Journal of Applied Ecology

Plant diversification across scales enhances biological pest control in agricultural landscapes

Journal:	*Journal of Applied Ecology*
Manuscript ID	JAPPL-2020-01405
Manuscript Type:	Research Article
Date Submitted by the Author:	11-Dec-2020
Complete List of Authors:	Beaumelle, Léa; INRAE, UMR SAVE Auriol, Arthur; INRA Grasset, Marie; INRAE, UMR SAVE Pavy, Alice; INRAE, UMR SAVE Thiéry, Denis; French National Institute for Agricultural Research (INRA), UMR1065 Santé et Agroécologie du Vignoble Rusch, Adrien; French National Institute for Agricultural Research (INRA), UMR1065 Santé et Agroécologie du Vignoble;
Key-words:	agroecology, arthropods, biological pest control, landscape ecology, biodiversity, ecosystem services, vineyards

SCHOLARONE™
Manuscripts

1   **Plant diversification across scales enhances biological pest control in agricultural**

2   **landscapes**

3   Léa Beaumelle*, Arthur Auriol, Marie Grasset, Alice Pavy, Denis Thiéry, Adrien Rusch

4   INRAE, UMR 1065 SAVE, Villenave-d'Ornon, France

5   * lea.beaumelle@inrae.fr

6

7   **Abstract**

8   1. Implementing plant diversification is a promising way to balance food production and

9   biodiversity conservation in agricultural systems. Biological pest control, a crucial

10   ecosystem service delivered by natural enemies, could particularly benefit from increased

11   plant diversity at the local scale. Such positive effects however often depend on the

12   landscape context that shapes the pool of natural enemy species available and their ability

13   to colonize newly created habitats. However, how the landscape context modulates the

14   local effect of plant diversity on natural enemies and pest control services remains unclear.

15   2. Here, we manipulated the diversity of cover crops (2 versus 20 plant species) in 9 pairs of

16   vineyards located along a gradient of landscape complexity (ranging from 20 to 60% of

17   semi-natural habitats). We sampled natural enemy communities in the soil and foliage, and

18   measured the predation rate of an important moth pest in European vineyards (*Lobesia*

19   *botrana*).

20   3. Diverse cover crops enhanced the abundance of natural enemies by 140% across the

21   experiment, but without changing their taxonomic richness and composition. We further

22   found a distance-decay effects of cover crops on natural enemy abundance across cover

23   crop types.

24   4. The landscape context remarkably modulated the effects of local plant diversity on natural

25   enemy abundance and predation rates. While predation rates were on average similar in the

26   low and high cover crop diversity treatments across the experiment, diverse cover crops

27   had higher positive effects on predation and natural enemies in simple (< 50% semi-natural

28   habitats) than complex landscapes.

29   5. *Synthesis and applications:* Our study demonstrates the benefits of increasing plant

30   diversity at the local scale to enhance the abundance of natural enemies as well as the level

31   of biological pest control services in vineyard agroecosystems. Diverse cover crops mostly

32   benefit natural enemies and biological pest control in simplified landscapes, highlighting

33   that the success of local agroecological practices in improving biodiversity and ecosystem

34   services depends on the landscape context. Thus, we suggest that strategic spatial

35   arrangement of local plant diversification practices within agricultural landscapes is

36   necessary to maximize beneficial effects on biodiversity and ecosystem services.

37

38   **Keywords**

39   Agroecology, arthropods, biological pest control, landscape ecology, biodiversity, ecosystem

40   services, vineyards

41

42   **Introduction**

43   Agricultural intensification is a main cause of biodiversity loss in terrestrial ecosystems (IPBES,

44   2019). By harnessing ecosystem functions supported by biodiversity, agroecology aims to design

45   agricultural landscapes that can maintain commodity production while preserving the

46   environment (Bommarco et al., 2013). Biological control of crop pests by their natural enemies

47   is a major ecosystem service that can increase the sustainability of agroecosystems (Lewis et al.,

48   1997; Rusch et al., 2017). It can contribute reducing the use of pesticides and their harmful

49   effects on the environment while maintaining crop productivity (Geiger et al., 2010; Rusch et al.,

50   2017). Identifying agroecological practices beneficial to biological pest control services by

51   enhancing natural enemies and their diversity is therefore crucial for future agriculture.

52

53   Multiple evidences show positive relationships between biodiversity and ecosystem functioning

54   across ecosystem types (Cardinale et al., 2012). In agroecosystems, biodiversity can strengthen

55   the delivery of key ecosystem services such as biological pest control (Dainese et al., 2019;

56   Ostandie et al., 2020). Plant diversity is particularly crucial to maintain multiple ecosystem

57   services as plants shape trophic interactions across several levels (Andow, 1991; Isbell et al.,

58   2011; Scherber et al., 2010). Increasing plant diversity is therefore often suggested as a key

59   management option to harness biodiversity-based ecosystem services (Aguilera et al., 2020;

60   Kremen and Merenlender, 2018). Plant diversification encompasses crop and non-crop diversity

61   as well as various management practices that can be implemented at multiple scales from field-

62   scale diversification (e.g., cover-cropping, intercropping) to landscape-scale diversification (e.g.,

63   diversifying crop rotation, semi-natural habitats) (Letourneau et al., 2011; Rusch et al., 2010).

64   While the separate effects of local and landscape plant diversification on biodiversity and

65   ecosystem services have been extensively studied, the relative and joint effects of plant

66   diversification practices across spatial scales on pest control services remain poorly explored.

67

68   At the field scale, increasing plant diversity can limit the density of insect pests as well as plant

69   damage (Barnes et al., 2020; Letourneau et al., 2011; Wan et al., 2020). It has been estimated

70   that crop diversification reduced by 23% insect pest abundance and crop damage compared to

71   monocultures (Letourneau et al., 2011). The effects of plant diversity on insect pests are

72   mediated by direct bottom-up effects (the resource concentration hypothesis) and indirect top-

73   down effects (the natural enemies hypothesis) (Letourneau et al., 2011; Wan et al., 2020).

74   According to the resource concentration hypothesis, insect pests are more likely to find and

75   remain on their host plant in monospecific plant communities due to the high density of resource

76   that increases immigration to, and decreases emigration from monospecific communities (Root,

77   1973). The mechanisms behind these bottom-up effects involve disruption of host localization

78   due to chemical or physical perturbations, as well as changes in host plant quality (Andow, 1991;

79   Castagneyrol and Jactel, 2012; Finch and Collier, 2000; Thiery and Visser, 1986). The natural

80   enemies hypothesis suggests that natural enemies are more abundant, diverse and efficient in

81   more diverse plant communities leading to lower pest densities (Russell, 1989). These indirect

82   top-down effects are mediated by the higher abundances of alternative prey or hosts, pollen,

83   nectar, as well as microhabitats in diverse than monospecific plant communities. Evidence

84   supporting these two non-exclusive hypotheses exists in the literature (Moreira et al., 2016) but

85   the extent to which the landscape context modulates their prevalence remain to be explored.

86

87   At the landscape scale, habitat diversity shapes natural enemy communities as well as the level

88   of biological pest control services they deliver (Bianchi et al., 2006; Chaplin-Kramer et al., 2011;

89   Rusch et al., 2016). Semi-natural habitats, such as hedgerows, grasslands or forests support

90   crucial resources and habitats for natural enemies such as alternative preys, nectar, pollen or

91   overwintering sites, (Landis et al., 2000; Rusch et al., 2010; Sarthou et al., 2014; Tena et al.,

92   2015). While several studies have demonstrated that natural enemies and trophic interactions are

93   affected by landscape structure, the direction and magnitude of such effects on pest populations

94   and crop damages remain highly variable (Karp et al., 2018). Such context-dependent effects of

95   landscape structure on biological pest control could be due to interactive effects between

96   landscape and local management. Indeed, according to the intermediate landscape complexity

97   hypothesis, the landscape context might non-linearly modulate the effect of local management on

98   biodiversity and ecosystem services (Tscharntke et al., 2012). According to this hypothesis, local

99   management options (such as flower strip, reduced tillage or organic farming) have limited

100   effects on biodiversity and ecosystem services in very simple and complex landscapes, while the

101   highest positive effects are expected in landscapes of intermediate complexity. In very simple

102   landscapes (less than 20% of semi-natural habitats), the species pool is supposed to be too low to

103   support an increase in species diversity in response to beneficial management options at the local

104   scale. In very complex landscapes, high levels of biodiversity and ecosystem services are

105   expected and might therefore limit any further positive effects of local management options

106   aiming to improve biodiversity and ecosystem services. The interactive effect between local-

107   scale plant diversification and landscape-scale habitat diversification on biodiversity and

108   ecosystem services remains largely unexplored. This is especially the case for natural enemy

109   communities and biological pest control.

110

111   In this study, we explored the effect of cover crop diversity on natural enemy communities and

112   pest control services along a gradient of landscape complexity. We asked if diverse cover crops

113   enhanced the abundance and richness of natural enemies and biological pest control

114   independently of the landscape context in vineyards. We focused on vineyards because they are

115   intensively managed (e.g. in France, 20% of the total pesticide use while they cover only 3% of

116   agricultural land (Sabatier et al., 2014)), and many efforts are currently undertaken to implement

117   agroecological practices. Furthermore, vineyards are perennial crops in which increasing local-

118   scale plant diversity is particularly challenging given that increasing crop diversity is not an

119   option. Implementing cover crops in vineyards' inter-row is however a practice that is gaining

120   attention due to their multiple beneficial effects on agroecosystem functioning (Daane et al.,

121   2018; Winter et al., 2018). However, the interactive effects of cover crop diversity and landscape

122   context on natural enemies and biological pest control remain unclear (Wilson et al., 2017).

123

124   We hypothesized that 1) diverse cover crops enhance natural enemy abundance and richness, as

125   well as pest control potential compared to lowly diverse cover crop (Letourneau et al., 2011), 2)

126   different guilds of natural enemies are affected differently by cover crop diversity (Muneret et

127   al., 2019), and 3) the positive effects of cover crop diversity are higher at intermediate landscape

128   complexity than in simplified or complex landscapes (Tscharntke et al., 2012; Wilson et al.,

129   2017).

130

131   **Materials and methods**

132   1. **Study design**

133   A field experiment was conducted in vineyards located in the Bordeaux area, France

134   (45°01'28"N, 0°21'13"W) in 2018. Nine sites were selected along a gradient of landscape

135   complexity (ranging from 22 to 63% of semi-natural habitats in a 1 km radius around each site).

136   At each site, a treatment with high cover crop diversity (flower strips) and a control with low

137   cover crop diversity (grassy strips) were applied each in one separate field under the same

138   management practices (plots were part of the same farm). The experimental design resulted in 9

139   pairs of vineyards. The high diversity treatment consisted in a mixture of 20 plant species

140   designed specifically for vineyards' inter-row and containing a range of functionally different

141   plants (such as Fabaceae, melliferous plants: see Supplementary materials for the full list of plant

142   species). The low diversity treatment consisted in a mixture of two Poaceae (*Lolium perenne* and

143   *Festuca rubra*). Plants were sown manually after soil tillage on April 24th and May 11th 2018 in

144   one out of two inter-rows, on a total of 8 inter-rows per plot. Cover crops were sown along a

145   distance of 20 m from the plot margin to the center of the plot (Fig. S1).

146

147   2. **Natural enemy sampling**

148   Two guilds of natural enemies (soil- and vine-dwelling) were sampled at increasing distance

149   from the cover crop treatments in each field. Soil enemies were sampled using pitfall traps and

150   vine enemies with beating nets. The samplings were conducted at three distances from the cover

151   crop treatments: in the middle of the cover crop (0 m), and at 15 and 30 m away from the middle

152   of the cover crops. Three sampling sessions were conducted (in June, August and September).

153   Each sampling session and at each distance (0, 15 or 30 m) in each field, two pitfall traps filled

154   with soap water were placed in the soil of different inter-rows for a week before being collected

155   and individuals pooled before identification. Vine arthropods were pooled from beating 15

156   randomly-located vines per distance per field at each sampling session. In the end, for each

157   distance, guild, treatment, and field, the sample size was n = 3 (one pooled sample per session),

158   yielding a total sample size of N = 324. Individuals were identified to the nearest possible

159   taxonomic level, but the high number of juvenile spiders limited species identification, and about

160   77% of all arthropod individuals were thus identified to the genus. We calculated taxonomic

161   richness as the number of taxonomic groups in each sample. Rarefied richness could not be used

162 due to a number of samples where the abundance was zero. As the sampling effort was identical

163 across the experiment, we focused on taxonomic richness instead of rarefied richness.

164

165   3. **Pest control measurements**

166 We evaluated the biological pest control potential of one of the main vineyard pest, the European

167 grapevine moth (*Lobesia botrana* Fam. Tortricidae) (Thiéry et al., 2018), using sentinel cards

168 (Muneret et al., 2019). Each sentinel card consisted of 10 moth eggs laid on parchment paper in

169 the laboratory, and then glued on a plastic card of about 1 x 8 cm. Moth eggs were obtained from

170 our own laboratory-rearing (temperature: 22°C, hygrometry: 60%, photoperiod: 16D/8N). In

171 each field, eight cards were attached to the vine stock, close to the grapes, at each distance from

172 the cover crop treatment, and left for three days before being collected. Biological control

173 potential was then measured based on the proportion of eggs removed from the card. Three

174 measurement sessions were conducted (in July, August and September). During the last sampling

175 session, only 4 egg cards were used due to low moth eggs availability in the laboratory and

176 incompatibility with pesticide spraying programs.

177

178   5. **Data analyses**

179 We tested the main and interactive effects of the plant diversity treatment (low versus high

180 diversity), the landscape context (proportion of semi-natural habitats), and the distance to the

181 center of the cover crop treatment (0, 15, 30 m) on the abundance, richness and community

182 composition of two guilds of natural enemies (soil and vine), and on pest predation rates. We

183 used the proportion of semi-natural habitats as a proxy of landscape complexity (Muneret et al.,

184 2018). The proportion of semi-natural habitats resulted from the sum of proportions of forests,

185   meadows and fallows. We used the regional database PIGMA (http://portail.pigma.org) and

186   calculated the proportion of different habitat types in a 1000 m radius around each site using

187   ArcGIS 10.1 (ESRI).

188

189   We used generalized linear mixed effect models (GLMMs) to analyze abundance and taxonomic

190   richness of natural enemies and biological pest control potential with the R package lme4 (Bates

191   et al., 2015; R Core Team, 2019). We analyzed natural enemy communities by constrained

192   ordination (partial Redundancy Analysis, pRDA) using the R package vegan (Oksanen et al.,

193   2019).

194

195   a. **Abundance**

196   GLMMs were fitted to natural enemy abundance with a negative binomial distribution to account

197   for the nature of the data (counts and overdispersion). We tested the following full model:

198   *Abundance ~Treatment*Guild*Landscape + Treatment*Guild*Distance + (1|site:session)*

199   The model included the fixed effects of the Treatment (two-level factor: low plant diversity and

200   high plant diversity); Guild (two-level factor: soil and vine guilds of natural enemies); Landscape

201   (continuous variable: scaled percentage of semi-natural habitats in a 1000m radius); and Distance

202   (continuous variable: scaled distance to the center of the cover crop). The model also included a

203   random effect of the session within each site on the intercept (factor with 27 levels) to account

204   for non-independent observations conducted the same date at each site. We first tested the full

205   model *vs.* null model (*Abundance ~ 1 + (1|site:session)*) and verified the residuals of the full

206   model using the R package DHARMa (Hartig and Lohse, 2020). Based on residuals patterns, we

207   included a quadratic effect of landscape complexity that significantly improved model fit and

208   residual plots, and was also biologically relevant (Tscharntke et al., 2012). We further evaluated

209   spatial autocorrelation by inspecting the residuals versus spatial coordinates of each plot, and

210   found no significant pattern. We tested the main effects of our variables and their interactions

211   using Wald Chi-square tests and likelihood ratio tests (LRT), using the R function *drop1* (Zuur et

212   al., 2009) both approaches yielded the same results. Following Harrison (2018) and Forstmeier

213   and Schielzeth (2011), we report the results of the full model instead of the optimal model.

214

215   **b. Diversity**

216   We used a similar approach and model structure to investigate the response of the taxa richness

217   of vine and soil natural enemies to the treatment, landscape and distance to cover crop treatment.

218   The model was identical to the abundance model above. We fitted a negative binomial GLMMs

219   that provided better fit than LMMs with gaussian distribution, even after log-transformation. We

220   also included a quadratic effect of the landscape based on residual diagnostic plots, and followed

221   the same protocol to model simplification and reporting (Harrison et al., 2018; Zuur et al., 2009).

222

223   **c. Biological pest control**

224   We modelled the number of eggs predated per sentinel card using a GLMM with negative

225   binomial distribution, after trying alternative distributions (binomial, poisson) that provided poor

226   fit to the data based on residual diagnostic plots. The following full model was tested:

227   *Predation ~Treatment*Landscape + Treatment*Distance + (1|site:session).* Again, we included

228   a quadratic effect of the landscape based on the residual diagnostic plots of initial models that did

229   not include such a non-linear effect.

230

231   d. **Community composition**

232   We used RDA using the same model structure as above to analyze the effect of Treatment,

233   Landscape, Guild and Distance on community composition of predators. We summed the

234   abundance of each taxa across sampling sessions before analysis. The community matrix was

235   Hellinger transformed prior to analysis. Permutation tests (using 999 permutations) were used to

236   test the significance of all constrained axes.

237

238   **Results**

239   A total of 5148 individuals belonging to 198 taxonomic groups were collected across the

240   experiment, 73% were spiders, 20% Coleoptera, 6% Opiliones, and a few Neuroptera (50

241   individuals) and Dermaptera (13 individuals). The soil guild was composed of 67% spiders, 28%

242   Coleoptera, and 5% Opiliones (with a total number of 156 taxa). The vine guild however was

243   dominated by 86% spiders, no Coleoptera, and 10% Opiliones (with a total number of 82 taxa).

244   In terms of biological pest control, the average predation rate was 0.30 (SD: 0.27, n = 999)
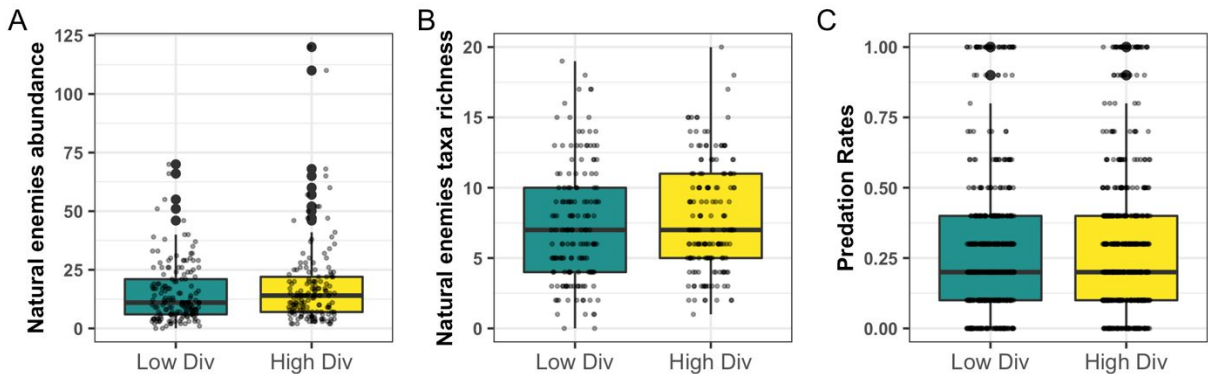
245   across the experiment.

246

247

248   **Figure 1. Cover crop diversity affects natural enemy abundance (A), but not richness (B)**

249   **and pest predation rates (C) in vineyards.** A) Total abundance of natural enemies in high and

250   low cover crop diversity treatments, across soil and vine guilds, and landscapes ($n_{high\ div}$ = 156,

251    $n_{low\ div}$ = 159). B) Taxonomic richness of natural enemies across guilds and landscapes ($n_{high\ div}$ =

252   156, $n_{low\ div}$ = 159). C) Proportion of sentinel grape moth eggs predated ($n_{high\ div}$ = 499, $n_{low\ div}$ =

253   500). Boxplots depict median values (horizontal bold lines), 25th and 75th percentiles (bottom

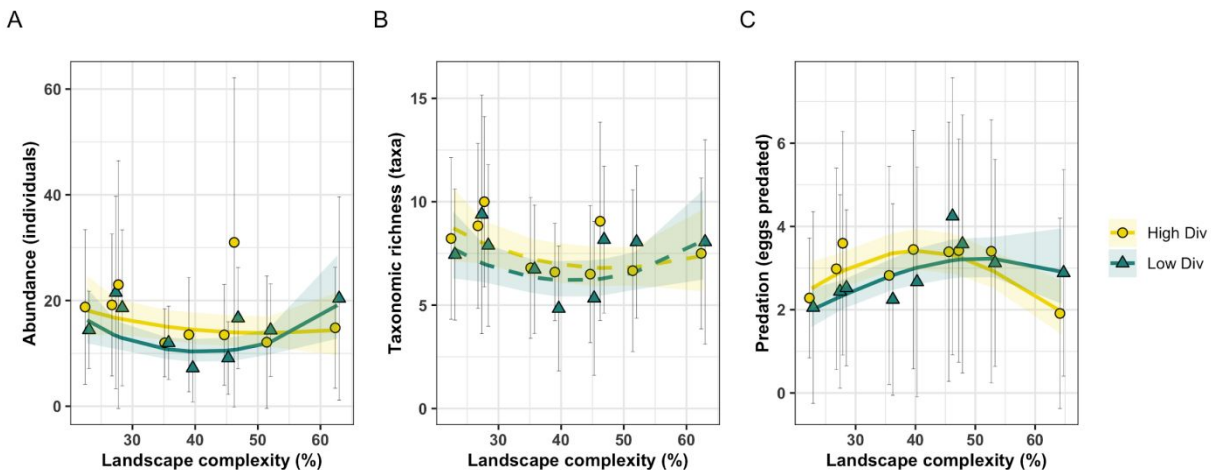254   and top of the boxes respectively), and vertical bars indicate 1.5 times the interquartile range.

255

256

257   **Figure 2 - Landscape context modulates the effect of cover crop diversity on natural enemy**

258   **abundance and pest predation.** Relationships between landscape complexity (% of semi-

259   natural habitats) and (A) the abundance of natural enemies across soil and vine guilds, (B) their

260   taxonomic richness, and (C) predation rates estimated by the number of sentinel eggs predated in

261   the high *vs.* low cover crop diversity treatments (High Div and Low Div, respectively). Slopes

262   and 95% CI from GLMMs : solid lines (p < 0.05); dashed lines (p > 0.05). Colored points

263   indicate mean values across sampling distances and guilds and error bars are standard deviations

264   (A and B: N = 315, n = 18 (n = 15 for landscape 36%, and High Div treatment in landscape

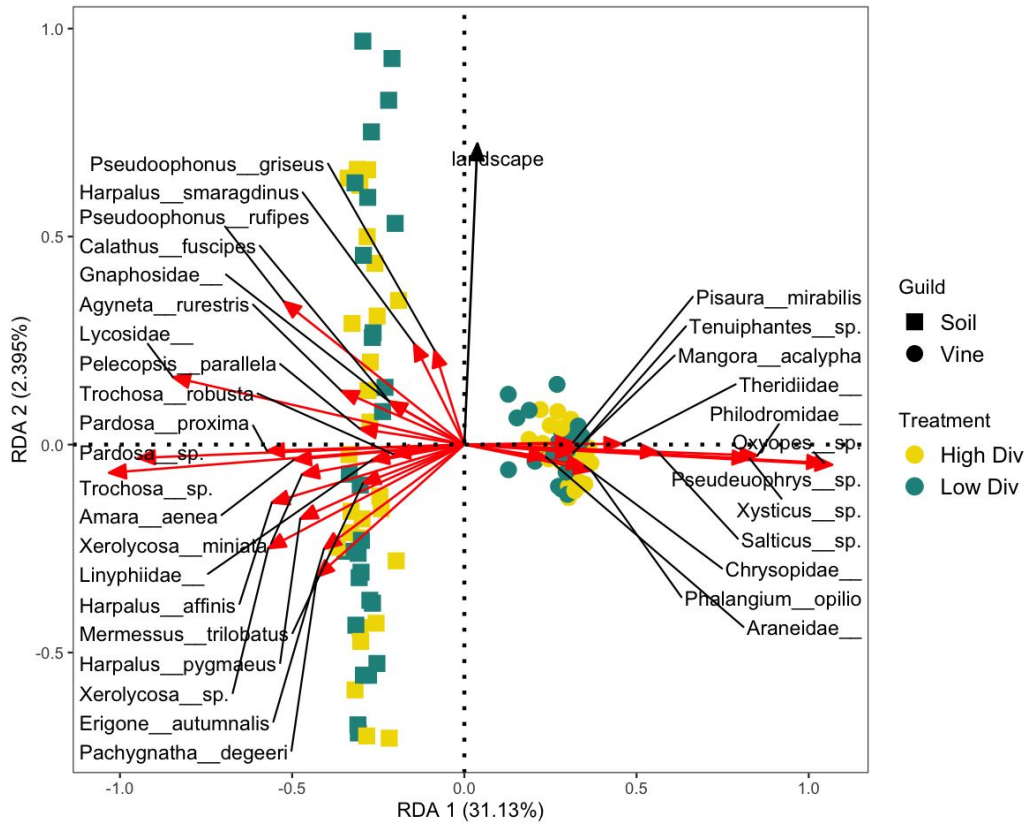265   39%); C: N = 999, n = 57 (n = 45 for landscape 62%)).

266

267

268   **Figure 3 - Cover crop diversity did not change natural enemy community composition.**

269   Redundancy analysis (RDA) plot of taxonomic groups and landscape complexity (% semi-

270   natural habitats) according to the guild of natural enemies (soil and vine) and to the cover crop

271   diversity treatment (High Div: high plant diversity, Low Div: low plant diversity). Red arrows

272   depict taxonomic groups that are the most correlated with each axis of the RDA.

273

274   **1. Abundance**

275   Cover crop diversity affected the abundance of natural enemies, with significantly higher

276   abundances in the high than in the low diversity treatment overall (Fig. 1A, Chi-square = 5.82, df

277 = 1, p = 0.016). The model predicted on average 140% more individuals in the diverse cover

278 crop treatment. However, the landscape context modulated the response of natural enemies to

279 plant diversity (significant interaction: Chi-square = 6.74, df = 2, p = 0.034). The model

280 predicted lower abundances at intermediate landscape complexity (i.e. around 40% of semi-

281 natural habitats), and higher abundances at low and high landscape complexities (Fig. 2A). There

282 was a slight negative effect of the distance to the cover crop (Chi-square = 4.92, df = 1, P =

283 0.027), indicating that the abundance of natural enemies progressively declined further away

284 from the center of the cover crop treatments (on average 17% less individuals at 30 m versus at

285 the center of the cover crop, Fig. S2)). Finally, the abundance of natural enemies differed

286 depending on the guild (Chi-square = 121.75, df = 1, p < 0.0001) with much higher densities of

287 soil compared to vine arthropods, but the two guilds showed similar responses to the landscape

288 context (interaction: Chi-square = 4.91, df = 2, p = 0.086) as well as the cover crop diversity

289 treatment (Chi-square = 1.39, df = 1, p = 0.239).

290

291   **2. Diversity**

292 There was no evidence that cover crop diversity changed the number of taxa of natural enemies

293 (Chi-square = 1.89, df = 1, p = 0.169). Taxonomic richness varied according to the guild (Chi-

294 square = 125.63, df = 1, p < 0.0001). Soil predators were more diverse than vine predators

295 (average predicted taxa richness of 8.37 (CI: 7.36-9.52) versus 5.16 (CI: 4.46-5.98) for the soil

296 and vine guilds, respectively). Landscape complexity had no significant effect on taxonomic

297 richness (Fig. 2B, Chi-square = 4.83, df = 2, p = 0.090), nor did the distance to the cover crop

298 treatment (Chi-square = 2.13, df = 1, p = 0.145).

299

300   **3. Community composition**

301   We further explored the response of natural enemy community composition and found no effect

302   of the plant diversity treatment (Fig. 3, F = 0.75, df = 1, p = 0.69). Taxa composition differed

303   with the guild considered (F = 49.2, df = 1, p < 0.001, Fig. 3), the proportion of semi-natural

304   habitats in the landscape (F = 3.01, df = 1, p = 0.01) as well as the interaction between guild and

305   landscape complexity (F = 2.79, df = 1, p = 0.01) (Fig. 3). The distance to cover crop treatment

306   did not modify the taxonomic composition of natural enemies (F = 1.08, df = 1, p = 0.26).

307

308   **4. Biological pest control**

309   The effect of cover crop diversity on predation rates depended on the landscape context

310   (interaction: Chi-square = 10.46, df = 2, p = 0.005; Fig. 2). Overall, the proportion of semi-

311   natural habitats affected predation rates non-linearly (Chi-square = 8.46, df = 2, p = 0.015), with

312   higher pest predation at intermediate landscape complexity, and lower rates at low and high

313   landscape complexities. As shown in Fig. 2C, we found higher predation rates under high cover

314   crop diversity than under low cover crop diversity at low landscape complexity, but similar or

315   even lower predation rates under high than low cover crop diversity at high landscape

316   complexity. There was no significant distance-decay effect of cover crops on predation rates

317   (Chi-square = 0.03, df = 1, p = 0.86).

318

319   **Discussion**

320   The present study sheds new light on the effect of cover crop diversity on biodiversity and

321   ecosystem services in agroecosystems. Our results reveal that locally increasing plant diversity

322   using cover crops enhances the abundance of natural enemies with positive cascading effect for

323   biological pest control. However, locally increasing plant diversity do not change taxonomic

324   richness and community composition of natural enemies. Importantly, our study highlights clear

325   interactive effects between plant diversity at the local scale and landscape complexity on

326   biological pest control. We find that local plant diversity had the most positive effects at

327   intermediate landscape complexities, confirming that the landscape context is a key moderator of

328   the success of local management options aiming to improve biodiversity and ecosystem services

329   in agroecosystems.

330

331   **Cover crop diversity affected the abundance but not the diversity of natural enemies**

332   We found that increasing the diversity of cover crops resulted in higher abundances of natural

333   enemies in vineyards. Our findings are in line with the natural enemies hypothesis (Letourneau et

334   al., 2011; Russell, 1989), and extend previous reports of the positive response of natural enemy

335   abundance to flower strips adjacent to crops or to higher plant diversity within-field in

336   agroecosystems (Sáenz-Romo et al., 2019; Tschumi et al., 2015, 2016). The high diversity

337   treatment included a mixture of 20 plant species belonging to different functional groups that

338   offered a wider range of habitats, refuges and additional food sources for arthropods than the low

339   diversity treatment, probably explaining the higher abundances of natural enemies (Balzan et al.,

340   2014; Frank and Reichhart, 2004; Koricheva and Hayes, 2018; Langellotto and Denno, 2004;

341   Wäckers et al., 2007). The abundance of natural enemies decreased with the distance to the cover

342   crop treatment across plant diversity treatments, confirming the positive effect of cover crops on

343   natural enemies in our experiment (Fig. S2). Indeed, the unsown parts of vineyards' inter-rows

344   were covered by spontaneous, sparse vegetation across the experiment and for both treatments.

345   These results further indicate that the positive effect of cover crops in vineyards remain localized

346   in the sown area. The absence of significant interaction between diversity treatment and distance

347   effects indicate that diverse cover crops also increased the abundance of natural enemies outside

348   of the sown area.

349

350   Contrary to our hypothesis, cover crop diversity did not change the diversity nor the community

351   composition of natural enemies. Our experiment involved a mixture of plants selected to improve

352   not only arthropods in general, but also soil quality. It is possible that plant species mixtures

353   specifically designed to benefit natural enemies would have yielded different results (Tschumi et

354   al., 2016). Furthermore, one of the mechanisms by which diverse cover crops or flower strips

355   enhance the diversity of arthropods on the relatively long term is by providing more

356   overwintering sites (Frank and Reichhart, 2004; Ganser et al., 2019; Holland et al., 2016). Here,

357   cover crops were sown in spring and arthropods were sampled during the following summer and

358   early autumn. The treatment probably increased the abundance of species or taxa that were

359   already present at these sites, but was not long enough to promote the establishment of new taxa.

360   The low and high cover crop diversity treatments were under similar agricultural practices

361   (pesticide use, tillage) in our experiment. Such practices probably filtered similar assemblages of

362   arthropod species from the available species pool, but the high diversity treatment may have

363   provided some of those species with more resources, allowing their abundance to increase.

364   Indeed, the composition of arthropod communities was not affected by the treatment. Thus, our

365   study reveals limited benefits of occasionally planting diverse cover crops to promote natural

366   enemy diversity in vineyards. Future studies should address the temporal effects of cover crop

367   diversity effects on natural enemy diversity, as well as the effects of functional plant diversity

368   (Gardarin et al., 2018).

369

The landscape context modulated cover crop diversity effects on natural enemies and

biological pest control

Our results indicate that the proportion of semi-natural habitats in the landscape modulates local

plant diversity effects on biological pest control services. Indeed, increasing cover crop diversity

had higher relative effect on predation rates and on natural enemy abundances in simplified

landscapes than in more complex ones. However, this pattern was the opposite in more complex

landscapes, where high cover crop diversity treatments had lower predation rates than low cover

crop diversity treatments overall. Overall, diverse cover crops had positive effects on natural

enemy abundance and predation rates below 50% of semi-natural habitats, but above, the effects

were inconsistent. These results are in line with the intermediate landscape-complexity

hypothesis (Tscharntke et al., 2012), and may reflect higher spill over in complex landscapes,

where natural enemies do find resources and refuges in semi-natural habitats around vineyards,

and are thus less affected by local management practices (Landis et al., 2000; Rusch et al., 2010).

While in simplified landscapes, natural enemies may have benefited more from highly diverse

cover crops, as refuges and habitats around vineyards are more limited.

385

Several studies have explored the interactive effect of local diversification and landscape context

on biodiversity or pest control services and found inconsistent results (Albrecht et al., 2020;

Haenke et al., 2009; Jönsson et al., 2015; Tschumi et al., 2015; Woltz et al., 2012). Evidently, the

extent to which the landscape context modulates the local effect of plant diversification on

natural enemies and biological pest control depends on multiple factors including farming

practices, species pool composition, or pedoclimatic conditions that may explain the contrasted

392   effects found in the literature (Karp et al., 2018; Muneret et al., 2019; Woltz et al., 2012). Our

393   findings are in line with the results of a recent study in Californian vineyards showing that

394   flowering cover crops increase the abundance of natural enemies as well as parasitism rate of

395   leafhoppers in landscapes with intermediate levels of diversity (Wilson et al., 2017). The

396   hypothesis of a non-linear interactive effect between local plant diversity and landscape

397   complexity on natural enemies and biological pest control could thus be particularly relevant in

398   vineyard landscapes (Tscharntke et al., 2012).

399

400   Our results further highlight the complex relationships between the structure of natural enemy

401   communities and the level of biological control services in agricultural landscapes. Indeed, high

402   predation rates observed at intermediate landscape complexity were not associated with highest

403   abundance or richness of natural enemies. Instead, the abundance of natural enemies (and to a

404   lesser extent their richness) was lower at intermediate landscape complexity in our experiment.

405   These results suggest that negative interactions between natural enemies may limit the top-down

406   control of insect pests. Indeed, our results may reflect lower levels of intra-guild predation or

407   negative behavioral interactions between predators at intermediate landscape complexity where

408   predators were overall less abundant. Furthermore, only a subset of the natural enemy

409   community is responsible for the predation of grape moth eggs, and recent evidence indicate that

410   small predator species are particularly important for the regulation of grape moth in vineyards

411   (Ostandie et al., 2020). The natural enemy species directly involved in the regulation of grape

412   moth may respond differently than the overall natural enemy community which probably

413   explains the contrasted patterns in natural enemy abundance and predation rates observed here.

414

415 **Conclusion**

416 The present study demonstrates that increasing local plant diversity benefits natural enemy

417 abundance and biological pest control services mostly in simple vineyard landscapes. By

418 illustrating how local and landscape scales diversification have interactive effects on natural

419 enemies and the ecosystem services they deliver, our study provides evidence that local plant

420 diversification schemes should be prioritized in rather simple landscapes (between 22% and 50%

421 of semi-natural habitats) to maximize beneficial effects on biological pest control services. The

422 results have important implications for the development of agroecology in vineyards, by

423 highlighting the landscape context as a key driver of the success of local management practices

424 aiming to improve biodiversity and ecosystem services.

425

426 **Authors' contributions**

427 AR, DT, and AA conceived the ideas and designed methodology; AA, MG and AP collected the

428 data; LB performed the analyses and led the writing of the manuscript. All authors contributed

429 critically to the drafts and gave final approval for publication.

430

431 **Data availability**

432 The data and R codes associated with the analyses will be made available publicly available on

433 the GitHub repository (https://github.com/leabeaumelle/EUCLID) upon publication.

434

References

445   Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B.,
446   Lindström, S.A.-M., Öckinger, E., Rundlöf, M., Rusch, A., et al. (2020). Crop diversity benefits
447   carabid and pollinator communities in landscapes with semi-natural habitats. Journal of Applied
448   Ecology *57*, 2170–2179.

449   Albrecht, M., Kleijn, D., Williams, N.M., Tschumi, M., Blaauw, B.R., Bommarco, R., Campbell,
450   A.J., Dainese, M., Drummond, F.A., Entling, M.H., et al. (2020). The effectiveness of flower
451   strips and hedgerows on pest control, pollination services and crop yield: a quantitative
452   synthesis. Ecology Letters *n/a*.

453   Andow, D.A. (1991). Vegetational Diversity and Arthropod Population Response. Annu. Rev.
454   Entomol. *36*, 561–586.

455   Balzan, M.V., Bocci, G., and Moonen, A.-C. (2014). Augmenting flower trait diversity in
456   wildflower strips to optimise the conservation of arthropod functional groups for multiple
457   agroecosystem services. J Insect Conserv *18*, 713–728.

458   Barnes, A.D., Scherber, C., Brose, U., Borer, E.T., Ebeling, A., Gauzens, B., Giling, D.P., Hines,
459   J., Isbell, F., Ristok, C., et al. (2020). Biodiversity enhances the multitrophic control of arthropod
460   herbivory. Science Advances *6*, eabb6603.

461   Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models
462   Using lme4. Journal of Statistical Software *67*, 1–48.

463   Bianchi, F. j. j. a, Booij, C. j. h, and Tscharntke, T. (2006). Sustainable pest regulation in
464   agricultural landscapes: a review on landscape composition, biodiversity and natural pest control.
465   Proceedings of the Royal Society B: Biological Sciences *273*, 1715–1727.

466   Bommarco, R., Kleijn, D., and Potts, S.G. (2013). Ecological intensification: harnessing
467   ecosystem services for food security. Trends in Ecology & Evolution *28*, 230–238.

468   Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,
469   Mace, G.M., Tilman, D., Wardle, D.A., et al. (2012). Biodiversity loss and its impact on
470   humanity. Nature *486*, 59–67.

471   Castagneyrol, B., and Jactel, H. (2012). Unraveling plant–animal diversity relationships: a meta-
472   regression analysis. Ecology *93*, 2115–2124.

473   Chaplin-Kramer, R., O'Rourke, M.E., Blitzer, E.J., and Kremen, C. (2011). A meta-analysis of
474   crop pest and natural enemy response to landscape complexity. Ecol Lett *14*, 922–932.

475   Daane, K.M., Hogg, B.N., Wilson, H., and Yokota, G.Y. (2018). Native grass ground covers
476   provide multiple ecosystem services in Californian vineyards. Journal of Applied Ecology *55*,
477   2473–2483.

478   Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R.,
479   Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., et al. (2019). A global
480   synthesis reveals biodiversity-mediated benefits for crop production. Science Advances *5*,
481   eaax0121.

482   Finch, S., and Collier, R.H. (2000). Host-plant selection by insects – a theory based on
483   'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomologia
484   Experimentalis et Applicata *96*, 91–102.

485   Forstmeier, W., and Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models:
486   overestimated effect sizes and the winner's curse. Behav Ecol Sociobiol *65*, 47–55.

487   Frank, T., and Reichhart, B. (2004). Staphylinidae and Carabidae overwintering in wheat and
488   sown wildflower areas of different age. Bulletin of Entomological Research *94*, 209–217.

489   Ganser, D., Knop, E., and Albrecht, M. (2019). Sown wildflower strips as overwintering habitat
490   for arthropods: Effective measure or ecological trap? Agriculture, Ecosystems & Environment
491   *275*, 123–131.

492   Gardarin, A., Plantegenest, M., Bischoff, A., and Valantin-Morison, M. (2018). Understanding
493   plant–arthropod interactions in multitrophic communities to improve conservation biological
494   control: useful traits and metrics. J Pest Sci *91*, 943–955.

495   Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B.,
496   Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., et al. (2010). Persistent negative effects of
497   pesticides on biodiversity and biological control potential on European farmland. Basic and
498   Applied Ecology *11*, 97–105.

499   Haenke, S., Scheid, B., Schaefer, M., Tscharntke, T., and Thies, C. (2009). Increasing syrphid fly
500   diversity and density in sown flower strips within simple vs. complex landscapes. Journal of
501   Applied Ecology *46*, 1106–1114.

502   Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D.,
503   Robinson, B.S., Hodgson, D.J., and Inger, R. (2018). A brief introduction to mixed effects
504   modelling and multi-model inference in ecology. PeerJ *6*, e4794.

505   Hartig, F., and Lohse, L. (2020). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /
506   Mixed) Regression Models.

507   Holland, J.M., Bianchi, F.J., Entling, M.H., Moonen, A.-C., Smith, B.M., and Jeanneret, P.
508   (2016). Structure, function and management of semi-natural habitats for conservation biological
509   control: a review of European studies. Pest Management Science *72*, 1638–1651.

510   IPBES (2019). Summary for policymakers of the global assessment report on biodiversity and
511   ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and
512   Ecosystem Services. IPBES Secretariat, Bonn, Germany 44.

513   Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen,
514   M., Schmid, B., Tilman, D., van Ruijven, J., et al. (2011). High plant diversity is needed to
515   maintain ecosystem services. Nature *477*, 199–202.

516   Jönsson, A.M., Ekroos, J., Dänhardt, J., Andersson, G.K.S., Olsson, O., and Smith, H.G. (2015).
517   Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the
518   wider landscape. Biological Conservation *184*, 51–58.

519   Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton,
520   C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., et al. (2018). Crop pests and predators exhibit
521   inconsistent responses to surrounding landscape composition. Proc Natl Acad Sci USA *115*,
522   E7863–E7870.

523   Koricheva, J., and Hayes, D. (2018). The relative importance of plant intraspecific diversity in
524   structuring arthropod communities: A meta-analysis. Functional Ecology *32*, 1704–1717.

525   Kremen, C., and Merenlender, A.M. (2018). Landscapes that work for biodiversity and people.
526   Science *362*.

527   Landis, D.A., Wratten, S.D., and Gurr, G.M. (2000). Habitat Management to Conserve Natural
528   Enemies of Arthropod Pests in Agriculture. Annual Review of Entomology *45*, 175–201.

529   Langellotto, G.A., and Denno, R.F. (2004). Responses of invertebrate natural enemies to
530   complex-structured habitats: a meta-analytical synthesis. Oecologia *139*, 1–10.

531   Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar,
532   S., Galindo, V., Gutiérrez, C., López, S.D., et al. (2011). Does plant diversity benefit
533   agroecosystems? A synthetic review. Ecological Applications *21*, 9–21.

534   Lewis, W.J., Lenteren, J.C. van, Phatak, S.C., and Tumlinson, J.H. (1997). A total system
535   approach to sustainable pest management. PNAS *94*, 12243–12248.

536   Moreira, X., Abdala-Roberts, L., Rasmann, S., Castagneyrol, B., and Mooney, K.A. (2016).
537   Plant diversity effects on insect herbivores and their natural enemies: current thinking, recent
538   findings, and future directions. Current Opinion in Insect Science *14*, 1–7.

539   Muneret, L., Thiéry, D., Joubard, B., and Rusch, A. (2018). Deployment of organic farming at a
540   landscape scale maintains low pest infestation and high crop productivity levels in vineyards.
541   Journal of Applied Ecology *55*, 1516–1525.

542   Muneret, L., Auriol, A., Thiéry, D., and Rusch, A. (2019). Organic farming at local and
543   landscape scales fosters biological pest control in vineyards. Ecological Applications *29*, e01818.

544   Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R.,
545   O'Hara, R.B., Simpson, G.L., Solymos, P., et al. (2019). vegan: Community Ecology Package.

546   Ostandie, N., Muneret, L., Giffard, B., Thiéry, D., and Rusch, A. (2020). The shape of the
547   predator biomass distribution affects biological pest control services in agricultural landscapes.
548   Functional Ecology *n/a*.

549   R Core Team (2019). R: A language and environment for statistical computing (Vienna,
550   Austria).

551   Root, R.B. (1973). Organization of a Plant-Arthropod Association in Simple and Diverse
552   Habitats: The Fauna of Collards (Brassica Oleracea). Ecological Monographs *43*, 95–124.

553   Rusch, A., Valantin-Morison, M., Sarthou, J.-P., and Roger-Estrade, J. (2010). Chapter six -
554   Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming
555   Systems, and Seminatural Habitats at the Landscape Scale: A Review. In Advances in
556   Agronomy, D.L. Sparks, ed. pp. 219–259.

557   Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C.,
558   Tscharntke, T., Weisser, W.W., Winqvist, C., et al. (2016). Agricultural landscape simplification
559   reduces natural pest control: A quantitative synthesis. Agriculture, Ecosystems & Environment
560   *221*, 198–204.

561   Rusch, A., Bommarco, R., and Ekbom, B. (2017). Chapter Ten - Conservation Biological
562   Control in Agricultural Landscapes. In Advances in Botanical Research, N. Sauvion, D. Thiéry,
563   and P.-A. Calatayud, eds. (Academic Press), pp. 333–360.

564   Russell, E.P. (1989). Enemies Hypothesis: A Review of the Effect of Vegetational Diversity on
565   Predatory Insects and Parasitoids. Environ Entomol *18*, 590–599.

566   Sabatier, P., Poulenard, J., Fanget, B., Reyss, J.-L., Develle, A.-L., Wilhelm, B., Ployon, E.,
567   Pignol, C., Naffrechoux, E., Dorioz, J.-M., et al. (2014). Long-term relationships among
568   pesticide applications, mobility, and soil erosion in a vineyard watershed. Proceedings of the
569   National Academy of Sciences *111*, 15647–15652.

570   Sáenz-Romo, M.G., Veas-Bernal, A., Martínez-García, H., Campos-Herrera, R., Ibáñez-Pascual,
571   S., Martínez-Villar, E., Pérez-Moreno, I., and Marco-Mancebón, V.S. (2019). Ground cover

572   management in a Mediterranean vineyard: Impact on insect abundance and diversity.
573   Agriculture, Ecosystems & Environment *283*, 106571.

574   Sarthou, J.-P., Badoz, A., Vaissière, B., Chevallier, A., and Rusch, A. (2014). Local more than
575   landscape parameters structure natural enemy communities during their overwintering in semi-
576   natural habitats. Agriculture, Ecosystems & Environment *194*, 17–28.

577   Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M., Schulze, E.-
578   D., Roscher, C., Weigelt, A., Allan, E., et al. (2010). Bottom-up effects of plant diversity on
579   multitrophic interactions in a biodiversity experiment. Nature *468*, 553–556.

580   Tena, A., Pekas, A., Cano, D., Wäckers, F.L., and Urbaneja, A. (2015). Sugar provisioning
581   maximizes the biocontrol service of parasitoids. Journal of Applied Ecology *52*, 795–804.

582   Thiery, D., and Visser, J.H. (1986). Masking of host plant odour in the olfactory orientation of
583   the Colorado potato beetle. Entomologia Experimentalis et Applicata *41*, 165–172.

584   Thiéry, D., Louâpre, P., Muneret, L., Rusch, A., Sentenac, G., Vogelweith, F., Iltis, C., and
585   Moreau, J. (2018). Biological protection against grape berry moths. A review. Agron. Sustain.
586   Dev. *38*, 15.

587   Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J.,
588   Clough, Y., Crist, T.O., Dormann, C.F., et al. (2012). Landscape moderation of biodiversity
589   patterns and processes - eight hypotheses. Biological Reviews *87*, 661–685.

590   Tschumi, M., Albrecht, M., Entling, M.H., and Jacot, K. (2015). High effectiveness of tailored
591   flower strips in reducing pests and crop plant damage. Proceedings of the Royal Society B:
592   Biological Sciences *282*, 20151369.

593   Tschumi, M., Albrecht, M., Collatz, J., Dubsky, V., Entling, M.H., Najar-Rodriguez, A.J., and
594   Jacot, K. (2016). Tailored flower strips promote natural enemy biodiversity and pest control in
595   potato crops. Journal of Applied Ecology *53*, 1169–1176.

596   Wäckers, F.L., Romeis, J., and van Rijn, P. (2007). Nectar and Pollen Feeding by Insect
597   Herbivores and Implications for Multitrophic Interactions. Annual Review of Entomology *52*,
598   301–323.

599   Wan, N.-F., Zheng, X.-R., Fu, L.-W., Kiær, L.P., Zhang, Z., Chaplin-Kramer, R., Dainese, M.,
600   Tan, J., Qiu, S.-Y., Hu, Y.-Q., et al. (2020). Global synthesis of effects of plant species diversity
601   on trophic groups and interactions. Nature Plants *6*, 503–510.

602   Wilson, H., Miles, A.F., Daane, K.M., and Altieri, M.A. (2017). Landscape diversity and crop
603   vigor outweigh influence of local diversification on biological control of a vineyard pest.
604   Ecosphere *8*, e01736.

605   Winter, S., Bauer, T., Strauss, P., Kratschmer, S., Paredes, D., Popescu, D., Landa, B., Guzmán,
606   G., Gómez, J.A., Guernion, M., et al. (2018). Effects of vegetation management intensity on

607   biodiversity and ecosystem services in vineyards: A meta-analysis. Journal of Applied Ecology
608   *55*, 2484–2495.

609   Woltz, J.M., Isaacs, R., and Landis, D.A. (2012). Landscape structure and habitat management
610   differentially influence insect natural enemies in an agricultural landscape. Agriculture,
611   Ecosystems & Environment *152*, 40–49.

612   Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. (2009). Mixed effects
613   models and extensions in ecology with R (New York, NY: Springer New York).

614

Supporting information

Beaumelle et al. "Plant diversification across scales enhances biological pest control in agricultural landscapes"

List of plant species in the high cover crop diversity treatment

Anethum graveolens, Carum carvi, Foeniculum vulgare, Coriandrum sativum (Fam. Apiaceae), *Borago officinalis* (Fam. Boraginaceae), *Centaurea cyanus* (Fam. Asteraceae), *Sinapis arvensis, Raphanus sativus* (Fam. Brassicaceae), *Vicia sativa, Ornithopus sativus, Calendula officinalis, Melilotus officinalis, Trifolium incarnatum, T. alexandrinum, T. aureum, Medicago lupulina* (Fam. Fabaceae)*, Malva sylvestris* (Fam. Malvaceae), *Phacelia tanacetifolia* (Fam. Hydrophyllaceae), *Origanum vulgare* (Fam. Lamiaceae), *Fagopyrum esculentum* (Fam. Polygonaceae).
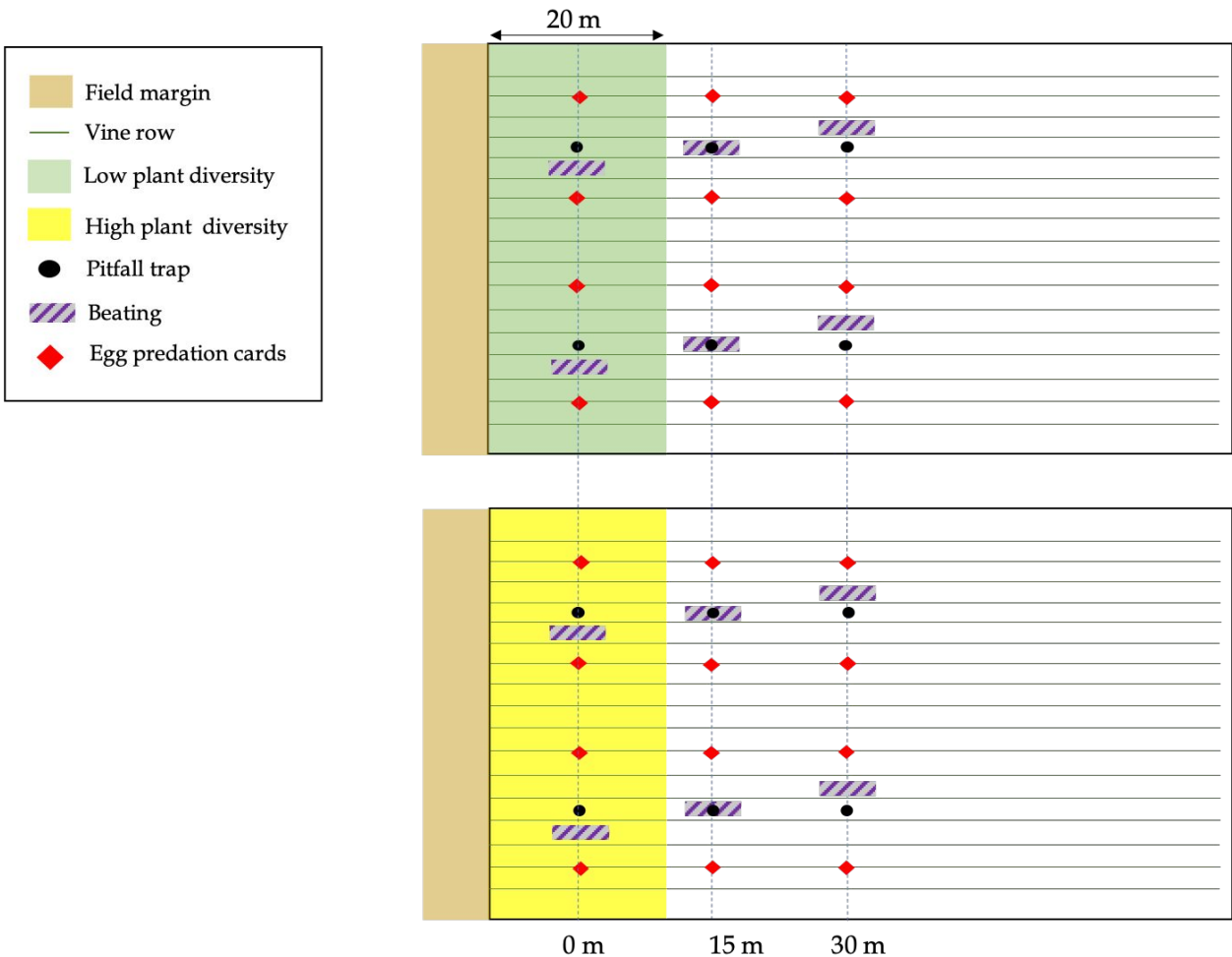

Figure S1. Experimental design showing the location of cover crop treatments (high versus low diversity) and of arthropod samplings and sentinel cards on vineyard plots. Sweeping samplings and sentinel larvae cards were conducted but not presented here.
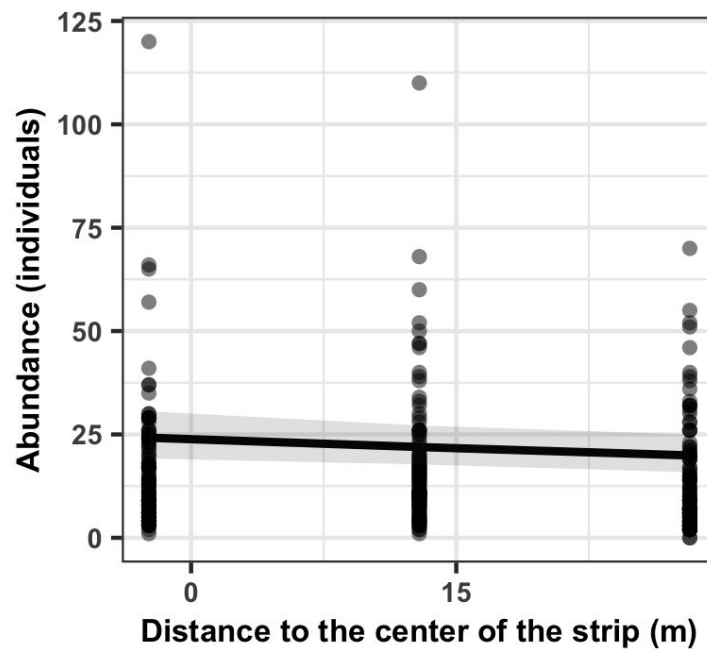
Figure S2 - The abundance of natural enemies decreased with increasing distance to the center of the cover crop treatments across cover crop diversity treatments. Points are individual observations across sampling sessions, guilds and landscapes. Slope and 95% confidence interval estimated from GLMM (Estimate = -0.08, SE = 0.04, p = 0.032).

Table S1 - Results of GLMMs of natural enemy abundance, taxonomic richness, and predation rates (number of sentinel eggs predated).

Predictors	Abundance			Taxa Richness			Predation (predated eggs)		
	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p	Incidence Rate Ratios	CI	p
(Intercept)	22.11	18.64 – 26.23	**<0.001**	9.34	8.39 – 10.40	**<0.001**	2.94	2.65 – 3.26	**<0.001**
Ldscp [1st degree]	0.10	0.00 – 2.14	0.141	0.18	0.03 – 1.20	0.077	0.31	0.01 – 8.24	0.486
Ldscp [2nd degree]	2.72	0.13 – 55.57	0.516	2.98	0.44 – 20.00	0.262	0.01	0.00 – 0.20	**0.003**
Treatment [Low Div]	0.90	0.75 – 1.10	0.304	0.99	0.88 – 1.12	0.916	0.93	0.84 – 1.04	0.189
Guild [Vine]	0.49	0.40 – 0.60	**<0.001**	0.64	0.56 – 0.73	**<0.001**			
Distance	0.95	0.83 – 1.09	0.451	0.99	0.91 – 1.07	0.752	0.99	0.92 – 1.07	0.893
Ldscp [1st degree] * Treatment [Low Div]	3.91	0.13 – 115.53	0.430	2.60	0.35 – 19.27	0.350	237.53	7.34 – 7691.55	**0.002**
Ldscp [2nd degree] * Treatment [Low Div]	88.76	2.81 – 2808.65	**0.011**	4.08	0.52 – 31.71	0.179	6.77	0.21 – 221.85	0.283
Ldscp [1st degree] * Guild [Vine]	5.80	0.17 – 202.88	0.332	3.51	0.37 – 33.17	0.273			
Ldscp [2nd degree] * Guild [Vine]	0.77	0.02 – 27.54	0.884	0.93	0.09 – 9.54	0.948			
Treatment [Low Div] * Guild [Vine]	0.84	0.63 – 1.11	0.221	0.86	0.71 – 1.04	0.116			
Treatment [Low Div] * Distance	1.02	0.84 – 1.24	0.851	0.98	0.88 – 1.11	0.789	1.00	0.90 – 1.11	0.990
Guild [Vine] * Distance	0.87	0.71 – 1.07	0.194	0.95	0.83 – 1.08	0.433			
(Ldscp [1st degree] * Treatment [Low Div]) * Guild [Vine]	1.96	0.01 – 279.97	0.791	1.28	0.05 – 31.83	0.880			
(Ldscp [2nd degree] * Treatment [Low Div]) * Guild [Vine]	0.03	0.00 – 4.63	0.172	0.20	0.01 – 5.53	0.344			
(Treatment [Low Div] * Guild [Vine]) * Distance	1.11	0.82 – 1.49	0.501	1.04	0.86 – 1.26	0.697			
Random Effects									
σ^2	0.33			0.15			0.55		
τ_{00}	0.07 Site:session			0.03 Site:session			0.03 Site:Session		
ICC	0.18			0.18			0.05		
N	9 Site			9 Site			9 Site		
	3 session			3 session			3 Session		
Observations	315			315			999		
Marginal R^2 Conditional R^2	0.353			0.317			0.045		
	0.471			0.437			0.096		

Table S2: Results of partial RDA of natural enemy community composition

Explanatory variables	Df	Variance	F	p	
Treatment	1	0.003	0.75	0.69	
Guild	1	0.21	49.26	0.001	***
Landscape complexity	1	0.01	3.01	0.01	**
Distance to the cover crop	1	0	1.08	0.26	
Treatment x Guild	1	0	0.77	0.62	
Treatment x Landscape complexity	1	0	1.13	0.25	
Guild x Landscape complexity	1	0	2.79	0.015	**
Treatment x Distance to the cover crop	1	0	0.95	0.39	
Guild x Distance to the cover crop	1	0	0.89	0.48	
Treatment x Guild x Landscape complexity	1	0	1.09	0.27	
Treatment x Guild x Distance to the cover crop	1	0	0.97	0.4	
Residuals	96				

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.'