi-natural habitats (Billeter et al. 2008;
60 Ridding et al. 2020) and this loss is among the major causes for the decline in biodiversity of
61 many taxonomic groups (Hallmann et al. 2017; Ridding et al. 2020). Biodiversity linked to semi-
62 natural habitats provides several important ecosystem services such as pollination, carbon
63 sequestration, reduction in fertilizer and pesticide run off, as well as pest control (Holland et al.
64 2017). European Union member states have implemented agri-environment schemes to restore
65 biodiversity in agricultural landscapes involving the creation or conservation of semi-natural
66 habitats (Haaland et al. 2011; Holland et al. 2017). One of the most widespread agri-environment
67 schemes is the sowing of wildflower strips (Haaland et al. 2011). Wildflower strips are flower-
68 rich mixtures of indigenous herbaceous species usually sown to the edges of arable fields.
69 Although initially developed in the late 1980ies to enhance biodiversity in general (neutral and
70 functional), effects on ecosystem services such as biocontrol are increasingly discussed
71 (Tschumi et al. 2016; Pollier et al. 2019). In France, the research on this topic has been strongly
72 revived since the governmental plan to reduce pesticide use by 50% between 2008 and 2018
73 failed (“Ecophyto 2018”: Guichard et al. 2017) and the deadline was extended to 2025 in order
74 to provide more time and resources for the development of alternative pest control measures.
75 Wildflower strips or equivalent semi-natural field margins provide shelter, overwintering
76 habitats, and food resources such as nectar or alternative prey to different groups of natural

77 enemies of pest insects (Bischoff et al. 2016; Holland et al. 2017). The provisioning of floral
78 resources is crucial for several important natural enemies such as parasitic wasps, hoverflies and
79 lacewings that change nutrition from carnivorous during larval stages to herbivorous (pollen,
80 nectar) during the adult period (Winkler et al. 2009; Araj and Wratten 2015). For this reason,
81 quantity, quality and period of floral resource availability are key traits in designing wildflower
82 strip mixtures (Gardarin et al. 2018). The positive effects of flower-rich semi-natural habitats
83 including wildflower strips on abundance and diversity of natural enemies are well documented
84 but a corresponding effect on pest abundance and/or crop damage has rarely been shown
85 (Chaplin-Kramer et al. 2011; Haaland et al. 2011). The reasons for this potential lack in the
86 desired response of pest insect activity to an increased number of natural enemies in field
87 margins are complex and not yet well understood (Tscharntke et al. 2016). One problem is the
88 possible concomitant positive effect of such habitats on natural enemies and important pest
89 insects (Bischoff et al. 2016; Tscharntke et al. 2016). Another important constraint may be
90 energetic costs of movements combined with a relative attractiveness of semi-natural habitats
91 resulting in a strong reduction of biocontrol efficiency (Heimpel & Jervis 2005; Wanner et al.
92 2006). Thus effects on crop herbivory need to be better studied and integrated when evaluating
93 the biocontrol service of sown wildflower strips.

94 Climate has a large influence on plant diversity and community composition (Thuiller et al.
95 2005). Additionally, climate may change plant-insect interactions even on the same plant species
96 (Rasmann et al. 2014). So far, it is not well known at which scale such changes occur and
97 whether plant mixtures for wildflower strips need to be adapted to climatic conditions in order to
98 obtain a desired biocontrol effect. Currently, European species mixtures for wildflower strips are
99 usually suggested at country scale although local origin is recommended (Vander Mijnsbrugge et
100 al. 2010; Haaland et al. 2011). Robust mixtures performing well under different climatic
101 conditions may be a solution to simplify logistics of involved seed companies if regional seed

102 sourcing is respected. They would also improve the resilience of established plant communities
103 and associated insects to global climate change and the resulting increase in the probability of
104 extreme weather events.

105 In our study, we tested the performance of a species-rich wildflower strip mixture in five French
106 regions with different climate. We analysed the response of major natural enemy groups in the
107 strips and the resulting effects on pest insects in adjacent winter wheat fields using a subset of
108 four regions. To evaluate the biocontrol effects, we compared wildflower strips with both grass
109 strips and spontaneously emerging vegetation. Sowing of grass strips to field margins is
110 supported in French agri-environment schemes to reduce machinery impact on soil structure, soil
111 erosion and water pollution by fertilizer and pesticide run-off close to water bodies (Cordeau et
112 al. 2012). Such commonly used, species-poor grass mixtures were thus the first baseline to which
113 the biocontrol efficiency of wildflower strips was compared. Spontaneous vegetation was used as
114 a second baseline because natural field margin succession is also common and thus more
115 straightforward than using bare soil or cereal strips as controls (Haaland et al. 2011). Wildflower
116 strips involving costs for seed material, soil preparation and sowing need to improve biocontrol
117 performance compared to less costly practices representing our baselines. Both grass strips
118 (Collins et al. 2002) and spontaneous margins (Bischoff et al. 2016) have been shown to provide
119 resources and shelter to natural enemies of crop pests. We further used a correlative analysis to
120 compare the influence of vegetation (independent of strip type) and climate on biological
121 control.

122 In order to test the effect of sown wildflower strips on conservation biological control and the
123 robustness of effects under different climatic conditions, we addressed the following research
124 questions: (i) Does the selected wildflower strip mixture develop well under different French
125 climates and increase floral resource provisioning in all study regions? (ii) Is this mixture in all
126 regions successful in increasing natural enemy abundance and predation compared with grass

127 strips and spontaneous vegetation? (iii) Does the potential increase in mixture-related resources
128 translate in higher natural enemy densities in the field (spill-over) and in a better regulation of
129 pest insects? (iv) How strong is the influence of vegetation characteristics compared to regional
130 climate?

131

132 **Material and methods**

133

134 *Study sites and design*

135 The experimental design includes five study regions with three (Rennes) to five (Angers,
136 Avignon, Grignon, Dijon) fields per region (Appendix A: Fig. A.1). Three study regions are
137 located in North-Western France with temperate Atlantic climate characterised by mild winters
138 and relatively low summer temperatures (Grignon, Rennes, Angers, Table 1). Among these three
139 regions, the average annual temperature is higher in Angers than in the other two regions
140 whereas winters are colder in Grignon. The Dijon region is located in central-eastern France. The
141 climate is thus more continental, in particular with lower winter temperatures. The Avignon
142 region is characterised by Mediterranean climate with high summer temperatures, mild winters
143 and summer drought.

144 The experiment was set up in 2014 and analysed for two seasons. Both study years were warmer
145 than the long-term average with a mild winter in 2014 and a warm summer in 2015 but
146 differences between regions corresponded to the long-term climatic data (Appendix A: Table
147 A.1).

148 In the regions of Rennes and Dijon, one field was lost in 2015 due to unexpected changes in crop
149 and strip management. At the Grignon, Rennes, Angers and Dijon sites, the experiment was set
150 up in oilseed rape field followed by wheat. In Avignon, the experiment was run in apple
151 orchards. Thus, Avignon data were only included for measurements within margins. In Grignon,

152 no data were available from the first year. In March 2014, three strip treatments were established
153 in each of the 23 fields: (1) a wildflower strip (WS) with 32 flowering indigenous plant species
154 (Appendix A: Table A.2). Cultivars or species non-native to the five study regions were
155 excluded. The sowing density was 300 seeds/m² (0.8 g/m²) and density proportion of all species
156 equal. The sown mixture comprised plant species of different height and flower morphology that
157 produce high quantities of floral or extrafloral nectar at complementary flowering periods.
158 Annual, biennial and perennial plants were included to guarantee a sufficient cover in the first
159 and subsequent years and to avoid expensive re-sowing. (2) A grass strip mixture (GS) with
160 *Lolium perenne* (0.84 g/m² = 420 seeds/m²) and *Festuca arundinacea* (2.16 g/m² = 1540
161 seeds/m²). The two species are commonly used in France to obtain a fast vegetation cover
162 outcompeting weed species and avoiding soil erosion. (3) A strip of spontaneously emerging
163 vegetation (C). The soil of all treatments was ploughed and harrowed prior to sowing. The strip
164 area was 30 m x 3 m and the three treatments were randomly assigned to a 90 m long field
165 margin of each field. The strips were mown after the growing season in autumn 2014. The
166 establishment of the three treatments in the same fields reduced bias resulting from differences in
167 soil, microclimate and land use intensity but limited the analysis of long-distance spill-over since
168 distance differences to different strip types were getting smaller in central parts of the field.

169 ***Measurements***

170 *Vegetation*

171 The vegetation of margin strips was monitored in early June 2014 and in late June 2015. The
172 presence of all vascular plant species was recorded in a survey area of 15 m x 3 m in the centre
173 of the margin strips. Percentage cover of each plant species was visually estimated as the vertical
174 projection of all aboveground organs. At the same time, the percentage of flowering plants was
175 evaluated for each species. Individual flower cover was calculated by multiplying plant cover

176 and the proportion of flowering plants in each species. The sum of individual flower cover was
177 used as a proxy of total flower cover.

178 *Natural enemies and predation in field margin strips*

179 The insect surveys were conducted in the same week as vegetation surveys corresponding to
180 peak abundance of major pest insects. We selected hoverflies and ladybirds as natural enemy
181 groups that occurred at all sites. In order to avoid disturbance, adult individuals were first
182 counted from outside the strip in walking slowly along the edges of a 10 m x 3 m segment.
183 Afterwards hoverfly and ladybird larvae were recorded on the plants requiring a penetration of
184 strips (observation time: 10 min in total x 2 observers). Hoverfly and ladybird counts for adults
185 and larvae were pooled for analysis to avoid zero inflation. The observation period was between
186 10 AM and 4 PM under favourable weather conditions (sunny, not windy, no rain).

187 Aphid predation pressure was evaluated using bait aphids glued to sand paper (predation cards).
188 We used the commercially available pea aphid *Acyrtosiphon pisum* as sentinel prey, assuming
189 that predator identity and predation rates are similar for different aphid species (Östman 2004).
190 Predation cards were prepared by gluing (contact spray 'Cléopâtre ltd') three aphids on 5cm x
191 5cm black sand paper sheets. Aphid predation was evaluated after 24 h. An aphid was considered
192 as predated when damaged or missing. We fixed one card on the ground in the centre of each
193 margin strip in the Rennes, Angers, Grignon and Avignon region.

194 *Crop herbivores, natural enemies and predation in adjacent fields*

195 In June 2015, the effect of different strip types was also tested in adjacent winter wheat fields
196 (n=17) at a distance of 5 m and 30 m from the margins. In addition to natural enemies and aphid
197 predation, the abundance of cereal aphids and cereal leaf beetle larvae as major crop herbivores
198 were included. For hoverflies and ladybirds, the observation method was similar to that used
199 within margin strips: adult insects were first counted by observation along a segment of 3m x

200 10m parallel to the margin, from a distance and without touching the wheat tillers. In a second
201 step, the number of larvae was recorded by close observation. Cereal leaf beetles (*Oulema* sp.,
202 larvae), cereal aphids (dominant species: *Sitobion avenae* and *Metopolophium dirhodum*) and
203 aphid mummies were counted on 50 consecutive tillers along each segment. Aphid parasitism
204 rate was estimated by dividing the total number of mummies by the sum of aphids and
205 mummies. Aphid predation was measured as inside the margin strips by attaching a predation
206 card to the ground of each segment corresponding to two cards per margin strip treatment. Aphid
207 abundance, leaf beetle abundance and aphid parasitism were recorded in all experimental fields
208 with winter wheat (Rennes, Angers, Grignon, Dijon) whereas hoverfly abundance, ladybird
209 abundance and aphid predation were measured in a subset of three regions (Rennes, Angers,
210 Grignon).

211 *Analysis*

212 Prior to statistical analysis, entomophilous flower cover was calculated based on total flower
213 cover to obtain a more straightforward proxy of floral resource provisioning. The Bioflor
214 database (Klotz et al. 2002) was used to identify entomophilous plants and to eliminate wind-
215 pollinated species that do not produce nectar.

216 The strip treatment effect on vegetation characteristics, natural enemy abundance and aphid
217 predation inside margin strips was analysed using generalized linear mixed models. Treatment,
218 region and the region-by-treatment interaction were included as fixed, field within region as a
219 random effect. Vegetation data and arcsin(sqrt(x))-transformed aphid predation were normally
220 distributed and thus analysed using a Gaussian distribution and identity link. Count data were
221 fitted using a Poisson distribution with log-link function. When overdispersion was detected, a
222 negative binomial model with log-link function was applied. The glht function (multcomp
223 package, Tukey) was used for multiple comparisons when treatment main effects were
224 significant.

225 We used the same statistical model to analyse strip treatment effects within wheat fields but
226 additionally included distance as a fixed effect. Thus the model comprised three fixed effects
227 (region, treatment, distance), field within region as random effect and the two-way interactions
228 region-by-treatment (fixed) and treatment-by-distance (fixed). For a higher parsimony of the
229 model, we did not include the interaction between region and distance and the three-way
230 interaction between region, treatment and distance. All GLMM analyses were run in R, version
231 3.3.1, using the glmer function of lme4 package (R Development Core Team 2015).

232 In order to compare the influence of climatic variables and vegetation characteristics beyond
233 strip treatments on natural enemies and pest insects, a Redundancy Analysis (RDA) was applied
234 to field margin data. Response variables were log-transformed to homogenise variances and to
235 obtain similar scales. Independent of strip treatment, plant species number and entomophilous
236 flower cover were included as explanatory variables to characterise vegetation. Summer
237 temperature, the number of winter frost days and annual precipitation were used as major
238 climatic variable potentially influencing response variables. Pseudo-F statistics using
239 permutation tests with 499 unrestricted permutations was applied to evaluate the relative
240 significance of explanatory variables in the full model. RDA including permutation tests was run
241 in Canoco 5 (ter Braak & Smilauer 2012).

242

243 **Results**

244 Compared with the unsown strips with spontaneous vegetation, the wildflower strip treatment
245 added on average eight plant species to the first year community and nine species in the second
246 year (Fig. 1). Twenty-four sown species developed well in all regions, eight sown species were
247 rare or absent (Table A2). In the first year, annual species from the soil seed bank dominated in
248 all regions with sown species only representing on average 25% of soil cover and 40% of total

249 vegetation cover in wildflower strips. All annuals such as *Capsella bursa-pastoris*, *Cyanus*
250 *segetum*, *Matricaria chamomilla*, *Papaver rhoeas* and *Sinapis arvensis* but also some perennials
251 such as *Malva sylvestris* flowered in the first year. In the second year, the cover of sown
252 wildflower species increased to 50% with nearly all biennial and perennial species flowering.
253 The cover of *Lolium perenne* and *Festuca arundinacea* sown to grass strips reached on average
254 17% in the first and 40% in the second year. Several species sown to wildflower strips were part
255 of the soil seed bank explaining their relatively high cover in unsown strips (Appendix A: Fig.
256 A.2).

257 The strip treatment had a significant effect on plant species richness, on the cover of sown
258 wildflower strip species and on entomophilous flower cover, with the highest values for
259 wildflower strips followed by spontaneous vegetation (Table 2, Fig. 1, Appendix A: Fig. A.2).
260 The strip treatment effect on flower cover did not significantly differ between regions. Strip
261 treatment effects were stronger between wildflower strips and grass strips than between other
262 treatments. In the first year, differences between wildflower strips and strips of spontaneous
263 vegetation were for example not significant for flower cover ($P=0.22$) whereas differences
264 between wildflower and grass strips were marginally significant ($P=0.09$). Differences between
265 spontaneous vegetation and grass strips were never significant. Strip treatment effects on sown
266 wildflower species and flower cover increased from the first to the second year.

267 Corresponding to the significant effect of strip treatment on flower cover, strip treatment also
268 had a significant effect on hoverfly abundance with highest abundance in wildflower strips and
269 lowest in grass strips (Table 2, Fig. 2). Interactions with region were not significant suggesting a
270 similar strip treatment effect under different climatic conditions of the study regions. The
271 significant strip treatment effect was mainly explained by a significant difference between
272 wildflower strips and grass strips (year 1 marginally significant: $P=0.092$, year 2: $P=0.016$)
273 whereas the difference between wildflower strips and spontaneous vegetation was not or

274 marginally significant (year 1: $P=0.097$, year 2: $P=0.142$). Neither strip treatment nor region had
275 a significant effect on ladybird abundance. Aphid predation was significantly affected by strip
276 treatment in the second year again being the highest in wildflower strips and the lowest in grass
277 strips. In the first year, there was no treatment main effect on aphid predation but a significant
278 interaction of treatment with regions. Predation was higher in wildflower than in grass strips in
279 Angers and Rennes regions whereas in the Avignon region, the highest predation was measured
280 in spontaneous vegetation.

281 In adjacent wheat fields, the significant effect on hoverfly abundance and aphid predation found
282 within strips was confirmed (Table 3, Fig. 3). Again significant differences were observed
283 between wildflower strips and grass strips (hoverflies: $P<0.001$, aphid predation: $P=0.04$)
284 whereas the difference between wildflower strips and spontaneous vegetation was only
285 significant for hoverflies ($P<0.001$). For hoverflies, a significant distance-by-strip type
286 interaction occurred. The positive wildflower strip effect was limited to crop plants close to the
287 margin (5 m, $P<0.001$) whereas the strip type effect on hoverflies was not significant at inner
288 parts of the field (30 m). A marginally significant effect of strip type was detected for aphid
289 parasitism with a higher parasitism of aphids at both distances of the wildflower strips.
290 Corresponding to the absence of significant differences within margins, the effect of strip type on
291 ladybird abundance within wheat fields was not significant. The positive effects of wildflower
292 strips on hoverflies, aphid predation and aphid parasitism did not result in a reduction of aphid
293 abundance, nor leaf beetle abundance was affected by strip treatments.

294 A comparison of major climatic variables and characteristics of the field margin vegetation
295 pooled for margin strip treatments showed a dominant influence of flower cover on natural
296 enemies and aphid predation observed in field margins (Fig. 4). Flower cover was the only
297 significant explanatory variable in the RDA on natural enemy abundance and predation in
298 margin strips (PseudoF=14.4, $P=0.004$). It was strongly correlated with the first RDA axis

299 explaining 30% of the total variation (second axis only 2%). At the same time, hoverfly
300 abundance was correlated with flower cover whereas no correlation was observed for ladybirds.
301 Neither annual precipitation nor summer temperature nor winter harshness (number of frost
302 days) were significantly correlated with natural enemy abundance and aphid predation.

303

304 **Discussion**

305 *Treatment effects within strips and stability under different climate*

306 The wildflower strip treatment had a consistent positive effect on plant species richness and
307 flower cover in all study regions. The establishment rate of the sown species and the increase in
308 plant species richness are in line with the results of a European scale experiment in orchards
309 using country-specific wildflower strip mixtures (Pfiffner et al. 2019). Wildflower strip species
310 spontaneously establishing from the soil seed bank had a higher cover in unsown than in grass
311 strips. Thus, differences to sown wildflower strips were only significant to grass strips in the first
312 year but not to unsown strips with spontaneous vegetation. Accordingly, first year flower cover
313 was only different between wildflower strips and grass strips. Although treatment differences
314 were not very strong between grass strips and spontaneous vegetation, these results suggest that
315 sowing of competitive grasses may hamper the establishment of wildflowers known to improve
316 pest biocontrol service.

317 Hoverfly abundance within margin strips followed the pattern of flower cover with a
318 significantly higher density in margin strips of all study regions. The lack of significant
319 interactions with region demonstrated the robustness of the positive wildflower strip effect under
320 different climate from temperate oceanic to temperate subcontinental and Mediterranean. Again,
321 the differences to grass strips were significant in both years whereas the differences to
322 spontaneous vegetation were only significant in one year confirming the trend of floral

323 suppression by grass sowing. Nectar accessibility is a key trait for positive interactions between
324 flowering plants and hoverflies (van Rijn & Wäckers 2016; Gardarin et al. 2018). Zoophagous
325 hoverflies need flowers with a short corolla tube or with an open corolla to access nectar or even
326 extra-floral nectar (Campbell et al., 2012; van Rijn & Wäckers, 2016), which was considered in
327 the choice of wildflower strip species. Correlative studies analysing the influence of unsown
328 semi-natural habitats such as herbaceous field margins did not always show such a clear positive
329 relationship between hoverfly abundance and floral cover (Pollier et al. 2018; Bartual et al.
330 2019). The stronger positive signal obtained for sown wildflower strips taking into account the
331 floral requirements of hoverflies (Tschumi et al. 2016; Pollier et al. 2019) demonstrated the
332 potential for improving conservation biological control by optimising floral resource
333 provisioning. The analysis of floral visits at two of the five sites demonstrated the high
334 attractiveness of sown wildflower strip species compared with spontaneous vegetation (Pollier et
335 al. 2019).

336 Ladybirds did not show any significant response to the strip treatments and no interaction with
337 study region was observed. Larvae and adults are predominantly carnivorous but gut content
338 analyses showed that ladybirds also feed on floral resources and flowering plants may thus
339 increase their lifespan (Walton & Isaac 2011). Accordingly, several studies have found a positive
340 relationship between flower cover in semi-natural habitats and ladybird abundance (Bischoff et
341 al. 2016; Tschumi et al. 2015; Pollier et al. 2018, 2019). In our study, ladybird abundances were
342 both low and highly variable between fields within regions limiting the probability to detect
343 significant differences.

344 Aphid predation was significantly affected by strip treatment in the second year when wildflower
345 strip species were well established. Corresponding to the results on hoverfly abundance, highest
346 predation was observed in wildflower strips and lowest in grass strips. Again, the result was
347 robust under the different climates of our study regions resulting in a non-significant region-by-

348 strip type interaction. The corresponding results of aphid predation and hoverfly abundance
349 suggest a causal relationship since hoverfly larvae are major predators of aphids (Laubertie et al.,
350 2012). However, ground dwelling arthropods contribute to the predation of aphids on predation
351 cards (Blaise et al. 2021). Thus, the increase in predation may also be explained by a positive
352 effect of wildflower strips on these arthropod groups (Tschumi et al. 2015).

353 The multivariate analysis comparing the influence of climatic factors and vegetation traits on
354 predators and predation in the margin strips confirmed the particularly strong influence of floral
355 cover on hoverflies (van Rijn & Wäckers 2016; Gardarin et al. 2018) and to a lesser degree on
356 aphid predation. Floral cover explained much better the variation of response variables than
357 climate. Climate may change plant-insect interactions as studies on latitudinal or altitudinal
358 gradient showed (Rasmann & Agrawal, 2011; Rasmann et al., 2014). Often biotic interactions
359 are getting stronger with warmer climate since the number of insects associated to plant species
360 increases. However, in our study we sowed the same species everywhere limiting climate-related
361 responses based on long-term adaptive processes.

362 *Spill-over to adjacent wheat fields and control of pest insects*

363

364 Insects depending on floral resources show limited movements from flower-rich margins into the
365 field, and parasitism or predation rates may decrease far below maximum distances of
366 movements (Lavandero et al. 2005; Wanner et al. 2006). Additionally, the higher availability of
367 resources in semi-natural habitats may prevent natural enemies from moving into crop fields
368 (Heimpel & Jervis 2005).

369 In our study, positive wildflower strip effects on aphid parasitism and predation combined with
370 the absence of a significant distance-by-strip type interaction indicated a spill-over of parasitoids
371 and generalist predators to central parts of our fields. Although strip effects were weaker in the
372 field than in field margins (predation: only wildflower vs grass strip significant, parasitism: only

373 significant at $P < 0.1$), the results clearly demonstrated the potential of wildflower strips in aphid
374 control. Such an increase of aphid parasitism and/or predation in central parts of the field has not
375 been found in previous studies (Hatt et al. 2017 at 15 m; Pollier et al. 2018 at 50 m) but mark-
376 recapture experiments showed that parasitoids can move over whole fields (Lavandero et al.
377 2005; Wanner et al. 2006).

378 Hoverflies showed a higher abundance close to wildflower strips at 5m in the wheat fields but
379 not at 30m suggesting dilution effects (treatment effects diminishing with distance from the
380 margin) and limited spill-over. Such limited spill-over of hoverflies was also found in studies by
381 Tschumi et al. (2016: potatoes, 1m) and Pollier et al. (2018: wheat, 5m) whereas Hatt et al.
382 (2017) observed an increased hoverfly abundance in central parts of fields with wildflower strip
383 margins. However, our study design may underestimate spill-over since inner parts of the fields
384 may have been influenced by different strip treatments. This may have been avoided by
385 establishing treatments in different fields but a one field - one treatment design increases the risk
386 of confounding effects with other environmental factors such as field management, soil
387 conditions, neighbouring habitats and microclimate.

388 The positive effect of wildflower strips on hoverflies, aphid predation and aphid parasitism in
389 wheat fields did not result in lower aphid abundance close to the margin. The presence of
390 wildflower strips had also no effect on cereal leaf beetles as the second major pest insect group.
391 Reviews by Chaplin-Kramer et al. (2011) and by Haaland et al. (2011) confirm that such a
392 response of pest insects to an increase in natural enemy abundance is often lacking. In a study on
393 cereal aphid regulation, the density of semi-natural habitats increased for example both natural
394 enemy but also aphid abundance (Thies et al. 2005). A lower abundance of aphids and cereal leaf
395 beetles in crop fields adjacent to wildflower strips was found by Tschumi et al. (2016: aphids in
396 potato), Hatt et al. (2017: cereal aphids) and Tschumi et al. (2015: cereal leaf beetles),
397 corresponding to a higher natural enemy density. However, controls of these studies were cereal

398 strips instead of spontaneous vegetation which increases the magnitude of wildflower strip
399 effects on natural enemy abundance and thus the probability of detecting spill-over.

400

401

402 ***Conclusions and implications***

403

404 The tested wildflower strip mixture established well in all study regions involving a large
405 climatic gradient and increased plant diversity and flower cover compared with spontaneously
406 emerging vegetation and sown grass strips. Such a robust plant species combination represents a
407 cost-efficient and environmentally sound alternative to regionally differentiated species
408 composition, in particular if local provenance can be provided in each region. Core mixtures of
409 wide ecological amplitude may be complemented by several region-specific plant species if
410 logistics is sufficiently developed (Pffiffner et al. 2019). Further tests are needed to adjust the
411 optimum diversity level required for efficient biological control (Gardarin et al. 2021).

412 The increase in flower cover and diversity resulted in a consistent positive effect of wildflower
413 strips on hoverfly abundance and aphid predation within the margin strips potentially improving
414 the control of aphids as major herbivores in several arable crops (Tschumi et al. 2016; Pollier et
415 al. 2018). The widespread practice in France to sow grass mixtures in field margins showed
416 rather negative effects on entomophilous flower cover and parameters of biocontrol since
417 competitive grasses may hamper the development of herbaceous species.

418 We also demonstrated a spill-over effect of natural enemies into winter wheat fields but no
419 reduction in major pest insect abundance was detected. Further multi-site experiments are needed
420 to develop methods increasing the spill-over into crop fields and to obtain consistent and
421 sufficiently strong effects on pest insect regulation.

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429

430 **Appendix A. Supplementary data**

431

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538

Table 1. Climate data of the five study sites (1981-2010). Annual and monthly averages of the nearest meteorological stations.

Region	Coordinates	Precipitation (mm·year ⁻¹)	Temperature (°C) Mean [Jan/Jul]	Nights T<0
Grignon	48°50'28"N, 1°56'42"E	657	10.9 [4.0/18.7]	54
Rennes	48°07'11"N, 1°73'69"W	711	11.2 [4.7/18.0]	34
Angers	47°45'58"N, 0°33'09"W	693	11.8 [5.0/19.2]	46
Dijon	47°31'66"N, 5°01'66"E	768	10.5 [1.4/19.3]	68
Avignon	43°54'54"N, 4°52'46"E	676	14.6 [5.9/24.2]	33

Table 2. Chi-square values of Generalised Linear Mixed Models testing the effect of different strip treatments on vegetation, natural enemies and predation within field margins of different regions. Significant effects and interactions are indicated: (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

a) Year 1

	Df	Plant richness	Sown cover	Flower cover	Hoverfly number	Ladybird number	Aphid predation
Region	3	8.87*	1.71	1.12	15.92**	3.14	0.78
Strip type	2	27.80***	20.50***	5.18(*)	6.50*	4.72	4.26
Region x strip	6	10.11	4.80	3.02	9.18	4.02	11.27*

b) Year 2

	Df	Plant richness	Sown cover	Flower cover	Hoverfly number	Ladybird number	Aphid predation
Region	4	8.85(*)	10.12*	19.41***	10.68*	6.93	7.09*
Strip type	2	49.64***	22.66***	14.57***	8.65*	1.43	4.99*
Region x strip	8	18.92*	15.75*	11.03	5.50	4.14	0.72

Table 3. Chi square values of Generalised Linear Mixed Models testing different strip treatments at 3 to 4 regions and two distances on pest insects, natural enemies and parasitism/predation within winter wheat fields (year 2). Significance levels: see Table 2.

	Df	Hoverfly number	Ladybird number	Leaf beetle number	Aphid number	Aphid predation	Aphid parasitism
Region	2-3	6.88*	0.06	4.16	16.32***	1.24	22.24***
Strip type	2	33.74***	1.71	1.01	3.23	3.71*	2.46(*)
Distance	1	4.53*	0.63	0.02	0.19	0.03	0.78
Region x strip	4-6	19.64***	1.59	1.02	7.64	1.18	2.44*
Distance x strip	2	28.39***	0.12	1.09	0.38	2.41	0.52

Fig. 1. Number of plant species (A, B), and flower cover (C, D) in different margin strip types and regions with different climate, in the first (A, C) and second year (B, D); means \pm SE. Differences between strip types are indicated using “>” ($P < 0.05$), “(<)” ($P < 0.1$) and “=” (not significant) with WS: wildflower strip, SV: spontaneous vegetation (unsown) and GS: grass strip. Region-by-strip type interactions are presented if significant.

Fig. 2. Hoverfly abundance (A, B), ladybird abundance (C, D) and sentinel aphid predation (E, F) in different margin strip types and regions with different climate, measured in the first (A, C, E) and second year (B, D, F); means \pm SE. WS: wildflower strip, SV: spontaneous vegetation (unsown) and GS: grass strip. Region-by-strip type interactions are presented if significant.

Fig. 3. Hoverfly (A), ladybird (B), leaf beetle (C) and aphid abundance (D) measured on 50 tillers, aphid predation and aphid parasitism (parasitoids) in winter wheat fields (year 2, 2015) at two distances to the different margin strip types; means \pm SE. WS: wildflower strip, SV: spontaneous vegetation (unsown) and GS: grass strip. Distance-by-strip type interactions are presented if significant.

Fig. 4. Ordination biplots of Redundancy Analysis (RDA) showing relations between environmental variables (climate, characteristics of margin strip flora) and pest insects, natural enemies and aphid parasitism/predation as response variables in second year field margins. Data are pooled for strip treatments.

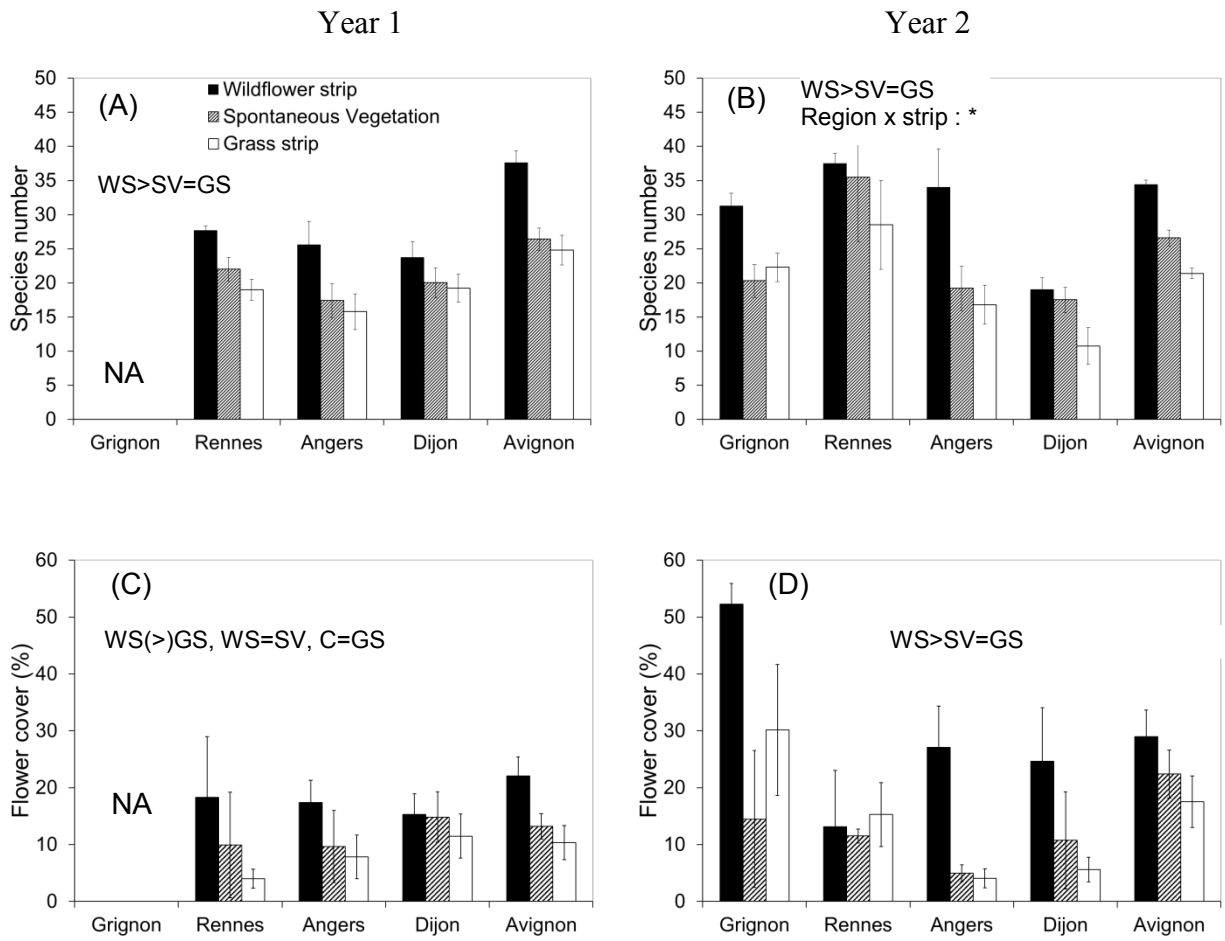


Fig. 1.

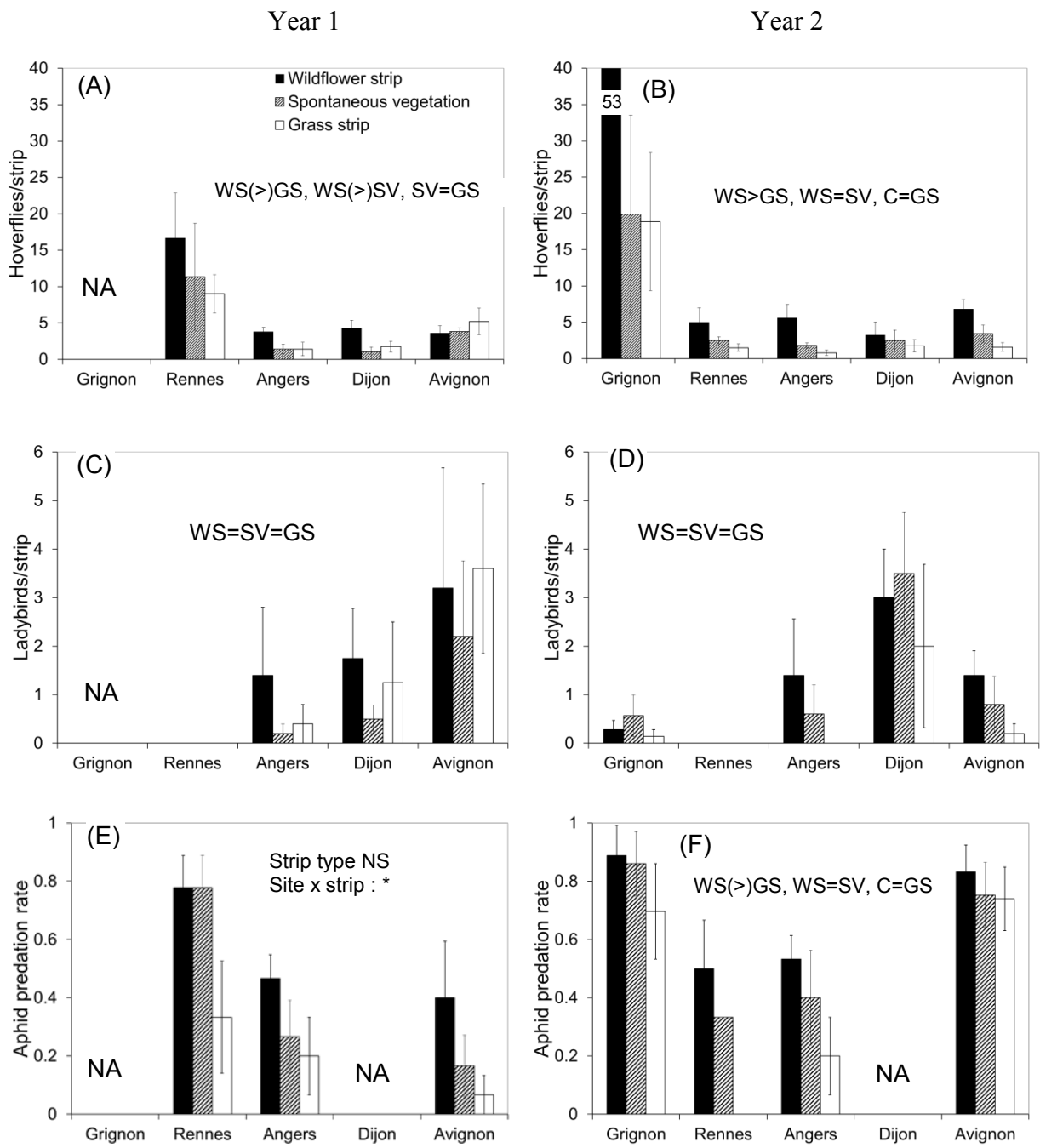


Fig. 2.

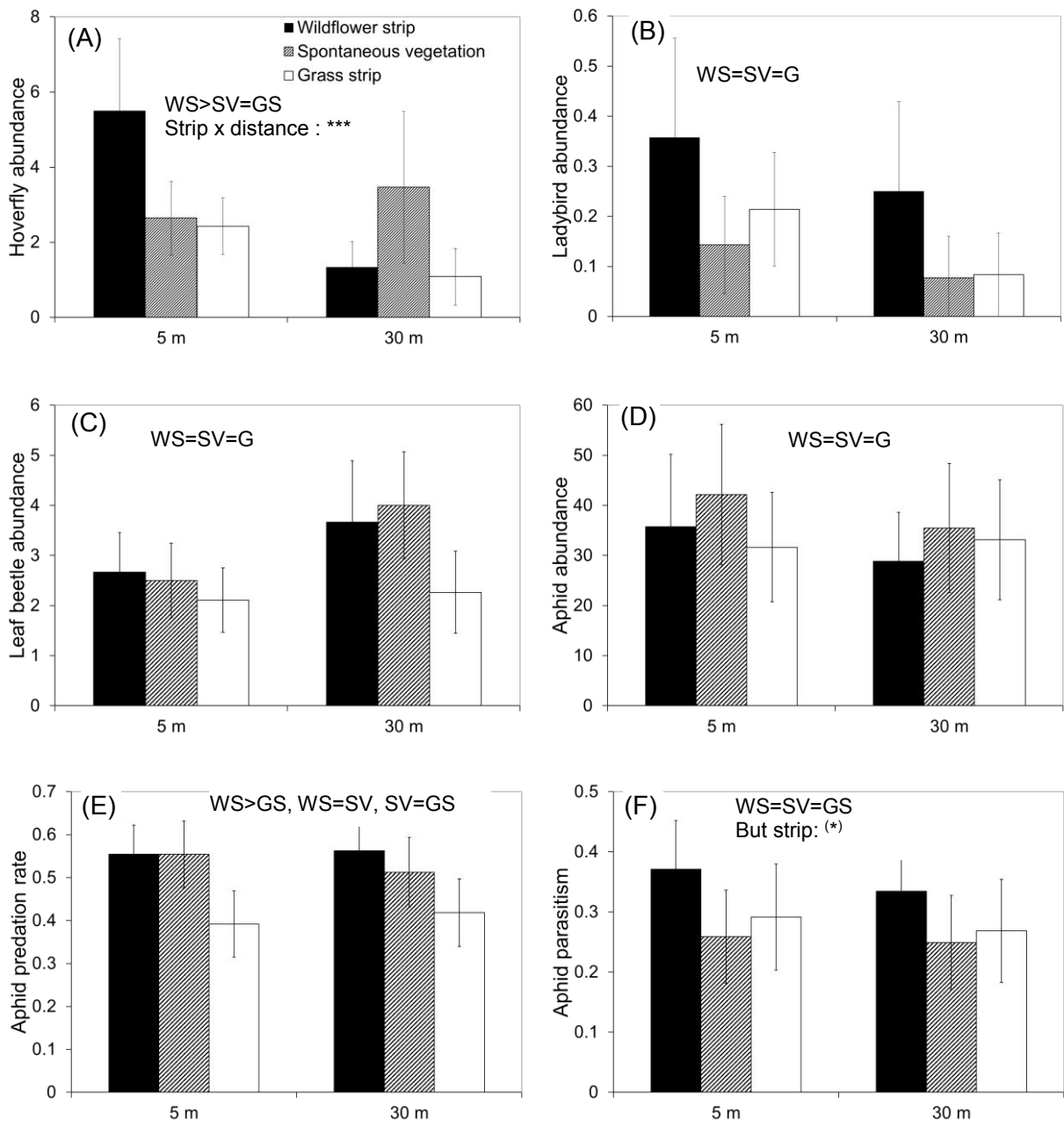


Fig. 3.

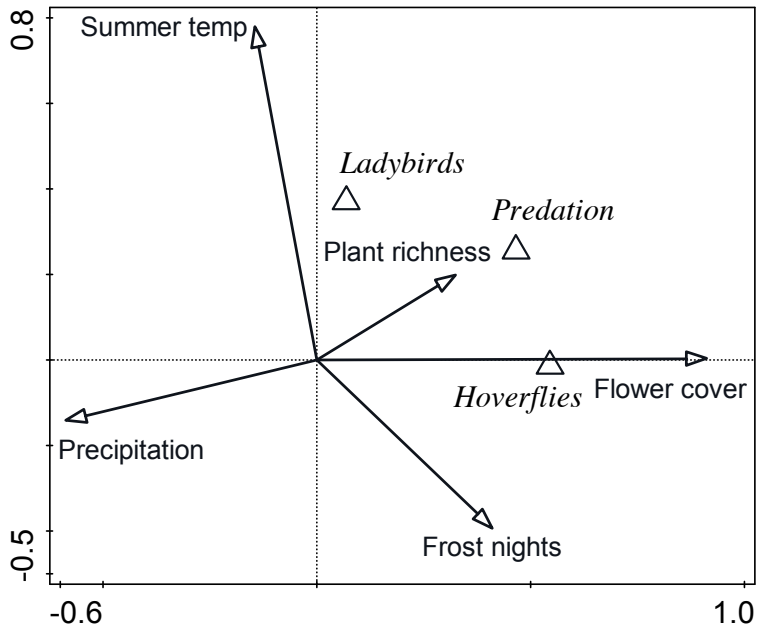


Fig. 4.

Appendix A

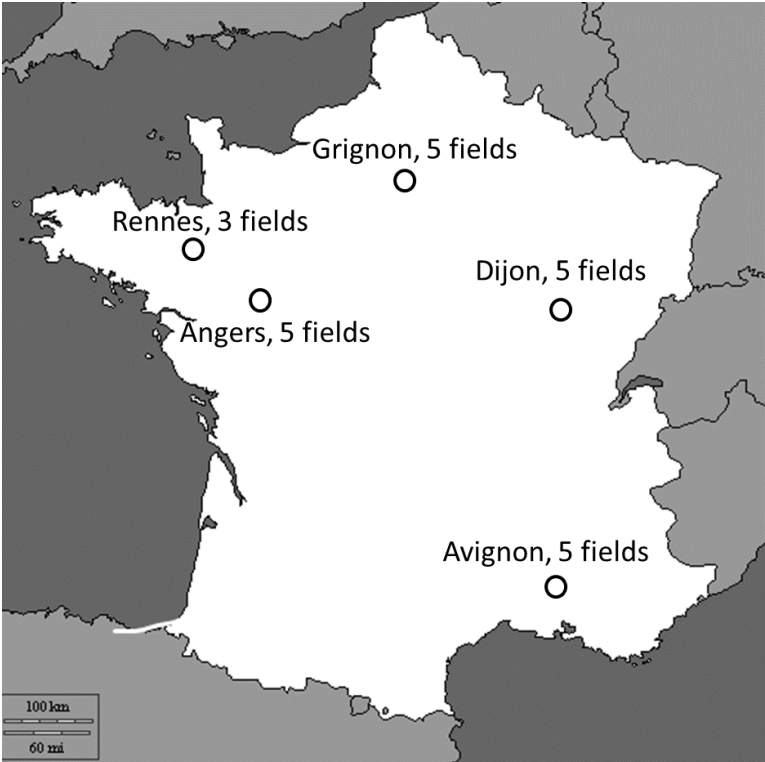


Fig. A.1. Position of the five study regions in France

Table A.1. Meteorological data of the five study regions. Annual and monthly averages during the study period.

a) 2014

Region	Coordinates	Precipitation (mm·a ⁻¹)	Temperature (°C) Mean [Jan/Jul]
Grignon	48°50'28"N, 1°56'42"E	687	12.2 [5.8/19.4]
Rennes	48°07'11"N, 1°73'69"W	838	12.9 [7.6/19.5]
Angers	47°45'58"N, 0°33'09"W	781	13.3 [6.6/20.4]
Dijon	47°31'66"N, 5°01'66"E	816	12.3 [4.9/20.0]
Avignon	43°54'54"N, 4°52'46"E	848	15.7 [8.4/22.9]

b) 2015

Region	Coordinates	Precipitation (mm·a ⁻¹)	Temperature (°C) Mean [Jan/Jul]
Grignon	48°50'28"N, 1°56'42"E	567	11.9 [3.5/20.6]
Rennes	48°11'07"N, 1°73'69"W	588	12.6 [5.0/19.5]
Angers	47°45'58"N, 0°33'09"W	660	13.0 [5.1/20.6]
Dijon	47°31'66"N, 5°01'66"E	536	12.1 [2.9/23.6]
Avignon	43°54'54"N, 4°52'46"E	690	15.6 [6.7/26.8]

Table A.2. Plant species composition of the sown wildflower strip mixture: sowing density, mean cover and number of region with at least one occurrence in relation to total number of regions (in parenthesis).

Species	Seed density (mg/m ²)	Cover (%) June 2014	Cover (%) June 2015
<i>Achillea millefolium</i> L.	1.69	0.20 (3/4)	0.92 (5/5)
<i>Ajuga reptans</i> L.	12.28	0.00 (0/4)	0.00 (0/5)
<i>Alliaria petiolata</i> Cavara & Grande	26.63	0.00 (0/4)	0.00 (0/5)
<i>Anthriscus sylvestris</i> (L.) Hoffm.	31.53	0.00 (0/4)	0.00 (0/5)
<i>Arctium minus</i> (Hill) Bernh.	98.53	0.01 (2/4)	0.05 (1/5)
<i>Arrhenatherum elatius</i> (L.) P.Beauv.	46.94	0.04 (3/4)	7.48 (5/5)
<i>Bellis perennis</i> L.	1.55	0.33 (4/4)	1.91 (5/5)
<i>Capsella bursa-pastoris</i> (L.) Med.	1.16	0.21 (4/4)	0.01 (2/5)
<i>Cyanus segetum</i> L.	36.64	2.09 (4/4)	0.20 (2/5)
<i>Centaurea jacea</i> L.	32.60	0.12 (3/4)	0.46 (5/5)
<i>Dactylis glomerata</i> L.	12.40	6.73 (2/4)	6.55 (5/5)
<i>Echium vulgare</i> L.	27.38	0.00 (0/4)	1.08 (5/5)
<i>Euphorbia cyparissias</i> L.	22.21	0.01 (1/4)	0.02 (1/5)
<i>Festuca arundinacea</i> Schreb.	28.30	0.15 (3/4)	1.13 (5/5)
<i>Foeniculum vulgare</i> Mill.	65.47	0.75 (3/4)	0.05 (3/5)
<i>Galium odoratum</i> (L.) Scop.	39.60	0.00 (0/4)	0.03 (1/5)
<i>Heracleum sphondylium</i> L.	77.87	0.00 (0/4)	0.24 (3/5)
<i>Hesperis matronalis</i> L.	21.25	0.01 (0/4)	6.35 (5/5)
<i>Hypericum perforatum</i> L.	1.24	0.00 (0/4)	0.00 (1/5)
<i>Leucanthemum vulgare</i> Lam.	6.23	0.01 (1/4)	7.15 (5/5)
<i>Malva sylvestris</i> L.	20.61	0.64 (4/4)	1.60 (5/5)
<i>Matricaria chamomilla</i> L.	3.75	3.07 (4/4)	0.84 (3/5)
<i>Medicago sativa</i> L.	20.18	1.03 (4/4)	3.22 (4/5)
<i>Papaver rhoeas</i> L.	2.12	3.38 (4/4)	5.37 (4/5)
<i>Potentilla erecta</i> (L.) Raeusch.	0.84	0.00 (0/4)	0.00 (0/5)
<i>Securigera varia</i> (L.) Lassen	41.86	0.05 (1/4)	2.21 (3/5)
<i>Sinapis arvensis</i> L.	25.33	10.30 (4/4)	0.63 (4/5)
<i>Tanacetum vulgare</i> L.	1.09	0.00 (0/4)	0.69 (4/5)
<i>Trifolium pratense</i> L.	23.15	1.91 (4/4)	3.22 (5/5)
<i>Trifolium repens</i> L.	6.73	0.74 (4/4)	7.47 (5/5)
<i>Verbascum densiflorum</i> Bertol.	1.31	0.03 (1/4)	0.00 (0/5)
<i>Veronica hederifolia</i> L.	40.80	0.06 (2/4)	0.03 (2/5)

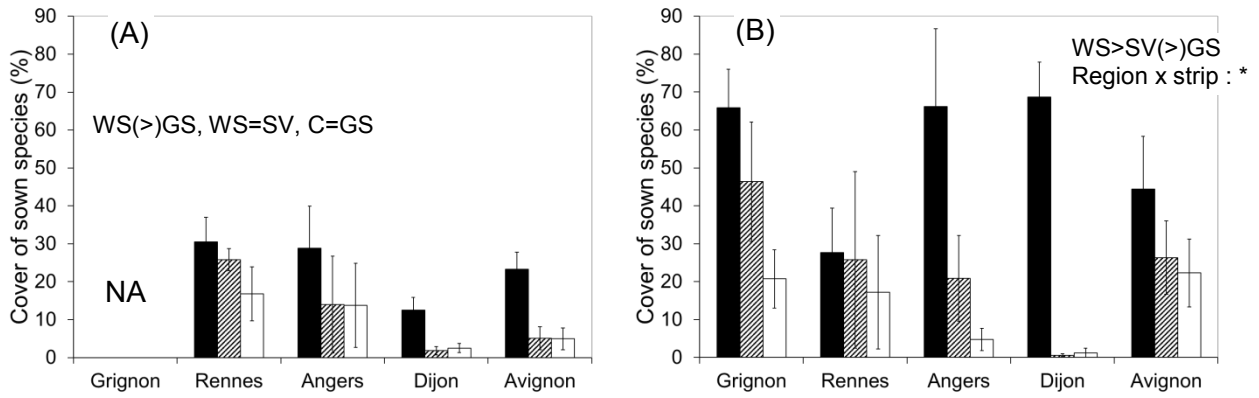


Fig. A.2. Cover of plant species of the wildflower strip mixture (Table A2) in different margin strip types and regions with different climate. in the first (A) and second year (B); means \pm SE. Differences between strip types are indicated using “>” ($P < 0.05$), “<” ($P < 0.1$) and “=” (not significant) with WS: wildflower strip. SV: spontaneous vegetation (unsown and GS: grass strip. Region-by-strip type interactions are presented if significant.