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**Title** : Key carabid species drive spring weed seed predation of *Viola arvensis*.

Benjamin Carbonne<sup>1</sup>, David A. Bohan<sup>1</sup>, & Sandrine Petit<sup>1</sup>

<sup>1</sup>Agroécologie, AgroSup Dijon, INRA, Université de Bourgogne Franche-Comté, F-21000  
Dijon, France

Corresponding author: Benjamin Carbonne<sup>1</sup>

Email address: [benjamin.carbonne@inra.fr](mailto:benjamin.carbonne@inra.fr)

Postal address: 17 rue Sully, BP 86510, 21065 Dijon cedex, France

## 1 **1. Introduction**

2 Conservation biological control could contribute to the sustainable management of pests  
3 and weeds through the enhancement of the abundance and activity of pest natural enemies  
4 that are naturally present in agroecosystems (Begg et al., 2017; Karp et al.,  
5 2018). Understanding the complex interactions within predator communities and the level of  
6 biological control exerted by these natural enemies remains difficult, however, notably for  
7 generalist predators (Kulkarni et al., 2015; Symondson et al., 2002).

8 Communities of natural enemies can have disparate biological control effects because of  
9 variation in species efficacy and interspecific interactions (Letourneau et al., 2009). Negative  
10 interactions, such as intraguild predation (Finke and Denno, 2004) or interference (Lang,  
11 2003) may disrupt prey depletion efficacy (Prasad and Snyder, 2004). Conversely, positive  
12 interactions such as complementarity, which can result from facilitation (Losey and Denno,  
13 1998) and/or resource partitioning (Straub and Snyder, 2008), can lead to an increase in the  
14 level of biological control. In some instances, positive and negative interactions cancel out  
15 one another (Cardinale et al., 2003; Finke and Snyder, 2010), or interactions between natural  
16 enemies are weak and predators have similar and independent additive effects (Roubinet et  
17 al., 2015).

18 The intensity of biological control can also be strongly influenced by the occurrence of  
19 “keystone” or “key” natural enemy species within a community (Gotelli et al., 2011; Gurr et  
20 al., 2012; Letoumeau, 1998; Letourneau et al., 2009; Snyder, 2019). These species exert a  
21 strong mortality on pests via characteristics such as relative greater abundance (Newman et  
22 al., 1998), high searching or competitive ability (Letourneau et al., 2009), or by exerting  
23 direct density-dependent predation (Holling, 1959; Turchin, 1995). Identifying predator  
24 assemblages that are the most effective for the suppression of specific pests is a challenge  
25 (Gotelli et al., 2011; Paredes et al., 2015). That is a prerequisite for management guidelines

26 promoting conservation biological control (Greenop et al., 2018; Gurr et al., 2012; Jonsson et  
27 al., 2017; Landis, 2017).

28 The biological control of weeds is receiving increased attention due to policy pressure to  
29 reduce herbicide use (Begg et al., 2017; Petit et al., 2018, 2015). Seed predator invertebrates,  
30 and in particular carabid beetles, have been shown to contribute to the depletion of weed  
31 seeds and weed population regulation (Westerman et al., 2003; Bohan et al., 2011; Blubaugh  
32 and Kaplan, 2016).

33 Carabid beetles are abundant generalist predators in agricultural fields. Certain species are  
34 specialist granivores, feeding mainly on seeds and only occasionally on animal prey, while  
35 many are omnivores feeding on both plant and animal items (Hengeveld, 1980). Trophic  
36 interactions within carabid communities have been found to impact predation (Russell et al.,  
37 2017). For example, the presence of intraguild predators can disrupt (Prasad and Snyder,  
38 2004) or enhance (Charalabidis et al., 2017) prey suppression. Conversely, interactions  
39 between some species appear to be complementary arising from contrasting species foraging  
40 strategies for seeds (Charalabidis et al., 2019). Although several authors have demonstrated a  
41 positive effect of seed-eating carabid abundance or diversity on the level of seed predation in  
42 the field (Jonason et al., 2013; Menalled et al., 2000; Petit et al., 2017; Trichard et al., 2013),  
43 such relationship does not appear to be generic to all field situations (Saska et al., 2008). Few  
44 studies have conducted in-depth analyses of the relationships between carabid community  
45 composition and individual carabid species and effective weed seed predation (Bohan et al.,  
46 2011), or of seed consumption in the laboratory when transposed to field situations (Honek et  
47 al., 2003; Petit et al., 2014). Petit et al. (2014) underlined the importance of carabid identity in  
48 improving the prediction of weed seed predation levels using laboratory- and field-measured  
49 consumption rates in models.

50 As carabid beetles are mobile organisms, the spatial resolution at which the carabid  
51 community interacts with weeds, resulting in weed seed predation, should be investigated.  
52 Similarly, the resolution of study of carabid taxonomy necessary to explain predation  
53 relationships is unclear. While a species-level taxonomic approach would highlight key  
54 species for predation, higher functional group approaches, such as grouping by genus or  
55 trophic behaviour, might be a better predictor of predation (Gagic et al., 2015). Clarifying the  
56 best spatial and taxonomic resolution required to explain the predation of seeds by carabids  
57 would therefore provide advances for conservation biocontrol, and be used as a guide to better  
58 predict seed predation.

59 In this study, we performed an analysis of the relative contribution of selected carabid taxa to  
60 the level of weed seed depletion in order to test the expectations that key carabid species  
61 and/or genera drive this process. We compiled a dataset of 1582 field records of carabid  
62 assemblages and associated seed predation rates of the weed *Viola arvensis* gathered in 111  
63 fields under contrasted farm management and landscape settings. Regression tree methods  
64 were applied to identify the key components (species or genera) of carabid assemblages that  
65 structure seed depletion and verify this against a null-model. These methods were applied to  
66 the dataset at taxonomic (species, genus) and spatial scales (plot, transect) in order to identify  
67 the resolution(s) at which relationships between carabid assemblages and seed depletion  
68 should be addressed.

## 69 **2. Materials and methods**

### 70 **2.1. Field data**

71 Data from five different experiments on the seed predation of *Viola arvensis* (Murray  
72 1770) were compiled. These five experiments were conducted within a 50km radius of the  
73 city of Dijon in Burgundy, France (47°19'18''N, 5°02'29''E) between 2012 and 2018 and

74 have previously been reported in Trichard et al., (2014); Lubac, (2014), Minvielle-Debat,  
75 (2016), Petit et al., (2017); Ricci et al., (2019). Seed predation was quantified by seed cards  
76 (Westerman et al., 2003) enclosed in a mesh cage (18 x 11 x 9 cm, 1 cm<sup>2</sup> wire mesh) to  
77 exclude vertebrates. The number of seeds remaining on the cards after 4 or 7 days of exposure  
78 was used to estimate the amount of seeds removed, and to calculate a seed predation rate.  
79 Carabids were pitfall trapped with plastic containers of 10 cm depth and 8 cm diameter, filled  
80 with 150 ml of a mixture of salt water and anti-freeze or odourless dishwashing liquid. To  
81 protect the pitfall traps from rain inundation a plastic roof was suspended 10 cm above each  
82 of the traps. Carabid names have been updated following Gargominy et al. (2018).  
83 In total, 111 fields were sampled that were under diverse types of farm management (6  
84 organic farming, 86 conservation agriculture, 35 conventional agriculture) and covered a wide  
85 range of landscape settings. These landscape and farm management gradients were not  
86 included in analysis, but contribute to the diversity of carabid communities in our data set.  
87 Twenty of the fields were monitored over successive years. This gave a full data set  
88 containing 171 field-year records (15 organic farming, 86 conservation agriculture, 70  
89 conventional agriculture). These field-year records were predominantly conducted in winter  
90 cereals (69%, mostly wheat and a few barley fields), spring crop (9.3 %, mainly soybean), 9%  
91 oilseeds (oilseed rape and mustard), 6% of legume crops (alfalfa, spring peas and winter bean)  
92 and 1.75 % of grassland or a mix of grass and legumes. Several sampling dates were used in  
93 each field-year, with several locations also being sampled. The database therefore included  
94 1582 sample observations (Table 1), which corresponded to the carabid fauna caught in a  
95 single trap, and the predation rates measured on the associated seed card, defined as the ‘plot’  
96 level. This level corresponds to the most accurate spatial resolution tested. Plot carabid data  
97 from Trichard et al.(2014) were derived from two traps and the activity density of species  
98 were pooled and divided by two. A second database, designated the ‘transect’ level, was

99 created where 4 plots were spatially aggregated along transects. The transect scale covered a  
100 range of distances ranging from 48 m to 98 m, depending on the sampling design used in the  
101 original studies. The four traps was either placed along a line or formed a rectangle,  
102 depending on the study. This spatial level corresponds to the larger spatial resolution tested.  
103 Predation rates were averaged and carabid species abundances were summed. Depending to  
104 the study, the fields surveyed included 1 or several transects (see Table 1) to give 470 data  
105 records. We defined an ‘intermediate’ spatial level, with predation estimated at the plot level  
106 because predation is very local and seeds are immobile, and with carabid species abundances  
107 pooled at the transect level because carabids are mobile in the field.

## 108 **2.2. Linking carabid assemblages to seed predation**

109 Data for carabid species that were likely to affect seed predation were extracted from the  
110 carabid database. These included carabid species described as granivore or omnivore in the  
111 literature (Purtauf *et al.*, 2005a; Homburg *et al.*, 2014; Pakeman and Stockan, 2014; Pey *et*  
112 *al.*, 2014). We also considered potential intraguild predators, which we defined here as  
113 species described as carnivores in the literature and with body length greater than 1cm , i.e.  
114 larger than the seed feeding carabids (average size 9.26mm (SD=2.78)) (Woodward and  
115 Hildrew, 2002; Prasad and Snyder, 2004). We thus assumed that small carnivores (< 1cm) do  
116 not prey on similar or larger sized carabid species (Snyder and Wise, 1999; Prasad and  
117 Snyder, 2004, 2006). Due to functional redundancy, species of the same genus or tribes  
118 generally have similar food specialization and seed preference (Goldschmidt and Toft, 1997;  
119 Honek *et al.*, 2007; Talarico *et al.*, 2016). However, seed preference can also differ between  
120 species of the same genus, especially among species belonging to *Amara* genus (Klimeš and  
121 Saska, 2010). We thus decided to conduct two distinct analyses, one at the genus level and  
122 one at the species level. In the dataset, we identified 44 species and 26 genera of seed-eaters  
123 and 19 species belonging to 16 genera as potential intraguild predators (Table 2). In our

124 dataset, two genera of seed-eating carabids included numerous distinct species, the genus  
125 *Harpalus* (11 species) and the genus *Amara* (15 species) (Supplementary Table 1).

### 126 **2.3. Statistical analysis**

127 We combined two complementary methodologies that identify key predator taxa that are the  
128 most effective for the suppression of specific pest. A linear mixed model (LMM) tree  
129 algorithm methodology (Fokkema et al., 2017) was selected because it analyses the role of the  
130 assemblage of carabid species in seed depletion. This method identifies carabid taxa and the  
131 associated activity-density thresholds that repeatedly split observations into nodes that have  
132 dissimilar seed predation rates (Fokkema et al., 2017). The regression trees can  
133 simultaneously handle many potential predictor variables and their interactions to reveal  
134 antagonisms or complementarities between species in weed seed predation. The null model  
135 approach of Gotelli et al. (2011) was also used to analyze the contribution of individual  
136 carabid species to the intensity of seed depletion, and confirm the regression tree outputs. The  
137 advantage of the regression tree analysis, in comparison to the Gotelli (2011) approach was  
138 the identification of combinations of carabid taxa that exhibited particularly high predation  
139 effects, consistent with a positive interaction e.g. complementarity, and the estimation of the  
140 abundances of the carabid taxa necessary to obtain seed depletion.

141 The LMM tree algorithm is a model-based recursive partitioning algorithm (MOB, Zeileis et  
142 al., 2008; Fokkema et al., 2017) of 4 distinct steps: in step (1) the model is fitted to all  
143 observations in order to estimate parameters, with the clustered structure of datasets being  
144 considered by the inclusion of random effects. (2) Assessment is used to decide whether  
145 observations should be split by performing a fluctuation test for parameter instability for this  
146 model (Zeileis et al., 2008; Zeileis and Hornik, 2007). These tests assess whether the  
147 parameter estimates are stable over each particular ordering of the partitioning variables, or  
148 whether the observations can be divided with respect to one of the partitioning variables to

149 reduce the instability and improve the fit of the model in each of the splitting subgroups  
150 (Zeileis et al., 2008). A test statistic is applied to assess whether there is overall instability and  
151 to calculate a p-value for every partitioning variable (Zeileis and Hornik, 2007). The  
152 observation are split only if there is significant instability associated to any of the partitioning  
153 variables. In step (3), the partitioning variable associated with the highest parameter  
154 instability, corresponding to the minimal p-value, is selected. Then, the optimal partitioning  
155 threshold associated with this partitioning variable is identified and the sample is split.  
156 Finally, in step (4), the procedure is iterated on the splitting subgroups obtained, also called  
157 nodes, until there are no further splits.

158 We built the regression trees using the *lmertree* function (package *glmertree*), with the  
159 predation rate as the response variable, weighted by the initial number of seeds exposed on  
160 cards. The partitioning variables were the activity density of the selected carabid genera /  
161 species. For the parameter instability tests, the significance level  $\alpha$  was fixed to 0.05 to avoid  
162 overfitting and selected the most pertinent partitioning variables. We did not impose any  
163 constraints on tree size, which means that trees can have variable sizes and number of  
164 terminal nodes. For each node, we also present the three main surrogate splits, corresponding  
165 to the partitioning variables that were not selected in the tree, but had a p-value  $< 0.05$  for the  
166 parameter instability tests (Supplementary Table 5, 6 and 7). The random effects were the  
167 *Experiment name*, the *Field identifier*, and the *Month* in interaction with the *Year* of sampling,  
168 to take into account the structure of the data set. The stability of the selected partitioning  
169 variables was assessed graphically using the *stabletree* function (package *stablelearner*)  
170 (Philipp et al., 2016), by checking the variable selection frequencies based on regression trees  
171 built on 500 bootstraps keeping 80% of the initial data set. Once the regression tree is built, a  
172 global LMM is performed to fit the predation rates against the different subgroups obtained as  
173 a fixed effect. Based on this global LMM, the estimated marginal means (EMMs) of the

174 predation rates of each terminal node were compared by Tukey pairwise comparison using the  
175 functions *emmeans* and *pairs* (package *emmeans*) with Bonferroni correction (Supplementary  
176 Table 2). The performance of the regression trees was obtained by evaluating  $R^2$ , using the  
177 ratio of the sum of squared errors (SSE) of the observations around the mean of the terminal  
178 node, to the total sum of squares deviations (SST) of the observations around the mean of the  
179 entire dataset.

180 In parallel, all the regression trees were also performed with all the species, including super  
181 dominant small carnivorous species, to verify the stability of trees and the importance given to  
182 dominant species.

183 To validate the identity of key species identified by the regression trees, we adapted the null-  
184 model approach developed by Gotelli et al. (2011). We performed LMM regression between  
185 the abundance of each species and the predation rates of *V. arvensis*. The random effects were  
186 the *Experiment name*, the *Field identifier*, and the *Month* in interaction with *Year*. The  
187 observed slopes were compared with slopes obtained with LMM performed with 1000  
188 random permutations of the predation rate vector. A standardized effect size (SES) was  
189 calculated for each species as:

$$190 \quad \text{SES} = \frac{\text{Sobs} - \text{Ssim}}{\sigma_{\text{sim}}}$$

191 Where Sobs and Ssim are the observed and the average of the slopes obtained on permuted  
192 data, respectively, and  $\sigma_{\text{sim}}$  is the standardized deviation of the slopes obtained on the 1000  
193 permuted data. SES values  $> 2$  or  $< -2$  indicate significant relationships (Gotelli et al., 2011)  
194 between the abundance of a given species and the predation rate of *V. arvensis*.

195 All statistical analyses were performed using the R software version 3.5.1 (R Development  
196 Core Team, 2005).

### 197 3. Results

198 The dataset included 30686 carabids belonging to 99 species and 40 genera (Supplementary  
199 Table 3 and 4). The 44 seed-eating species observed represented 32.4 % of the catch and, in  
200 decreasing order, were *Poecilus cupreus* (58.4 %), the *Harpalus* genus (18.8 %) mainly  
201 represented by *H. dimidiatus* and *H. affinis*, and *Pseudoophonus rufipes* (8 %). The 19  
202 potential intraguild predator species represented 12 % of the total carabids catches and were  
203 dominated by *Pterostichus melanarius* (8 %) and *Carabus convexus* (1.5 %). At the plot level,  
204 there were on average 6.10 (SD = 11.22) individuals and 1.62 (SD = 1.40) species per plot of  
205 seed-eating carabids, and 2.26 (SD = 5.44) individuals and 0.79 (SD = 0.83) species per plot  
206 that were potential intraguild predators. At the transect level, there were on average 21.17 (SD  
207 = 37.46) individuals and 2.91 (SD = 2.04) species per transect of seed-eating carabids, and  
208 8.77 (SD = 17.07) individuals and 1.58 (SD = 1.12) species per transect that were potential  
209 intraguild predators. The predation rates of *V. arvensis* ranged from 0 to 1, at both the plot and  
210 transect level, with means of 0.43 (SD = 0.40) and 0.41 (SD = 0.33), respectively at the plot  
211 and transect level.

#### 212 3.1. Relating seed predation to carabid assemblages at the plot level

213 For carabid genera, we obtained a three terminal node tree that explained 10.6 % of the total  
214 variance in seed predation rate. The predation rate was best described by the activity density  
215 of the carabids from the genus *Harpalus* (Figure 1 A), with relatively high predation rates ( $\bar{x}$   
216 = 72 %, n = 197) being associated with high activity density of *Harpalus* (> 2.5). The  
217 predation rate was lower ( $\bar{x}$  = 34 %, n = 986) at low activity density of *Harpalus* ( $\leq$  0.5).  
218 Carabids of the genus *Harpalus* were present in 41.5 % of the traps, with an average of 2.77  
219 (SD = 3.62) individuals per plot where present. The genus *Harpalus* was selected in 98.2 % of  
220 the trees built on the bootstrapped data (Figure 2 A). Following *Harpalus*, the next most  
221 frequently selected splitting variables were the genera *Pseudoophonus* and *Poecilus*, which

222 appear respectively in 50.2 % and 28.6 % of trees (Figure 2 A). They were also present as a  
223 surrogate split for node 1 (Supplementary Table 5 A). The null model approach confirmed the  
224 significance of the genera *Harpalus* (SES 8.09), *Pseudoophonus* (SES 6.70) and *Poecilus*  
225 (SES 6.11). The genera *Pterostichus* and *Scybalicus* were also identified as groups exhibiting  
226 a positive, but more moderate (SES 3.9 and 3.1 respectively), effect on *V. arvensis* predation.

227 When implemented using carabid species, the tree explained 6.2 % of the predation rate  
228 variation and the abundance of *Harpalus dimidiatus* had the highest explanatory power for  
229 predation rate (Figure 3 A). Low abundances of *H. dimidiatus* ( $\leq 0.5$ ) were associated with  
230 low predation rates ( $\bar{x} = 39 \%$ ,  $n = 1292$ ), and conversely, higher abundances of *H. dimidiatus*  
231 ( $> 0.5$ ) were related to higher seed predation ( $\bar{x}=65 \%$ ,  $n=290$ ). *Harpalus dimidiatus* was  
232 selected in slightly less than 60 % of the regression trees from the bootstrapped samples.

233 *Harpalus affinis* did not appear on the principal regression tree but was selected in 76.6 % of  
234 the bootstrapped regression trees (Figure 4 A) and also appears as a surrogate split  
235 (Supplementary Table 5 B). The null model approach corroborated the significance of *H.*  
236 *affinis* (SES 4.68) and *H. dimidiatus* (SES 3.93), and also highlighted the role of *P. rufipes*  
237 (SES 4.63) and *P. cupreus* (SES 4.60).

### 238 **3.2. Relating plot level seed predation to transect level carabid assemblages**

239 When considering carabids at the genus level, a five terminal node regression tree was  
240 obtained that explained 19.7 % of the total variation in seed predation (Figure 1 B). Three  
241 important carabid genera were identified: *Harpalus*, *Poecilus* and *Pseudoophonus*, which is  
242 consistent with the variable selection frequencies barplot (Figure 2 B). Predation rate was  
243 high ( $\bar{x} = 86 \%$ ,  $n = 112$ ) when *Harpalus* was abundant ( $> 8$ ) and associated with high  
244 abundance of *Poecilus* ( $> 17$ ). More than 55 % of the observations were associated with low  
245 predation rates ( $\bar{x} = 29 \%$ ,  $n = 898$ ) and were related to low activity densities of *Harpalus* ( $\leq$   
246 4) and *Pseudoophonus* ( $\leq 1$ ). There were three intermediate nodes, the node 4 ( $\bar{x} = 61 \%$ ,  $n =$

223) related to presence of *Pseudoophonus* ( $> 1$ ) but low abundance of *Harpalus* ( $\leq 4$ ), the node 6 ( $\bar{x} = 55 \%$ ,  $n = 273$ ), associated with low AD of *Poecilus* ( $\leq 17$ ) and intermediate AD of *Harpalus* ( $4 <$  and  $\leq 8$ ), and the node 8 ( $\bar{x} = 61 \%$ ,  $n = 76$ ) related with high abundance of *Poecilus* ( $17 >$ ) and intermediate AD of *Harpalus* ( $4 <$  and  $\leq 8$ ). The predation rates of these three subgroups were not significantly different, and presented a high level of variability. The null model approach corroborated the significance of *Harpalus* (SES 5.37), *Pseudoophonus* (SES 4.88) and *Poecilus* (SES 4.49) found in the trees. *Pterostichus* and *Scybalicus* also had a positive but more moderate effect on seed predation rates (SES 3.07 and 2.87 respectively).

When considering carabid species, a six terminal node regression tree was obtained that explained 13.5 % of seed predation variation, with a key role of *H. dimidiatus*, *H. affinis*, *P. rufipes*, *Carabus auratus* and *Amara eurynota* (Figure 3 B). There were two nodes associated with very high predation rates, nodes 9 ( $\bar{x} = 86 \%$ ,  $n = 64$ ) and 10 ( $\bar{x} = 99 \%$ ,  $n = 16$ ), linked to *H. affinis* ( $> 1$ ), *P. rufipes* ( $> 2$ ) and absence of *C. auratus* ( $\leq 0$ ). Most of the observations indicate low rates of predation (node 3;  $\bar{x} = 34 \%$ ,  $n = 1037$ ) that were related to low abundance of *H. affinis* ( $\leq 1$ ) and *H. dimidiatus* ( $\leq 3$ ). *P. cupreus* was frequently present in the trees built on bootstrapped data (47 %), whereas it was not present on the main tree, in contrast to *C. auratus* and *A. eurynota* that were rarely selected (Figure 4 B). The null model approach corroborated the significance of *H. dimidiatus* (SES 7.22), *H. affinis* (SES 6.94), *P. rufipes* (SES 6.89) and *P. cupreus* (SES 6.35). *P. melanarius*, *S. oblongiusculus* and *A. equestris* also had a positive but moderate effect on seed predation rates (SES 4.12, 2.93 and 2.38 respectively).

### 3.3. Relating seed predation to carabid assemblages at the transect level

When considering carabid genera, we obtained a four terminal node regression tree that explained 29 % of seed predation variation. The genera *Harpalus*, *Poecilus* and *Pseudoophonus* explained the most variability in predation (Figure 1 C), and frequently

272 appeared in trees on bootstrapped data (Figure 2 C). Predation rate was high for node 7 ( $\bar{x}$  =  
273 74 %, n = 50) when *Poecilus* was abundant in the transect (> 15), and when the abundance of  
274 *Harpalus* exceeded 4 individuals. However, this situation was rather unusual in fields,  
275 occurring in only about 10% of observations. Most of the observations were associated with  
276 low predation rates ( $\bar{x}$  = 28 %, n = 301) and related to low abundance of *Harpalus* ( $\leq$  4) and  
277 *Pseudoophonus* ( $\leq$  2). There were two intermediate nodes presenting high level of predation  
278 variability, nodes 4 ( $\bar{x}$  = 65 %, n = 38) and 6 ( $\bar{x}$  = 58 %, n = 81) related to combination of low  
279 and high abundance of the three key genera. The null model approach confirmed the  
280 overriding importance of *Harpalus* (SES 5.43), *Pseudoophonus* (SES 4.74) and *Poecilus*  
281 (SES 4.54). *Pterostichus* and *Scybalicus* also had a positive but moderate effect on seed  
282 predation rates (SES 2.82 and 2.14 respectively).

283 When considering carabid species, the tree explains 30 % of predation variation and three  
284 species emerge as important: *H. affinis*, *H. dimidiatus* and *P. rufipes*. The highest level of  
285 predation (node 9;  $\bar{x}$  = 84 %, n = 26) was associated with *H. affinis* (> 1) and *P. rufipes* (> 2)  
286 (Figure 3 C). Although it did not appear on the main tree, *P. cupreus* was selected in 29 % of  
287 the trees based on bootstrapped data (Figure 4 C), and was a surrogate split (Supplementary  
288 Table 7 B). The null model approach corroborated the significance of *H. dimidiatus* (SES  
289 4.30), *H. affinis* (SES 5.36) and *P. rufipes* (SES 4.70). It also highlighted the role of *P.*  
290 *cupreus* (SES 4.45), *P. melanarius* (SES 2.81) and *S. oblongiusculus* (SES 2.14).

#### 291 **4. Discussion**

292 Our study provides some methodological advances and guidelines to explore the relative  
293 contribution of key taxa to pest regulation in field situations. We investigated this relationship  
294 at different spatial and taxonomic resolutions, with the objective of providing guidelines for  
295 future research. Our work consistently identifies four seed-eating carabid species, genera and  
296 their assemblages as key drivers of the depletion of *V. arvensis* seeds, and suggests that intra-

297 guild predators within carabid community and their trophic interactions only played a minor  
298 role in seed predation. Finally, our analysis shows that in many of the field situations explored  
299 in this paper, seed predation was limited because key carabid species driving seed predation  
300 were not present at high enough abundance.

#### 301 **4.1. The key taxa driving seed depletion**

302 Among the 44 species and 26 genera of seed-eating carabids present in our dataset, four key  
303 carabid taxa were consistently estimated to have a significant effect on the predation of *V.*  
304 *arvensis* seeds. The granivore genus *Harpalus*, appears as a key group that explains the  
305 predation of *V. arvensis*. Two species of *Harpalus* were found to be important, *H. affinis* and  
306 *H. dimidiatus*. These are two medium sized spring breeding granivores (Homburg et al., 2014)  
307 that made up approximately 6 % and 8.7 % of the seed feeders caught, respectively. After  
308 spatial aggregation of carabids, we detected effects of two other medium size species, *P.*  
309 *cupreus* and *P. rufipes*, which are spring and autumn breeder species respectively (Cole et al.,  
310 2002; Homburg et al., 2014; Pey et al., 2014), and are the dominant species of the genera  
311 *Poecilus* and *Pseudoophonus*, respectively, in our data. The importance of these key genera  
312 corroborates the findings of previous studies that have shown that genera from the tribe  
313 *Harpalini*, such as *Harpalus* or *Pseudoophonus*, consumed significant quantities of *V.*  
314 *arvensis* seeds in laboratory cafeteria tests (Honek et al., 2007; Petit et al., 2014; Deroulers  
315 and Bretagnolle, 2019). Interestingly, *P. cupreus* does not show a preference for *V. arvensis*  
316 seeds in cafeteria tests, eating some 0.40 seeds / day in comparison to 4.65 and 15.37 seeds /  
317 day for *H. affinis* and *P. rufipes*, respectively (Petit et al., 2014). *P. cupreus* is dominant,  
318 however, being present in 69.6 % of the sampled transects, with on average 12.11 (SD =  
319 28.79) individuals per trap. Thus, *Poecilus* appeared as a key species due to mass effect in the  
320 field, compensating for its low consumption of *V. arvensis* seeds, while *Pseudoophonus* and  
321 *Harpalus* are key species due to their high per capita consumption of *V. arvensis* seeds. The

322 genus *Amara*, known to consume substantial amounts of weed seeds (Honek et al., 2007; Petit  
323 et al., 2014) was rarely selected in the regression trees but this could be related to its low  
324 acceptance of *V. arvensis* seeds, as previously shown in laboratory cafeteria tests (Honek et  
325 al., 2007; Petit et al., 2014).

326 The highest predation rates were associated with the combination of relatively high  
327 abundances of *Harpalus* and *Poecilus*, at the genera level, and *H. affinis* and *P. rufipes*, at the  
328 species level. The combination of relatively high activity density of *Harpalus* and *Poecilus*  
329 better explained high predation rates than the two genera separately, which may be an  
330 indication of additivity or complementarity effects, such as resource partitioning or  
331 facilitation when they co-occur (Gurr et al., 2012; Letourneau et al., 2009). Charalabidis et al.  
332 (2019) highlighted the differences and complementarities of foraging strategies between *H.*  
333 *affinis* and *P. cupreus* under laboratory conditions, which may provide a mechanism for a  
334 positive association of these two species. *Poecilus cupreus* has a low latency time before  
335 consumption, but is limited in the range of weed seed species consumed, whereas *H. affinis*  
336 start consuming after a longer delay, but consume a wide range of weed species (Charalabidis  
337 et al., 2019). The per capita consumption of *V. arvensis* seeds seems to be unaffected by  
338 carabid conspecific density, suggesting that seed predation is proportional to the abundance of  
339 conspecific for both *H. affinis* and *P. cupreus* (Carbonne et al., 2019). In addition, seed  
340 consumption by *H. affinis* increases under risk of intraguild predation, in contrast to  
341 consumption by *P. cupreus* that remained unchanged (Charalabidis et al., 2019, 2017). In  
342 addition to presenting complementary foraging strategies, these two species present temporal  
343 complementarity, with *P. cupreus* mostly described as a day active carabid, and *H. affinis* as a  
344 night active species (Ribera et al., 1999; Barbaro and Van Halder, 2009).

345 Finally, although we expected that intraguild predators would be important drivers of the  
346 patterns of seed consumption in our field situations, our analysis did not support this

347 convention. While *Pterostichus melanarius* was identified as being important in our analysis,  
348 it appears in only 5 to 10% of the bootstrapped trees and is actually identified as a positive  
349 contributor to seed predation, contrary to expectation. The mechanisms that would explain  
350 this impact are, however, unclear. Charalabidis et al. (2019) showed that the risk of predation  
351 exercised by *P. melanarius* can increase the weed seed consumption by *H. affinis*. It is also  
352 not excluded that *P. melanarius* consumes seeds. Other large intraguild predators are  
353 sometimes selected in the main or bootstrapped regression trees. For example, when *H. affinis*  
354 (>1) and *P. rufipes* (>2) are in combination, the presence of *Carabus auratus* tends to increase  
355 the variability in seed predation rates, and it cannot be excluded that *C. auratus* reduces weed  
356 seed predation by preying upon seed-feeding carabids (Prasad and Snyder, 2004). The  
357 presence of complex habitats and heterogeneous vegetation can be a solution to dampen  
358 antagonistic interactions by reducing the chances of encounters among natural enemies  
359 (Gontijo, 2019; Snyder, 2019). Here, only indirect effects of intraguild predation within  
360 carabid communities are assessed, as information on other non-carabid predator groups was  
361 not available. The presence of other seed predators, like micro mammals (Blubaugh et al.,  
362 2017), might provide a better understanding of the effect of intraguild predation on the weed  
363 seed predation, and increase our explanatory power.

364 Finally, when regression trees were built on all genera or species without any selection,  
365 only the two trees with species at the plot and intermediate scale were slightly different  
366 (Supplementary Figure 1 and 2). Simply one new species, *Brachinus crepitans* (Linnaeus,  
367 1758), appears in the tree built with species at the plot scale. *B. crepitans* is an ectoparasitoid  
368 carabid which develop on pupae of spring breeding species, and can be highly correlated with  
369 some granivorous species, in particular with the genus *Amara* (Saska and Honek, 2008). Trees  
370 are therefore relatively stable, and did not seem to over-represent the dominant species.

#### 371 **4.2. The spatial and taxonomic resolution**

372 Although the identification of key taxa was consistent across the three spatial resolutions  
373 explored, our results indicate that the relationships between carabid assemblages and seed  
374 predation were much better explained at the transect scale than at the plot scale. The apparent  
375 mismatch between carabid abundance and predation rates at fine spatial scales has already  
376 been shown in field studies (Saska, 2008; Trichard et al., 2014). The higher explanatory  
377 power achieved at the transect scale may be explained by the aggregation of data, and  
378 particularly the pooling of the predation rate over several plots that averages away some of the  
379 variability of predation. It may also reflect the heterogeneous spatial distribution of carabids  
380 in arable fields (Thomas et al., 2002; Trichard et al., 2014) and that carabids caught in a  
381 specific plot location may have foraged at distances of up to 50 meters away (Wallin and  
382 Ekblom, 1988). Finally, aggregating the carabid data increased the pool of species considered  
383 with the inclusion of new taxa as partitioning variables in regression trees and to a more  
384 precise detection of species preying upon *V. arvensis* seeds. For future experiments, spatial  
385 aggregation of plots, by transect or zone, would provide a beneficial increase in prediction of  
386 seed predation by taking into account carabid mobility.

387 Finally, we assumed that analysing the relationship between carabid taxa and seed predation  
388 at the species level would provide more accurate results than an analysis at the genus level  
389 due to the potential difference in seed acceptance between species belonging to the same  
390 genus. Our results show, however, that there is an increase in explanation in considering  
391 predation at the genus level rather than the species level at the plot and intermediate scale. By  
392 grouping species at the genus level we formed functional groups including functionally  
393 redundant species that if considered separately would have little weight, and would not be  
394 included in the tree. This result is supported by previous studies showing that functional  
395 groups are more informative for predicting prey suppression than species (Gagic et al., 2015;  
396 Russell et al., 2017).

397 Overall, the 30% of variation in seed depletion explained by assemblages of carabid taxa, at  
398 the transect level, is fairly high. The use of regression trees permit the explanation of  
399 predation rates in situations where key species are absent or present. Nodes with component  
400 parts of the group of four key species identified or intermediate levels of activity-density have  
401 highly variable levels of predation (see for example Figure 1 A node 4 and B node 4, 6 and 8).  
402 The 70% of the unexplained variation in seed predation is likely due to the occurrence of  
403 other invertebrate seed predators such as crickets or ants (Baraibar et al., 2009; Brust, 1994)  
404 not accounted for here. Variability in the availability of alternative prey for carabids, but also  
405 the presence of competitor or predator, might also affect the predation of the target prey (Koss  
406 and Snyder, 2005; Symondson et al., 2006) and account for unexplained variation in the  
407 depletion of *V. arvensis* seeds in the sampled transects. Finally, a part of the seed loss can be  
408 due to environmental conditions such as rain, wind or loss of adhesive power of the cards  
409 (Westerman et al., 2003).

#### 410 **4.3. Enhancing weed seed predation in arable landscapes**

411 Beside the identification of key taxa delivering seed predation, our study also emphasizes the  
412 fact that in the vast majority of our field situations, the predation of *V. arvensis* was limited by  
413 the absence or low abundances of key carabid species. Our study was based on data collected  
414 in 111 farmer's fields conducted under contrasting farming managements and located in very  
415 different landscape settings. Yet, in more than 60% of the transects surveyed, key carabid taxa  
416 were absent or were poorly represented, and associated with low seed predation. Nodes of the  
417 regression trees exhibiting favourable key carabid assemblages delivering high seed predation  
418 gathered only a limited number of observations. This suggests that seed predation could be  
419 enhanced in arable landscapes, and that currently only a small proportion of the transects  
420 surveyed were favourable to the key carabid species associated with high seed predation rates.  
421 It is interesting to note that fields under conservation agriculture and organic fields tended to

422 be more represented in these nodes than conventional fields. Indeed, for the regression tree  
423 performed on genera at the transect scale, 17% and 18% of the conservation agriculture and  
424 organic field transects are associated to high seed predation (node 7), respectively, compared  
425 to only 2% of the conventional agriculture transects. This is in line with studies that have  
426 demonstrated the positive effect of conservation agriculture on seed-eating carabid species  
427 (Menalled et al., 2007), including *P. rufipes* (Trichard et al., 2014). Tillage is known to  
428 strongly reduced adult activity, oviposition rate and larval capture in fields (Blubaugh and  
429 Kaplan, 2015). Similarly, organic farming has been shown to enhance the abundance of seed-  
430 eating carabids such as *H. affinis* (Diekötter et al., 2016) and *P. rufipes* (Döring and Kromp,  
431 2003). These elements could explain the much higher proportion of fields exhibiting high  
432 predation rates in conservation and organic agriculture compared to conventional fields. Yet,  
433 our results also suggest that adopting organic or conservation farming practices do not seem  
434 to ensure high predation rates in all situations and there may be several reasons for this. First,  
435 conversion to organic or conservation agriculture may be too recent to result in significant  
436 changes in carabid communities and subsequent increases in weed seed predation rates. For  
437 example, increases in predation rates in conservation agriculture were shown to be apparent at  
438 least four years after (Petit et al., 2017). In addition, pesticide use can be high in conservation  
439 agriculture, with detrimental effects on key carabid species and weed seed predation (Ricci et  
440 al., 2019; Trichard et al., 2013). Second, the landscape context of arable fields can greatly  
441 affect the composition of carabid communities and modulate the effect of the local farming  
442 management in the focal field. For example, the presence of grassy field boundaries can  
443 positively affect the in-field abundance of *P. rufipes* (Labruyere et al., 2017, 2016b; Rouabah  
444 et al., 2015). At the landscape scale, the cover of grassland (Labruyere et al., 2016a; Purtauf et  
445 al., 2005b; Trichard et al., 2013) and the proportion of organic agriculture (Diekötter et al.,  
446 2016) enhance the key carabid taxa identified in this study. These elements suggest that

447 different combinations of local field and landscape scale management could increase the very  
448 low abundance of key species and the level of seed predation observed here in conventional  
449 arable fields.

450 Our study suggests that for the conservation biological control of *V. arvensis* it is necessary to  
451 promote the activity density of *Harpalus*, *Poecilus* and *Pseudoophonus*. The statistical  
452 modelling approach we develop could be a useful method to identify key natural enemies that  
453 exert high pest mortality, and can be a useful guide to select field management that  
454 specifically supports these species to improving the efficacy of biocontrol.

455

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463

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**Table 1:** Summary of the information on the five datasets contained in the database. For each dataset we specify year of data collection, number of session, number of fields, number of transect per field, and the number of records at the plot and transect level. More information about the protocols can be found on the corresponding publication (Trichard et al., (2013); Petit et al., (2017); Ricci et al., (2019)).

**Table 2:** Summary of all genus and species of seed eaters and intraguild predators integrated in the analysis with their corresponding activity-density (AD) and occurrence (%).

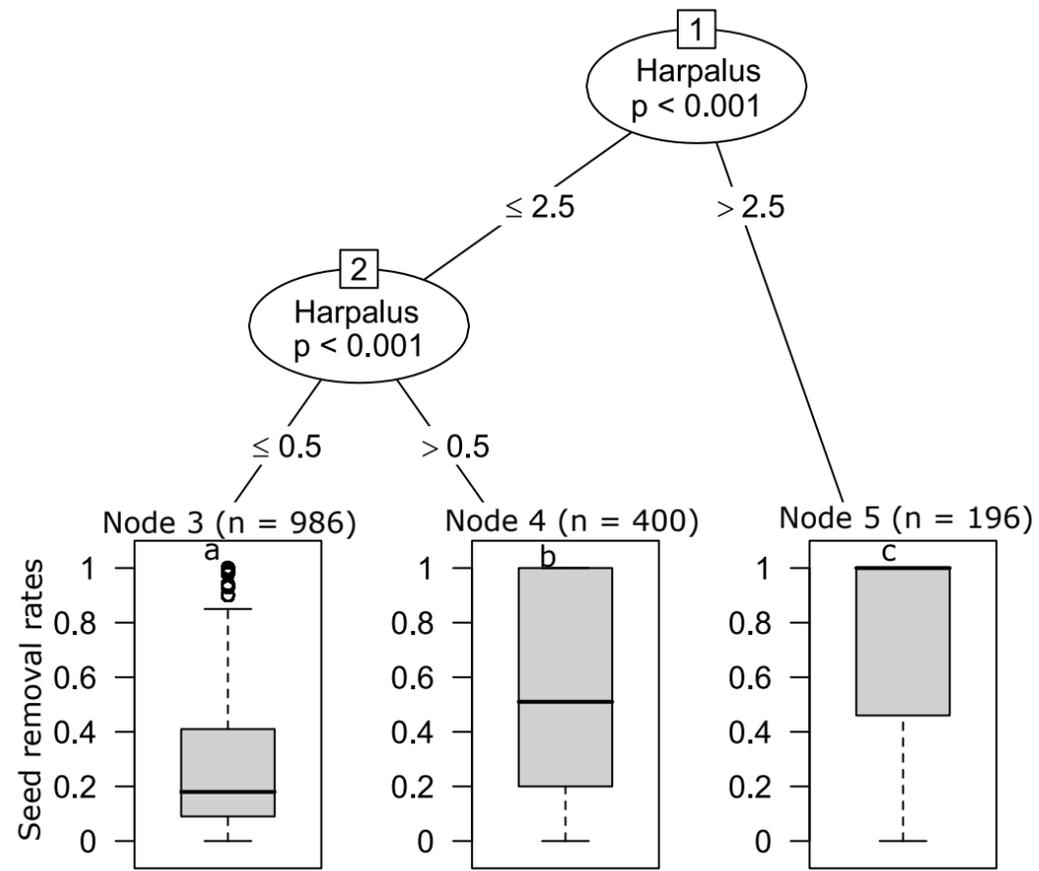
Figure 1: Regression trees displaying interaction among activity-density of seed eaters and potential intraguild predator carabid beetles genera on weed seed predation of *V. arvensis* at different spatial scale: **(A)** Plot scale ( $R^2 = 10.60\%$ ), **(B)** intermediate scale with predation measures at the plot level and carabid beetles at the transect level ( $R^2 = 19.7\%$ ), and **(C)** transect scale ( $R^2 = 29\%$ ). Box plots represent medians and upper and lower quartiles for each sub group of the regression trees. Difference between subgroup obtained are indicated by different letter on the top of each boxplot.

Figure 2: Relative frequency of selection of the most frequent carabid genera in the regression trees, built on 500 bootstraps of the data set, for explaining *V. arvensis* predation rates. The variables selected in the regression tree based on the initial data set are indicated in dark grey, and the associated genera names are underlined. Letters indicate the spatial aggregation tested: **(A)** plot scale, **(B)** intermediate scale (predation measure at the plot level, and carabid beetles at the transect level), and **(C)** transect scale.

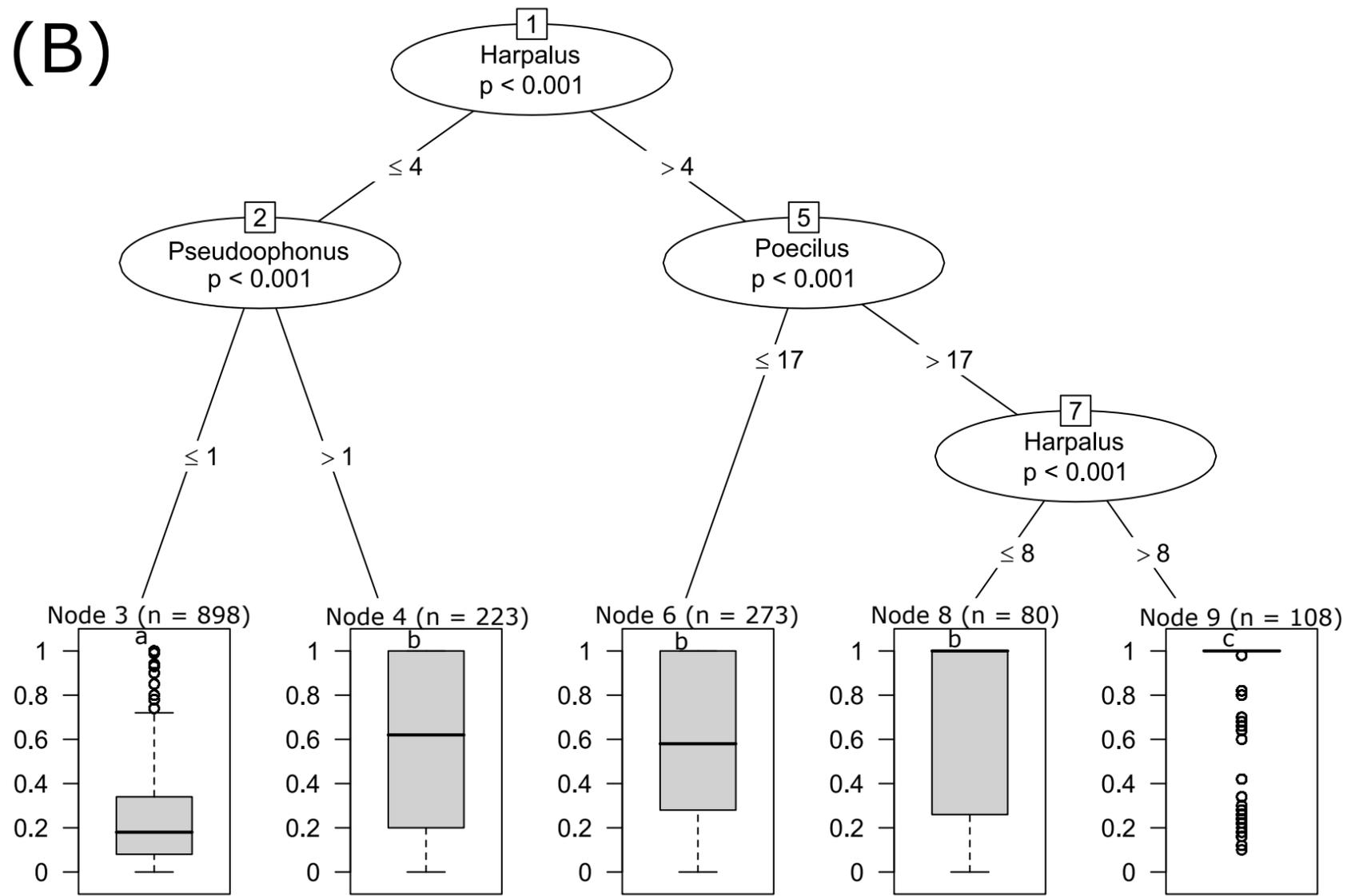
Figure 3: Regression trees displaying interaction among activity-density of seed eaters and potential intraguild predator carabid beetles species on weed seed predation of *V. arvensis* at different spatial scale: **(A)** Plot scale ( $R^2 = 6.20\%$ ), **(B)** intermediate scale with predation measures at the plot level, and carabid beetles at the transect level ( $R^2 = 13.5\%$ ), and **(C)** transect scale ( $R^2 = 29.7\%$ ). Box plots represent medians and upper and lower quartiles for each sub group of the regression trees. Difference between subgroup obtained are indicated by different letter on the top of each boxplot.

Figure 4: Relative frequency of selection of each carabid species in the regression trees built on 500 bootstraps of the data set, for explaining *V. arvensis* predation rates. The variables selected in the regression tree based on the initial data set are indicated in dark grey, and the associated genera names are underlined. Letters indicate the spatial aggregation tested: **(A)** plot scale, **(B)** intermediate scale (predation measure at the plot level, and carabid beetles at the transect level), and **(C)** transect scale.

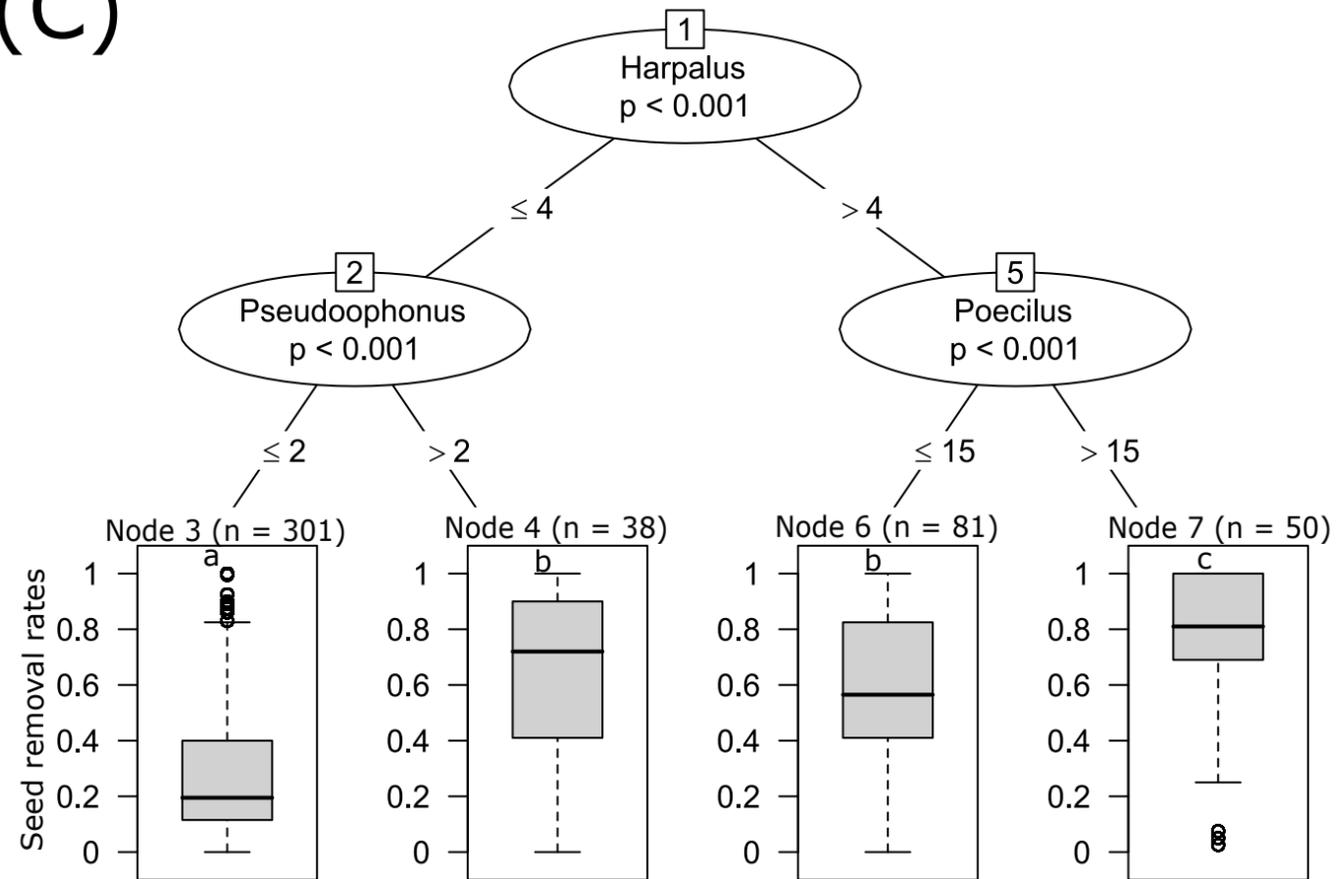
(A)

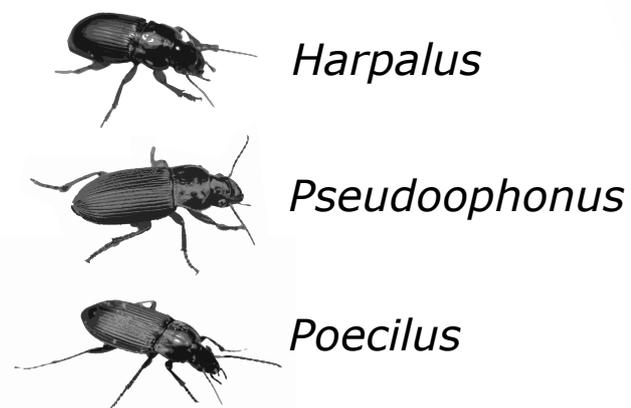
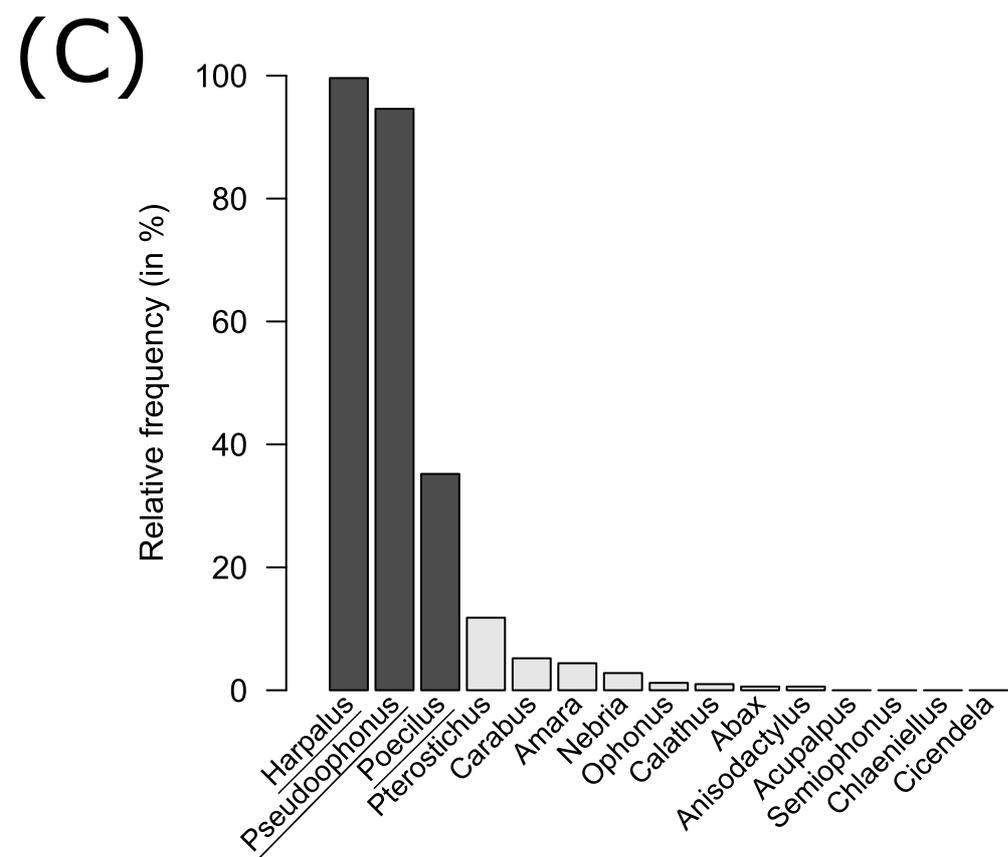
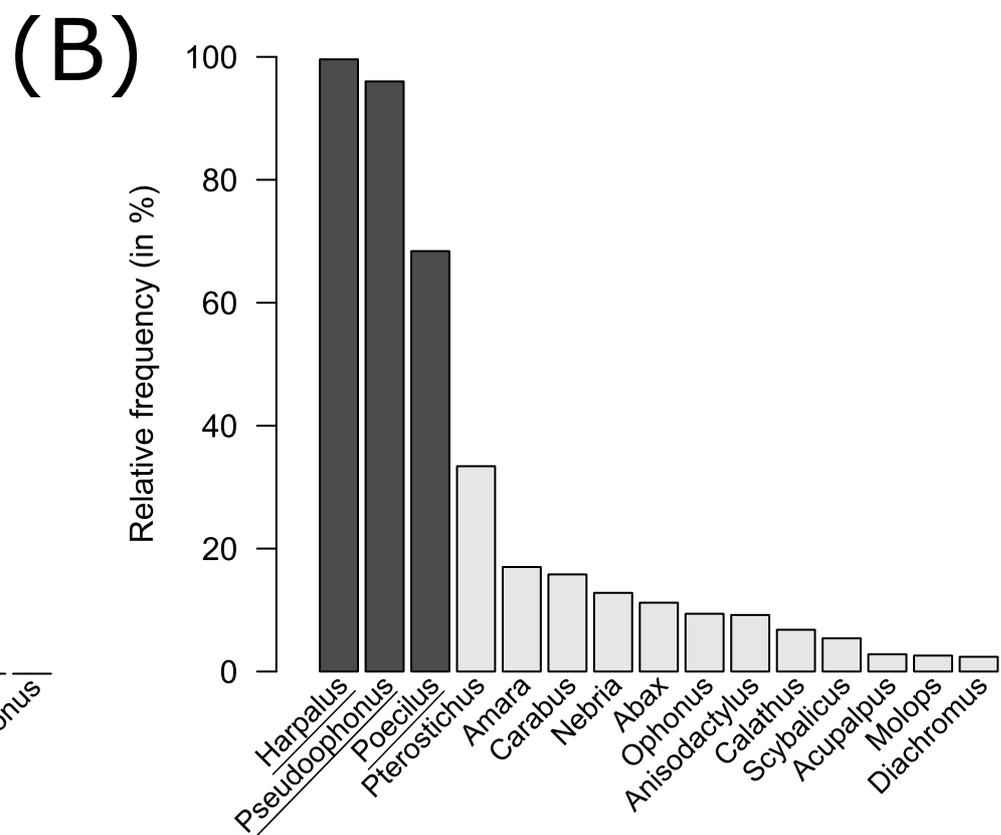
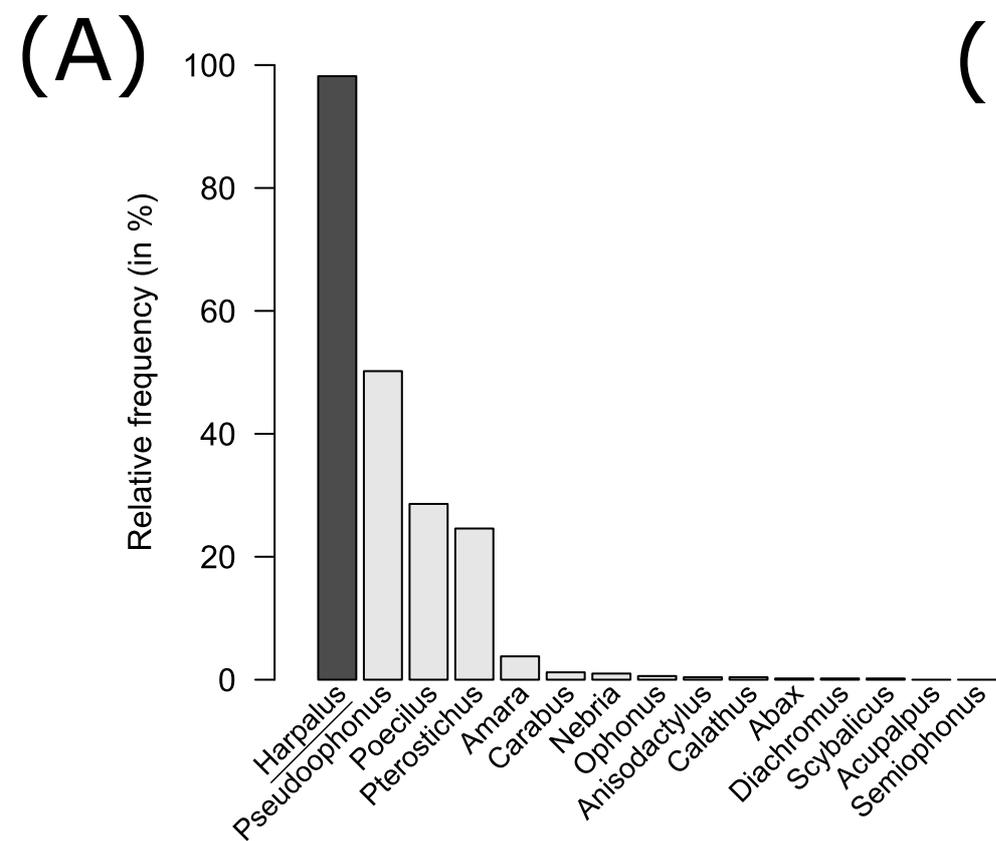


(B)

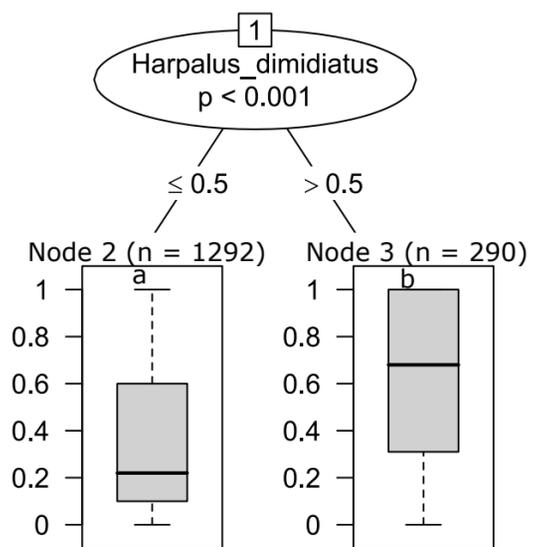


(C)

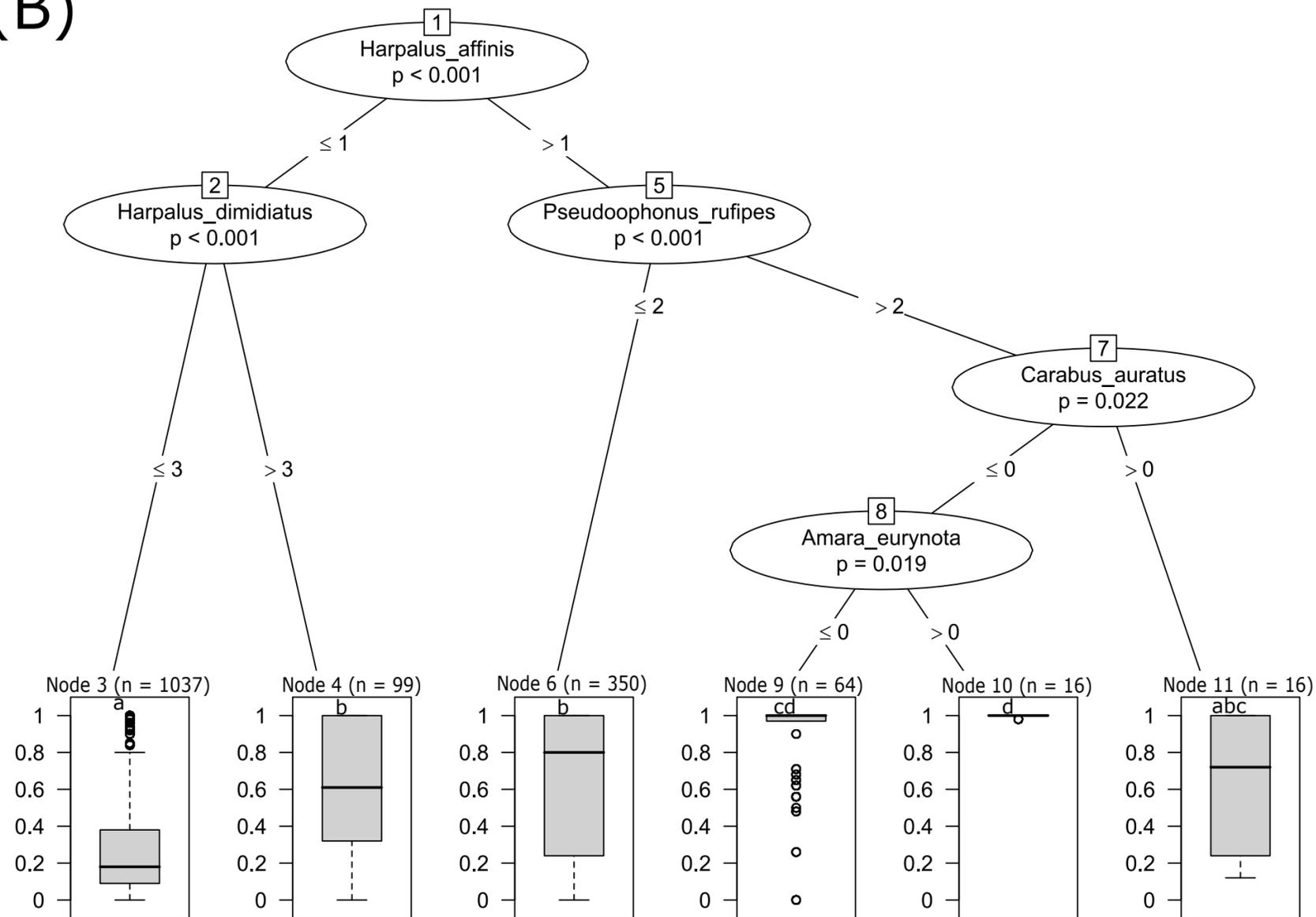




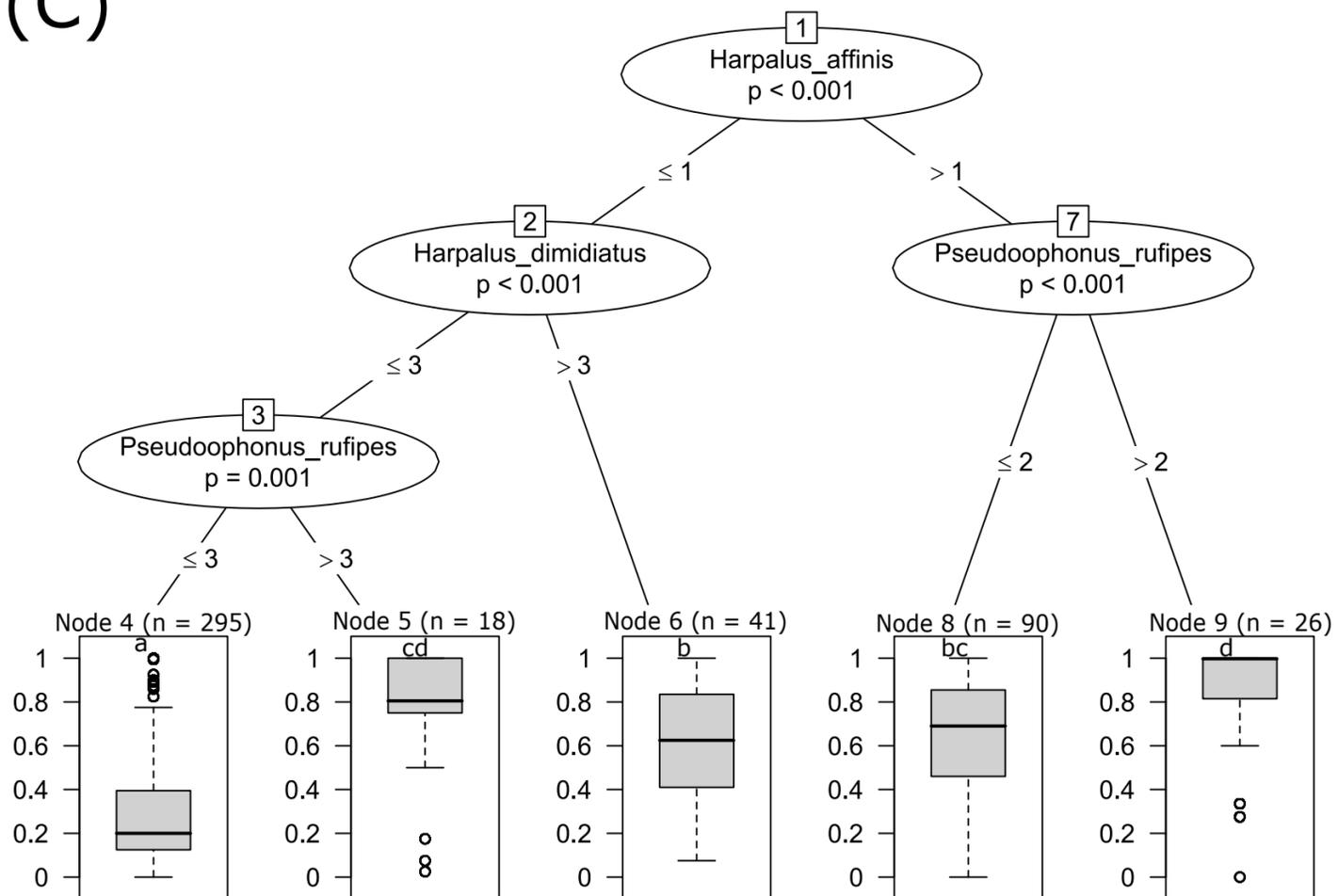
(A)

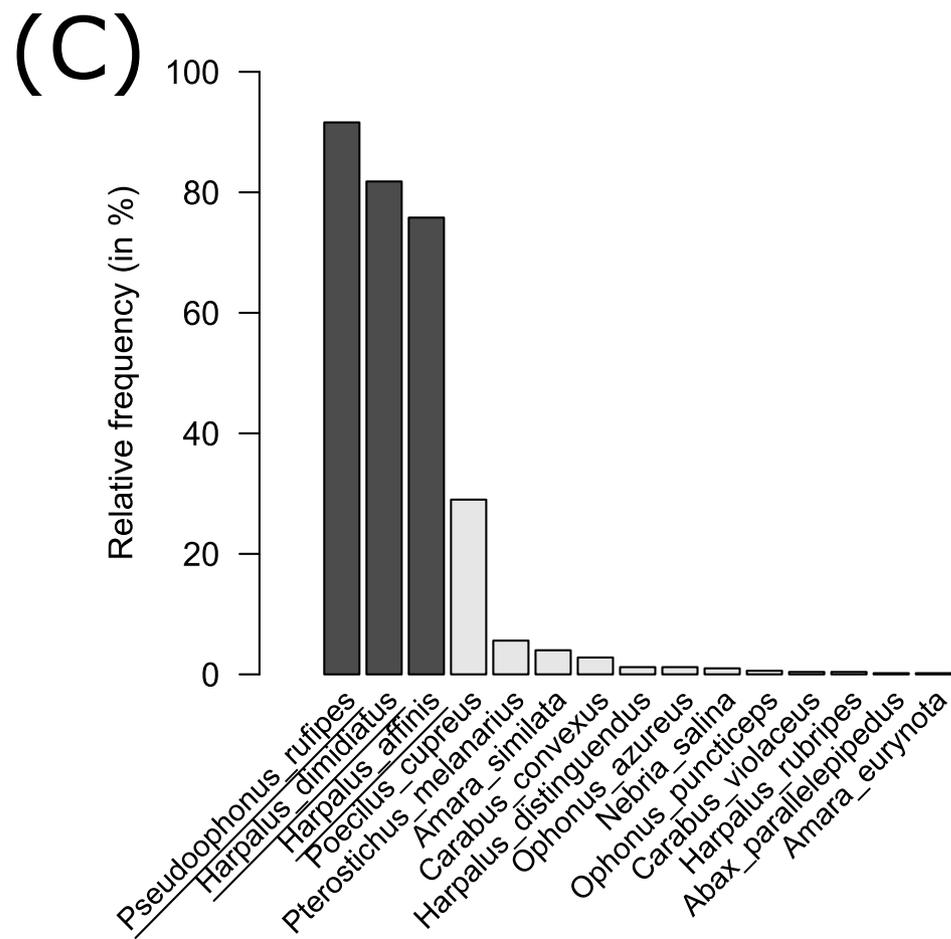
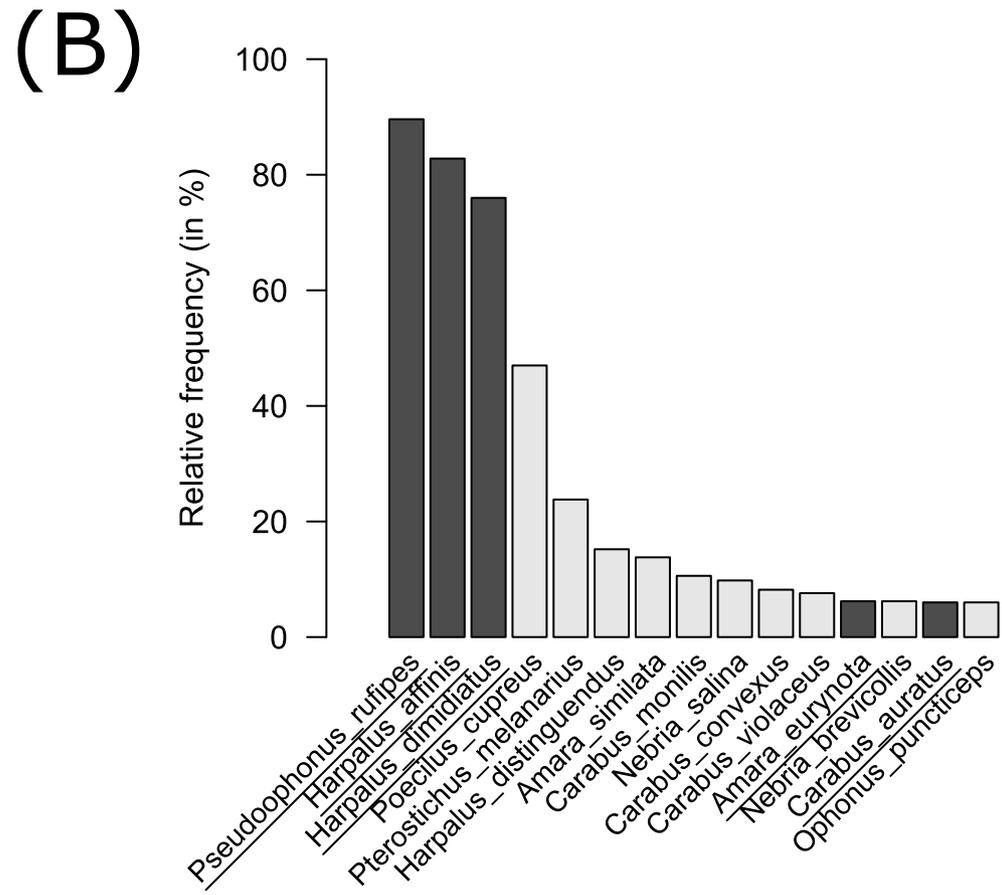
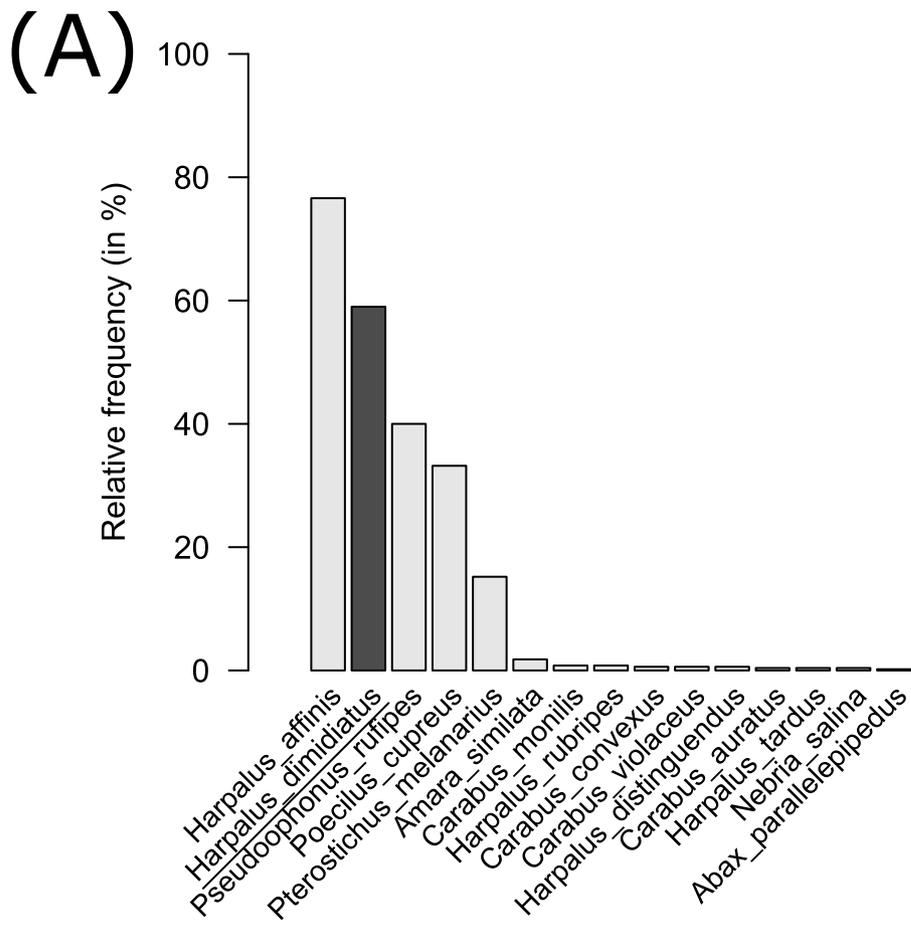


(B)



(C)





Project	Main objective	Year	No. sessions	No. of fields	No. of transects per field	Records at plot level	Records at transect level
Trichard et al., (2013)	Investigate spatio-temporal association between weed seed predation and carabids in two type of soil management: conventional and no tillage.	2011	5	2	14	280	140
Petit et al., (2017)	Investigate the effect of landscape and conservation agricultural practices, in interaction, on the weed seed predation in-field.	2012	1	69	2	546	138
Lubac (2014)	Investigate the effect of crop type on weed, carabid communities and weed seed predation.	2014	1	8	1	21	8
Ricci et al., (2019)	Investigate the effect of landscape and local pesticide use intensity, in interaction, on weed seed, aphids and Lepidoptera eggs predation.	2015 to 2018	2	20	1	640	160
Minvielle-Debat (2016)	Characterize carabid communities at different spatial scales.	2016	2	12	1	95	24

**Seed Eaters (44 species)**

Genus/Species:	Total AD	Occurrence (%)
<i>Poecilus cupreus</i>	5638	55.94
<i>Harpalus</i>	1815	41.53
<i>H. dimidiatus</i>	713	21.68
<i>H. affinis</i>	584	22.06
<i>H. distinguendus</i>	241	5.25
<i>H. rubripes</i>	132	4.80
<i>H. serripes</i>	70	2.47
<i>H. tardus</i>	50	2.47
<i>H. sp</i>	14	0.25
<i>H. atratus</i> , <i>H. latus</i> , <i>H. luteicornis</i> , <i>H. smaragdinus</i>	13	0.13-0.25
<i>Pseudoophonus rufipes</i>	788	20.42
<i>Amara</i>	465	12.20
<i>A. similata</i>	236	5.63
<i>A. eurynota</i>	83	2.97
<i>A. aenea</i>	45	1.14
<i>A. consularis</i>	40	1.45
<i>A. ovata</i>	34	1.20
<i>A. nitida</i> , <i>A. apricaria</i> , <i>A. aulica</i> , <i>A. plebeja</i> , <i>A. fulvipes</i> , <i>A. familiaris</i> , <i>A. montivaga</i> , <i>A. equestris</i> , <i>A. convexior</i> , <i>A. communis</i>	28	0.06-0.44

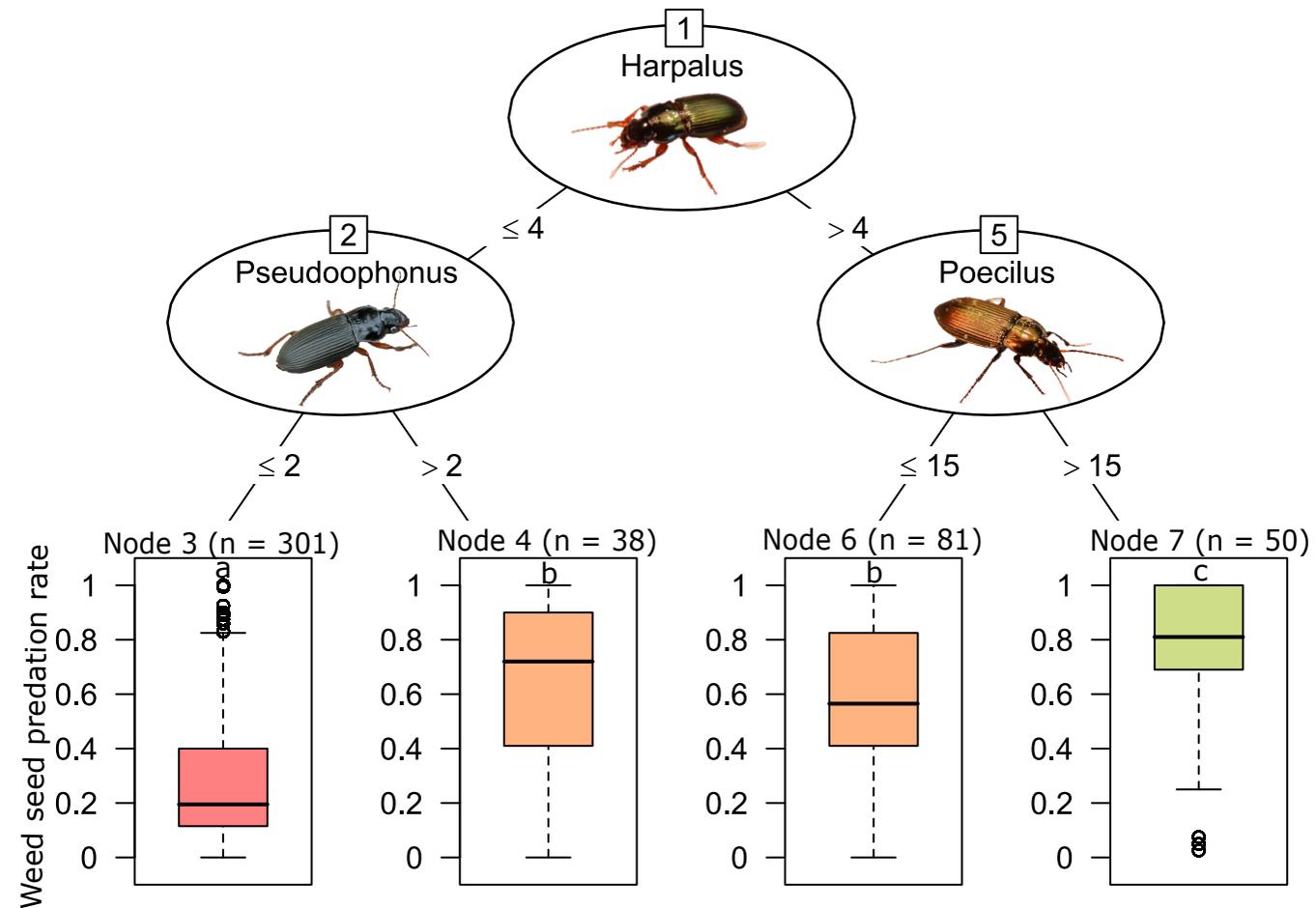
Genus/Species:	Total AD	Occurrence (%)
<i>Anisodactylus</i>	287	2.09
<i>A. signatus</i>	274	1.77
<i>A. binotatus</i>	13	0.63
<i>Ophonus</i>	265	4.74
<i>O. puncticeps</i>	224	2.34
<i>O. azureus</i>	39	2.53
<i>O. sabulicola</i>	2	0.13
<i>Scybalicus oblongiusculus</i>	230	1.33
<i>Diachromus germanus</i>	116	1.14
<i>Pterostichus madidus</i>	18	1.01
<i>Stenolophus teutonius</i> , <i>Acupalpus meridianus</i> , <i>Semiophonus signaticornis</i> , <i>Zabrus tenebrioides</i> , <i>Cryptophonus tenebrosus</i> , <i>Parophonus mendax</i> , <i>Polistichus connexus</i> , <i>Acupalpus dubius</i>	23	0.06-0.38

**Intraguild Predators (19 species)**

Genus/Species:	Total AD	Occurrence (%)
<i>Pterostichus</i>	2403	37.93
<i>P. melanarius</i>	2394	37.80
<i>P. anthracinus</i>	9	0.51
<i>Abax</i>	21	1.39
<i>A. parallelepipedus</i>	20	1.33
<i>A. parallelus</i>	1	0.06
<i>Carabus</i>	864	22.57
<i>C. convexus</i>	462	13.02
<i>C. auratus</i>	296	5.31
<i>C. violaceus</i>	50	3.48
<i>C. monilis</i>	49	2.53
<i>C. coriaceus</i>	7	0.76

Genus/Species:	Total AD	Occurrence (%)
<i>Nebria</i>	245	10.18
<i>N. salina</i>	203	8.15
<i>N. brevicollis</i>	42	2.47
<i>Calathus fuscipes</i>	32	2.15
<i>Molops piceus</i> , <i>Chlaenius nigricornis</i> , <i>Cylindera germanica</i> , <i>Poecilus versicolor</i> , <i>Bembidion lunulatum</i> , <i>Cicindela campestris</i> , <i>Platynus assimilis</i>	19	0.06-0.70

# Classification of weed seed predation of *Viola arvensis* according to the composition of carabid key genera



Weed seed predation intensity