

1 **Semi-natural habitats support populations of stink bug pests in agricultural landscapes**
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21 **Abstract**

22 Semi-natural habitats are considered fundamental for biodiversity conservation and the provision of
23 biological control services in agroecosystems. However, crop pests that exploit different types of
24 habitats during their life cycle might thrive in complex landscapes. Understanding how crop pests use
25 a range of resources across the agroecosystem is fundamental to plan sustainable crop protection
26 strategies. Here we explored the effects of local habitat type (i.e., annual crop, perennial crop, dry
27 grassland and forest) and landscape composition (increasing cover of forest and dry grassland) on
28 stink bug pests in Mediterranean agroecosystems. Stink bugs (Hemiptera: Pentatomoidea) are
29 polyphagous and highly mobile organisms considered a serious threat for numerous crops worldwide.
30 To better understand how stink bugs used different habitats, we sampled active adults and juveniles
31 in spring and summer, and overwintering individuals in autumn and winter. Our results showed that
32 semi-natural habitats supported more abundant stink bug populations, potentially providing
33 alternative feeding, reproduction, and overwintering sites. Specifically, we found more active adults
34 and juveniles in dry grasslands, while forests hosted greater numbers of overwintering individuals.
35 Moreover, forest cover in the landscape was positively related to active stink bug abundance in all
36 sampled habitats. Finally, we found complex landscapes rich in overall semi-natural habitats to
37 support higher abundance of overwintering individuals in both forests and dry grasslands, while
38 perennial crop might provide suitable overwintering sites in highly simplified landscape. These
39 results have important implications for pest management as crop fields situated in complex
40 landscapes might be more susceptible to pest infestation. Effective control strategies may require a
41 landscape-based approach.

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44 **Key words:** Crop, Dry grassland, Forest, Landscape, Mediterranean agroecosystems,

45 Pentatomoidea, Pest dynamics

46 **1. Introduction**

47 Since the beginning of the Green Revolution, broad-spectrum pesticides have been widely used to try
48 to control crop pests, leading to widespread environmental pollution and severe impacts on non-target
49 organisms (Geiger et al. 2010). Moreover, agricultural expansion has resulted in landscape
50 simplification, contributing to the decline of farmland biodiversity (Emmerson et al. 2016), further
51 threatening the provision of important ecosystem services such as biological control of pests (Dainese
52 et al. 2019). The implementation of integrated crop protection strategies that take advantage of natural
53 regulation mechanisms have been largely advocated to reduce the negative impacts of agricultural
54 production on the environment by reducing pesticide use (Bianchi et al. 2006; Gagic et al. 2021).
55 Identifying the main factors driving the dynamics of pest populations is crucial to support effective
56 and more eco-friendly pest control (Mazzi and Dorn 2012).

57 Pest management strategies often focus on the local field scale. However, many pest species are
58 mobile organisms that exploit and move across different habitat types during their life cycle (Kennedy
59 and Storer 2000). Several studies have hence highlighted the need for considering larger scales and
60 multiple habitats to better understand pest dynamics in agroecosystems (e.g., O'Rourke et al. 2011;
61 Rusch et al. 2013). Semi-natural habitats embedded in agricultural matrices are known to influence
62 pest populations both positively, providing alternative food resources, shelters, and overwintering
63 sites (Cullum et al. 2020; Santoiemma et al. 2019; Tschardt et al. 2016), and negatively, supporting
64 populations of natural enemies such as predators and parasitoids (Holland et al. 2017; Mele et al.
65 2021). Although biocontrol is generally expected to be stronger in landscapes rich in semi-natural
66 habitats (Bianchi et al. 2006), pest response to landscape composition in crop fields has been shown
67 to be largely inconsistent (Delaune et al. 2021; Karp et al. 2018) and potentially driven by species-
68 specific characteristics (Tamburini et al. 2020). Understanding how agricultural pests use a range of
69 resources across multiple habitats and respond to landscape characteristics is fundamental to plan
70 sustainable crop protection strategies beyond the field scale.

71 Phytophagous stink bugs (Heteroptera: Pentatomoidea) are responsible for important economic
72 losses to agriculture on a global scale (Schaefer and Panizzi 2000). Stink bugs can cause major
73 damage to important crops such as cotton, soybean, corn, rice, wheat, apple, kiwi, olive and cherry
74 (Panizzi et al. 1997; Sosa- Gómez et al. 2020). Reductions in both yield quantity and quality are due
75 to their feeding activity on fruits, seeds, leaves or stems (McPherson 2018; Panizzi 1997) and several
76 species are also vectors of plant pathogens (Mitchell et al. 2018). Highly polyphagous and mobile
77 species (e.g., the southern green stink bug, *Nezara viridula* L.) are considered particularly dangerous
78 as they can move across the agricultural matrix feeding on both wild and crop hosts (Reeves et al.
79 2010; Schaefer and Panizzi 2000; Taki et al. 2014; Venugopal et al. 2014), often reinvading sites
80 from which they were previously eliminated (e.g., Fauvel 1999). Previous studies explored how stink
81 bugs colonize crop fields from adjacent habitats (Bundy and McPherson 2000; Tillman et al. 2009;
82 Reeves et al. 2010; Venugopal et al. 2014, 2015), especially wooded ones, that support stink bug in
83 population build up (González et al. 2020; Lee et al. 2014a, 2015; Taki et al. 2014; Venugopal et al.
84 2014). Nevertheless, semi-natural habitats such as forests and riparian habitats have also been shown
85 to support the biological control of some species of stink bug pests (Conti et al. 2020; Mele et al.
86 2021; Ogburn et al. 2016). These habitats in fact support richer and more abundant communities of
87 parasitoids (mainly hymenopteran wasps, such as Scelionidae and Encyrtidae) and generalist
88 predators known to significantly impact stink bug egg survival (Schaefer and Panizzi 2000; González
89 et al. 2017, 2020). It is hence important to better understand how semi-natural habitats influence the
90 spatiotemporal dynamics of stink bug pest populations in heterogeneous agroecosystems.

91 The aim of this study was to explore the effects of habitat type and landscape composition on stink
92 bug pests in Mediterranean agroecosystems. We measured stink bug abundance in four habitats
93 characterizing the study region (i.e., annual crop, perennial crop, dry grassland and forest) along a
94 landscape gradient of semi-natural habitats (increasing cover of forest and dry grassland). The four
95 habitats provide different resources to stink bugs. Annual and perennial crops should both support
96 pest populations by providing host plants during spring and summer. Forests are expected to mainly

97 provide overwintering sites (Bakken et al. 2015). Dry grasslands should provide alternative host
98 plants (especially when crops are harvested) and suitable reproduction sites (i.e., habitats where adults
99 breed and juveniles can find enough resources for development) (Panizzi 1997). To better understand
100 how stink bugs use different habitats (i.e., as feeding, reproduction, or overwintering sites), we
101 sampled adults and juveniles in spring and summer (i.e., active adults and juveniles), and
102 overwintering individuals in autumn and winter. We hypothesized that i) semi-natural habitats would
103 generally support stink bug pests, and that ii) forests would mainly be used as overwintering sites and
104 dry grasslands for feeding and reproduction. We hence expected that iii) crop fields located in
105 landscapes rich in semi-natural habitats would present more abundant communities of stink bug pests.
106 We also tested whether species identity would influence stink bugs' response to habitat type and
107 landscape composition.

108

109 **2. Material and methods**

110 *2.1. Study area, experimental set-up and landscape analyses*

111 The study was carried out in 2020 in the agricultural landscape of Bari and Barletta-Andria-Trani
112 provinces in southeast Italy, within the boundaries of the Alta Murgia National Park. The park covers
113 a total area of nearly 68,000 ha, it is characterized by a Mediterranean semi-arid climate (mean annual
114 precipitation = 700 mm, mean annual temperature = 15 °C) and it consists of extensively farmed areas
115 interspersed with semi-natural habitats such as dry grasslands, mainly used as extensive pastures, and
116 forest patches (*Pinus halepensis* Mill. or *Quercus pubescens* Willd. forests). The arable land is
117 cultivated with annual crops (mainly cereals and legumes), and perennial crops (mostly almond, olive
118 and cherry).

119 We selected 12 non-overlapping circular landscapes with a 1 km radius along a gradient in the
120 cover of semi-natural habitats (range = 23.6 – 75.1 %). Landscapes were separated by at least 4.7 km,
121 except for two that were located at shorter distance (3.78 km). Within each landscape we selected
122 four sites corresponding to the four most abundant habitats in the region: annual crops, perennial

123 crops, dry grasslands, and forests (48 sites in total). The annual crops were all wheat, the perennial
124 crops were nine olive, one cherry and two stone fruit orchards, and the dry grasslands were all
125 characterized by grasses and few shrubs (mostly *Scorzoneretalia villosae* Horvatić dry grasslands
126 interspersed with *Pyrus spinosa* Forssk. trees). The forests comprised four oak and eight pine forests.
127 The sites were selected in order to minimize the distance from the landscape centroid (the maximum
128 distance from the centroid was 370 m, except for two sites that were distant 580 m and 647 m,
129 respectively). To quantify the cover of dry grasslands, forests and total semi-natural habitats within
130 each landscape (1km radius), we manually digitalized dry grassland and forest patches by visual
131 inspection of high-resolution satellite images in Google Earth Pro (Google Inc.© 2017). We also
132 measured the Shannon diversity index of land-cover types (habitat diversity) and the total number of
133 patches within each landscape. Landscape characteristics were also evaluated in a 2-km radius buffer
134 around the landscape centroid, to test for potential scale dependence (landscape variables' ranges and
135 correlations at different scales are presented in Table S1).

136

137 2.2. Insect sampling

138 The survey was carried out from May to December 2020 across the 48 sites. We conducted two
139 sampling campaigns to measure 1) the abundance of active stink bugs in spring and summer and 2)
140 the abundance of overwintering adults in autumn and winter. Specifically, from May to September
141 (five sampling rounds), active specimens present on ground vegetation were collected using a sweep
142 net on a total of six transects (100 m/transect) per site (three at the center and three at the edges).
143 Moreover, since many stink bugs are pests of perennial crops, we selected six trees per site (three at
144 the center and three at the edges) and we sampled the individuals present on the canopy, beating the
145 branches and collecting insects on a white cloth placed underneath (beating technique). Trees were
146 not present in annual crops, so the sampling on tree canopies was conducted only in perennial crops,
147 dry grasslands and forests. However, because of the low number of specimens collected with the

148 beating technique (32 specimens in total), only those collected by sweep netting were included in the
149 analyses.

150 The second sampling campaign was conducted to identify those habitats used by stink bugs as
151 overwintering sites. It took place from October to December (three sampling rounds) after the number
152 of active individuals strongly decreased (see Results). We sampled both trees and leaf litter, as stink
153 bugs typically overwinter as adults in sheltered environments such as litter or beneath the bark of
154 trees and shrubs (Schwertner et al. 2021). At the center of each site, we removed and carefully
155 examined the leaf litter from three randomly selected 1 x 1 m squares, and sampled three trees (the
156 same plant species were surveyed during spring and summer) both with the beating technique and
157 installing branch traps (i.e., a strip of cardboard mounted around one branch per tree that mimics tree
158 bark; Schwertner et al. 2021). Branch traps were installed at c. 1.5 m of height, on branches similar
159 in diameter (c. 55 cm) and checked monthly. This second sampling campaign was conducted only in
160 perennial crop, dry grassland and forest habitats and not in annual crops, as these mostly presented
161 bare soil and no trees or shrubs. Because of the low number of specimens found in the leaf litter (10
162 in total), only those collected on trees (i.e., via beating technique and branch traps) were included in
163 the analyses.

164 After collection, insects were stored at -20°C until identification which was made following the
165 main taxonomic keys of Heteroptera (Derjanschi and Péricart 2005; Lupoli and Dusoulhier 2015;
166 Ribes and Pagola-Cardé 2013).

167

168 2.3. *Data analysis*

169 We used general linear mixed-effects models to explore the effects of habitat type and landscape
170 composition on the abundance of active and overwintering stink bug pests. We considered as
171 landscape predictors the proportion of forest, dry grassland or total semi-natural habitats in the
172 landscape, habitat diversity and the number of patches in the landscape at both 1 and 2 km scale. Ten
173 models were hence run per response variable (see below), each including a different landscape

174 predictor (five landscape metrics at 2 different landscape scales). The model displaying the lowest
175 AIC was considered as the best fitting model (Akaike 2011; Table S2).

176 For the analyses of active stink bug pests (first sampling campaign, from May to September), we
177 averaged data at the site level for each sampling round, as preliminary analyses showed no effect of
178 sampling location (center *vs.* edge; ANOVA: $P = 0.928$). We set up a total of three different models.
179 With the first model (*model 1*) we explored the overall response of stink bugs to the tested factors.
180 We hence included the total abundance of active stink bugs (both adults and juveniles) as response
181 variable, and habitat type (categorical, four levels), landscape composition (continuous; % cover of
182 forests, dry grasslands, total semi-natural habitats in the landscape, habitat diversity or number of
183 patches), time (continuous; Julian days) and their interactions as predictors. With the second model
184 (*model 2*), we explored whether adults and juveniles responded differently to habitat type and
185 landscape composition. Stink bug abundance was hence averaged at the site level for adults and
186 juveniles, separately. We included in the model the abundance of active stink bugs for each
187 development stage as response variable, and habitat type, landscape composition, development stage
188 (categorical, two levels) and their interactions as predictors. We included also the quadratic and cubic
189 terms of time in these first two models to better fit the temporal dynamics of stink bug populations.
190 With the third model (*model 3*), we further tested whether species identity influenced stink bugs'
191 response to the tested variables. Stink bug abundance was hence averaged at the site level for each
192 species (i.e., time was not considered in this analysis to improve model residuals). We included in
193 this model the abundance of adult stink bugs for each species as response variable, and habitat type,
194 landscape composition, species identity (categorical; six levels) and their interactions as predictors.
195 Juveniles were not considered for this analysis as they could not be all reliably identified at the species
196 level. Species counting less than 30 individuals were not included in this analysis (Table S3). Tukey
197 multiple comparison test was applied to determine habitat preference for each stink bug species.
198 Standardizing stink bug abundance within species produced qualitatively similar results (not
199 presented). For all three models, landscape and site ID were included as random factors.

200 For the analyses of overwintering stink bug pests (second sampling campaign, October to
201 December) we averaged data at the site level (i.e., one record per site), as preliminary analyses
202 showed no effect of sampling method (beating vs. branch traps; ANOVA: $P = 0.417$) on the
203 abundance of stink bug pests. Time was not considered in this analysis to improve model residuals.
204 The model (*model 4*) included the total abundance of overwintering stink bugs as response variable,
205 and habitat type, landscape composition, and their interactions as predictors. Landscape ID was
206 included as random factor. Stink bug abundance was log-transformed in all four models to abide by
207 model assumptions. Normality and homoscedasticity of the model residuals were validated
208 graphically. To reduce model complexity, we did not consider three- and four-way interactions when
209 not significant. Moreover, we tested whether a different model selection procedure influenced model
210 outcomes: adopting an information-theoretic approach evaluating alternative competing models
211 produced quantitatively similar results (see Supporting information). All the analyses were performed
212 in R using the ‘lme4’ and vegan packages (Bates et al. 2017, Oksanen et al., 2019).

213

214 **3. Results**

215 During the first sampling campaign (from May to September) we collected a total of 1,645 adults
216 belonging to 9 species of stink bug pests and 1,908 juveniles (Heteroptera: Pentatomoidea:
217 Pentatomidae and Scutelleridae; Table S3). The most abundant species was *Eurygaster maura* L.
218 (37.6%) followed by *Aelia acuminata* L. (15.9%), *Aelia germari* K. (12.0%) and *Dolycoris baccarum*
219 L. (11.5%). Juveniles belonged mainly to the genus *Eurygaster* spp. (58.0%) and *Aelia* spp. (23.7%).
220 During the second sampling campaign (from October to December) we collected a total of 52
221 overwintering adults belonging to 5 stink bug species. The most abundant overwintering species was
222 *N. viridula* (53.8%) and *Piezodorus lituratus* F. (38.4%) (Table S3).

223 Abundance of active stink bugs was influenced by both habitat type and landscape composition
224 (Table 1). We found that the total abundance of active stink bugs (both adults and juveniles) was
225 higher in dry grassland compared to the other habitats and that, after peaking in late spring, the total

226 abundance declined (i.e., non-linear effect of time; Fig. 2A). However, forest habitat locally
227 supported higher abundance of stink bugs at the end of the summer compared to annual and perennial
228 crops (Habitat x Time interaction; *model 1*). When including development stage in the analyses
229 (*model 2*), we found that juveniles were more abundant than adults at the beginning of the sampling
230 period compared to late summer, but only in dry grasslands and forests (Habitat x Time x
231 Development stage interaction; Fig. S1). Moreover, habitat preference varied among species (Habitat
232 x Species ID interaction, *model 3*; Fig. 3). Specifically, we found more *E. maura* and *A. germari*
233 adults in dry grasslands, *E. austriaca* was more abundant in annual crops, *Eurydema ornata* L. and
234 *D. baccarum* in both perennial crops and dry grasslands, whereas *A. acuminata* did not present clear
235 differences (for statistical differences see Fig. 3 and Table S6). Including the proportion of forests at
236 2 km scale as landscape predictor always yielded the lowest AIC for all models on active stink bugs
237 (Table S2). We found that the total abundance of active stink bugs increased with forest cover in the
238 landscape in all the sampled habitats (*model 1*; Fig. 2B). However, the effect of the percentage of
239 forest cover on stink bug abundance depended on the species identity (Forest x Species ID interaction,
240 *model 3*): the positive effect of forest cover was observed for all the most abundant species except for
241 *A. germari* which did not respond to landscape (Fig. S2). The effects of habitat type and landscape
242 composition remained similar across models.

243 Abundance of overwintering adults was influenced by an interactive effect between habitat type
244 and landscape composition (Table 1). We found that the abundance of overwintering stink bugs was
245 generally higher in forest habitats, and that the effect of landscape composition depended on habitat
246 type. The abundance of overwintering individuals increased with the proportion of semi-natural
247 habitats (2 km scale), but only in forests and dry grasslands, whereas it showed the opposite trend in
248 perennial crops (Habitat x Semi-natural habitats interaction, *model 4*; Fig. 4).

249

250 **4. Discussion**

251 Our study shows that semi-natural habitats play an important role in supporting populations of stink
252 bug pests in Mediterranean agroecosystems. We found that stink bug pests were present in both crop
253 and non-crop habitats, with dry grasslands and forests providing potential alternative feeding,
254 reproduction, and overwintering sites. Agricultural landscapes with forest cover presented higher
255 local abundance of stink bug pests in both crop and non-crop habitats, whereas high cover of semi-
256 natural habitat in the landscape increased the abundance of overwintering individuals in non-crop
257 habitats. These results have important implications for the control of stink bug pests in agricultural
258 landscapes, as crop colonization can be affected by the type and the abundance of semi-natural
259 habitats in the surrounding landscape.

260 We found stink bug pests in both crop and non-crop habitats, confirming their ability to move
261 across the agricultural matrix and to exploit a variety of habitats and hosts. Most of stink bug species
262 are in fact polyphagous and highly mobile organisms (Lee et al. 2014b) and seasonal availability of
263 resources probably influenced the temporal occurrence of stink bugs in different habitats (Bundy and
264 McPherson 2000; Tillman et al. 2009; Venugopal et al. 2014). Annual and perennial crops seemed to
265 provide a suitable habitat for stink bug pests in spring and early summer, while abundance dropped
266 in August and September. Similar seasonal trends were previously observed for true bugs in
267 Mediterranean environments (e.g., Gessé et al. 2014), where severe late summer droughts can limit
268 availability of host plants. Moreover, within our study area, cereals were harvested in June and
269 herbaceous cover in orchards is often removed with machineries to avoid competition for water. This
270 can also explain why we found forests to present more abundant stink bug populations at the end of
271 the summer compared to annual and perennial crops, suggesting that this habitat might provide
272 aestivation opportunities and food resources not available in cultivated areas.

273 Contrary to our expectations, we did not find any perennial crop specialist feeding on fruits in
274 orchards after July, but only occasional pests of woody plants such as *D. baccarum* and *P. lituratus*,
275 feeding on herbaceous plants (Mutlu et al. 2018). Moreover, the invasive alien pest *Halyomorpha*
276 *halys* (Stål) was not found during the survey, despite the species has been recorded in Apulia region

277 in 2016 (Cianferoni et al. 2018). Dry grasslands presented the highest abundance of stink bug pests
278 from May to September and resulted to be a favorite habitat for four out of the six most abundant
279 species, i.e., *E. maura*, *A. germari*, *D. baccarum*, and *E. ornatum*. This is probably because dry
280 grasslands provide more abundant, diverse, and temporarily stable communities of host plants
281 (Malenovský et al. 2011). Our findings confirm the importance of this habitat for stink bugs
282 communities (Di Giulio et al. 2001; Gessé et al. 2014; Kőrösi et al. 2012). However, local
283 heterogeneity within the same habitat type (e.g., pine and oak forests were categorized both as forests)
284 probably increased variability in our dataset, making more difficult to identify habitat preferences.

285 The semi-natural habitats in the study area represented also suitable reproduction sites for the
286 populations of stink bug pests. We found more juveniles than adults at the beginning of the sampling
287 period, but this difference was evident only in forests and dry grasslands and not in cultivated habitats
288 (Fig. S1). This might indicate that stink bugs preferably used non-crop habitats for reproduction and
289 development of juveniles (Panizzi 1997). Nevertheless, more studies measuring egg mass abundance
290 and juvenile survival in multiple habitats are needed to better understand reproduction dynamics of
291 stink bug communities in heterogeneous agroecosystems. Our study also highlights the importance
292 of wooded habitats as overwintering sites. We found higher abundance of overwintering adults in
293 forests compared to dry grasslands and perennial crops. This is in accordance with previous studies
294 that found this type of habitat to provide diverse shelter opportunities such as bark cavities, dense tree
295 crowns and abundant soil litter (Jones et al. 1981; Lee et al. 2014a; Musolin 2012; Schaefer and
296 Panizzi 2000). Contrary to our expectations, we only found overwintering stink bugs on trees rather
297 than in the leaf litter. Moreover, we found few overwintering individuals of *Eurygaster* spp. (10
298 specimens; Table S3) and *Aelia* spp., the two most abundant genera in our study. Although reported
299 to overwinter in large groups under dry leaves in forest habitats, *Eurygaster* and *Aelia* species have
300 been previously found to migrate to elevated areas such as hills or mountains in late summer for both
301 aestivation and hibernation (Brown 1965; Critchley 1998; Schaefer and Panizzi 2000; Schuh and
302 Weirauch 2020), potentially explaining the lack of overwintering individuals in our study. Our results

303 also indicated that *Eurygaster* species positively responded to forest cover in the landscape (see
304 below) indicating that this habitat plays an important role in the life cycle of this genus. Nevertheless,
305 to better understand the influence of specific thermal needs and of other landscape features (i.e.,
306 elevation; Cullum et al. 2020) on the spatiotemporal dynamics of different pest species, future studies
307 could explore stink bug overwintering along elevation or temperature gradients.

308 The importance of semi-natural habitats in supporting populations of stink bug pests emerged also
309 when analyzing their response to landscape composition. We found that high cover of forests in the
310 landscape was associated with high abundance of active individuals in all the surveyed habitats.
311 Similar results were observed for stink bug pests in soybean in Argentina (González et al. 2020) and
312 for the brown-winged green bug, *Plautia stali* Scott, in fruit orchards in Japan, where severe orchard
313 infestations were associated with high forest cover in the landscape (Taki et al. 2014). Also, at a
314 smaller scale, many studies found both native and invasive stink bug species to move from woodlands
315 to adjacent crops (Bakken et al. 2015; González et al. 2017; Bundy and McPherson 2000; Reeves et
316 al. 2010; Tillman et al. 2016). As mentioned before, many Pentatomoidea species use forest habitats
317 for alternative food and shelters (Schwertner et al. 2021), potentially playing an important role in
318 stink bug life cycle and population build-up (Venugopal et al. 2014). We also found that abundant
319 semi-natural habitats in the landscape (forests and dry grasslands) were associated with high numbers
320 of overwintering individuals in forests and dry grasslands, but not in perennial crops (Fig. 4). This is
321 probably because the higher anthropic disturbance typical of cultivated crops, alters the optimal
322 microclimatic condition required for overwintering (Cullum et al. 2020), leading the individuals to
323 leave those sites and take refuge elsewhere. Our data also suggest that perennial crops might provide
324 suitable shelters for overwintering (e.g., under tree bark) when seminatural habitats are not available
325 (i.e., in highly simplified landscapes). Moreover, our analyses showed that stink bugs best responded
326 to landscape processes consistently at 2 km scale, confirming the available information in the
327 literature regarding their dispersal ability (Olson et al. 2018; Taki et al. 2014). Response to landscape
328 composition was similar for the most abundant species except for *A. germari*, which showed no

329 relationship with forest cover in the landscape. This pest of cereals probably overwinters and finds
330 shelter in other type of habitats. Studies considering pest species identity might be required when
331 planning specific control actions. Finally, including variables describing landscape configuration and
332 diversity in the models never yielded the lowest AIC. This suggests that the abundance of shelters
333 and food resources in the landscape was more important for stink bugs than the diversity of habitats
334 or the presence of landscape features that facilitate dispersion: stink bugs are in fact characterized by
335 high dispersal ability and are often generalists in terms of both habitats and hosts.

336 In conclusion, our study shows that semi-natural habitats play a key role in supporting the
337 community of stink bug pests in agroecosystems. This has important implications for pest control
338 strategies: crop fields situated in landscapes with high cover of semi-natural habitats might be more
339 exposed to pest invasion. For this reason, monitoring efforts should be reinforced in complex
340 landscapes to closely track pest dynamics in the field and to intervene when necessary. Forests in fact
341 may potentially serve as source of overwintered adults colonizing fields and orchards in early spring,
342 while dry grasslands as a season-long reservoir for crop infestations (Bakken et al. 2015; Cornara et
343 al. 2021). Nevertheless, semi-natural habitats have also been shown to support communities of natural
344 enemies in agricultural landscapes (Dainese et al. 2019; Roland and Taylor 1997) and might
345 contribute to the biological control of stink bug pests. For instance, high forest cover in the landscape
346 has been showed to promote the control of stink bugs in soybean in Argentina, without however
347 reducing their abundance in the field (González et al. 2017, 2020). Moreover, Mele et al. (2021)
348 recently found that both the abundance and the control by parasitoids of the invasive stink bug *H.*
349 *halys* in kiwifruit orchards, increased with the proximity to riparian vegetation. In this context, semi-
350 natural habitats might be a greater source of pests than natural enemies (Bianchi et al. 2006,
351 Tschardt et al. 2016). However, since the potential for biological control was not measured in this
352 study, we can not exclude that natural enemies influenced stink bug populations. Actions to
353 specifically support the communities of biological control agents in the landscape are probably
354 necessary (e.g., providing alternative floral resources) (Albrecht et al. 2020). Improving knowledge

355 regarding the factors driving stink bug population dynamics in agroecosystems could be useful to
356 plan effective and sustainable pest management strategies aimed at reducing the use of pesticides
357 (Grabarczyk et al. 2021; Taki et al. 2014). These strategies should consider pest dispersal across crop
358 and non-crop areas and may require a landscape-based approach.

359

360 **Declaration**

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535 **TABLES**

536 **Table 1.** Results of the best fitting linear mixed-effects models (lowest AIC) testing the effects of
 537 habitat type (annual crops, perennial crops, dry grasslands, forests) and landscape composition (2 km
 538 scale) on the abundance of stink bug pests. Other fixed factors included were time (Days; model 1
 539 and 2), development stage (Stage; model 2) and species identity (Species ID, model 3).

Variable	Chisq	P-value
<i>1) Total stink bug abundance</i>		
Habitat	56.65	< 0.001
Forest (2 km scale)	5.09	0.024
Days	16.77	< 0.001
Days^2	17.77	< 0.001
Days^3	17.74	< 0.001
Habitat : Forest	4.81	0.186
Habitat : Days	13.20	0.004
Forest : Days	0.13	0.714
<i>2) Stink bug abundance (adults vs. juveniles)</i>		
Habitat	53.21	< 0.001
Forest (2 km scale)	3.77	0.052
Days	27.59	< 0.001
Stage	4.22	0.040
Days^2	28.30	< 0.001
Days^3	27.42	< 0.001
Habitat : Forest	5.24	0.155
Habitat : Days	15.54	0.001
Forest : Days	1.12	0.290
Habitat : Stage	4.40	0.221
Forest : Stage	0.40	0.525
Days : Stage	26.17	< 0.001
Habitat : Forest : Days	5.34	0.149
Habitat : Forest : Stage	0.10	0.992
Habitat : Days: Stage	18.90	< 0.001
Forest : Julian days : Stage	0.56	0.455
<i>3) Stink bug abundance (by species)</i>		
Habitat	30.83	< 0.001
Forest (2 km scale)	4.97	0.026
Species ID	43.45	< 0.001
Habitat : Forest	2.11	0.550
Habitat : Species ID	120.69	< 0.001
Forest : Species ID	14.97	0.010
<i>4) Overwintering stink bug abundance</i>		
Habitat	10.24	0.006
Semi-natural habitats (2 km scale)	0.26	0.613
Habitat : Semi-natural habitats	7.42	0.024

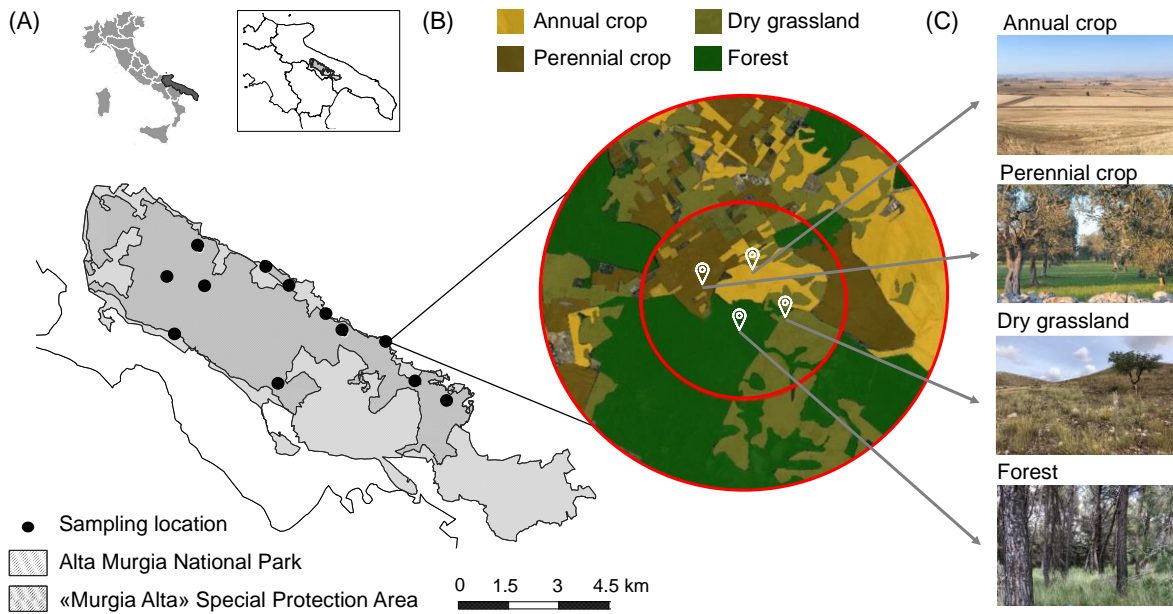
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FIGURES

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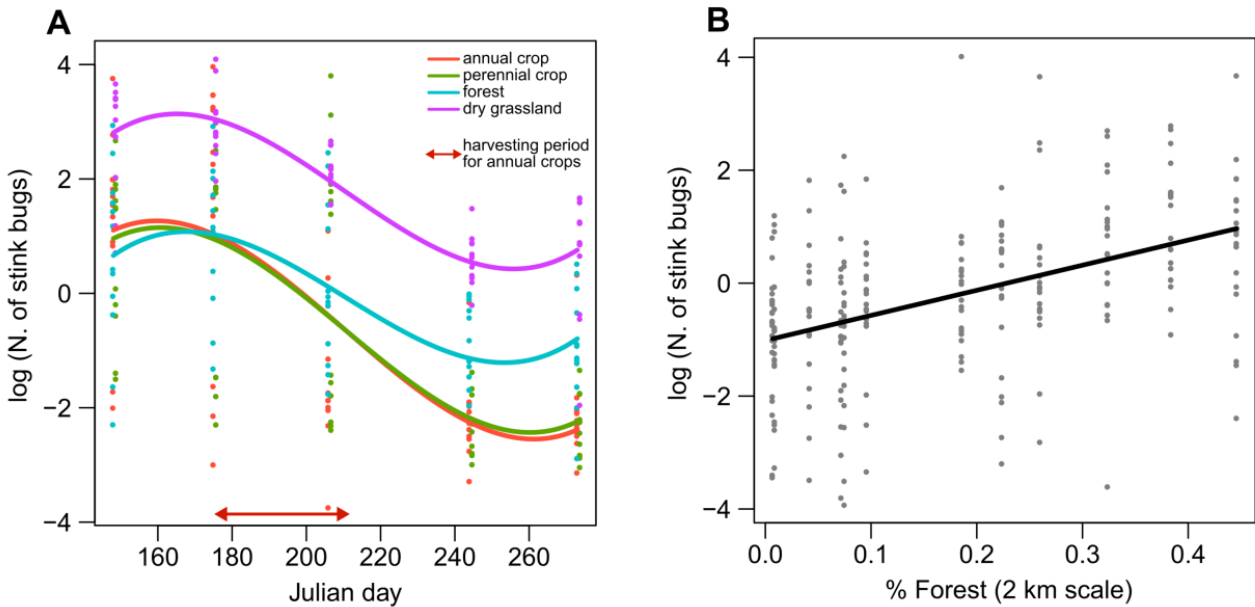


544

545 **Figure 1.** Map of the 12 sampling landscapes (A), example of landscape buffer at 1 and 2 km scale
546 (B), and of the four investigated habitats within each landscape (C). (Color figure)

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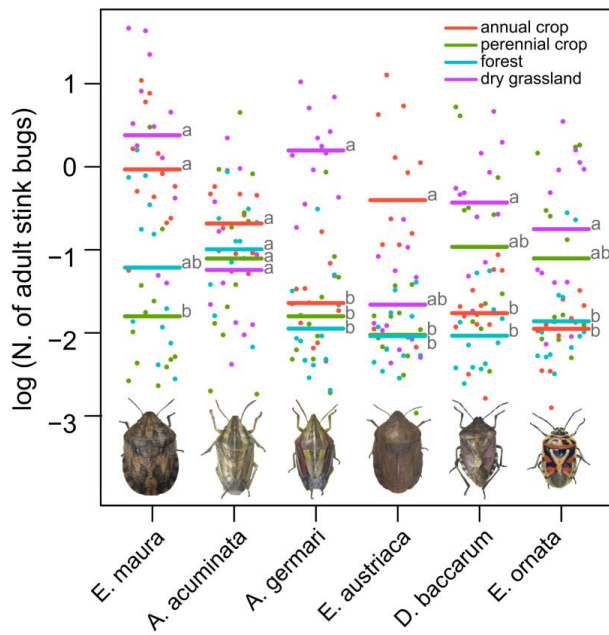
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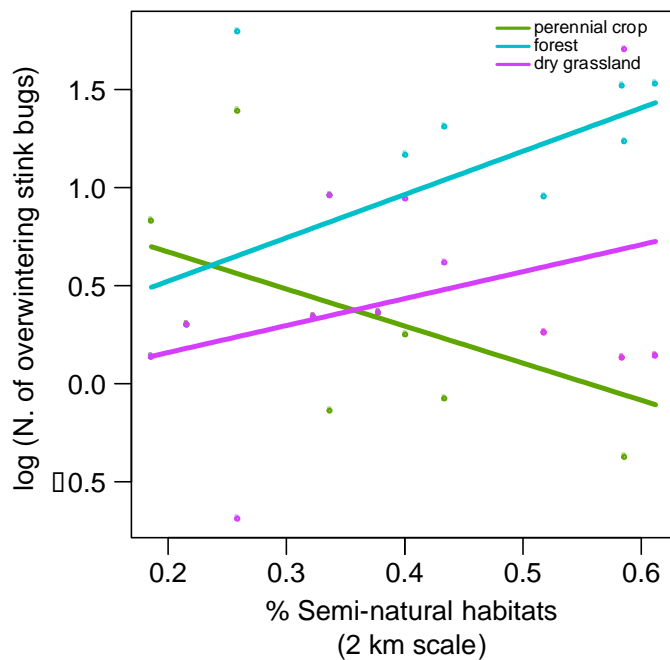
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550 **Figure 2.** Effects of (A) time in interaction with habitat type and (B) landscape composition (%
551 of forest cover at 2 km scale) on the overall abundance of stink bugs (i.e., both adults and juveniles)

552 during the first sampling campaign (May-September) (*model 1*). Plots display prediction lines and
553 partial residuals. (Color figure)



554
 555 **Figure 3.** Habitat preference of the most abundant stink bug species collected during the first
 556 sampling campaign (May-September) (*model 3*). Different letters indicate significant differences
 557 among habitat for each species ($p < 0.05$, Tukey multiple comparison test) Plots display prediction
 558 lines and partial residuals. (Color figure)
 559



560
 561 **Figure 4.** Effects of the interaction between habitat type and landscape composition (% of semi-
 562 natural habitat cover at 2 km scale) on the abundance of overwintering stink bugs (second sampling
 563 campaign, October-December) (*model 4*). Plots display prediction lines and partial residuals. (Color
 564 figure)
 565