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1 **Banker plants and landscape composition influence colonisation precocity of tomato**
2 **greenhouses by mirid predators**

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21

22 **Key Message**

- 23 • Effective biological control occurs when predators colonise crops and pests are low.
- 24 • We tested which greenhouse elements encourage the colonisation of tomato by mirid
25 predators.
- 26 • Herbaceous habitats promoted early colonisation of tomato by *Macrolophus pygmaeus*.
- 27 • *Calendula* banker plants favoured early colonisation by *M. pygmaeus*.
- 28 • Banker plants are a key low-cost tool to foster biological control in tomato.

29

30 **Abstract (150-200 words)**

31 Conservation biological control involves manipulation of the environment to enhance the
32 effectiveness of natural enemies in controlling crop pests. In this study we combined historical
33 data, sticky trap sampling of tomato greenhouses and beat-sampling of adjacent vegetation to
34 identify which greenhouse characteristics, habitat management practices and landscape features
35 favour an early colonisation of tomato greenhouses by the key mirid predator *Macrolophus*
36 *pygmaeus* and its establishment in NE Spain. Results show that landscape composition and the
37 use of *Calendula officinalis* banker plants inside the greenhouse are key factors. In general,
38 greater amounts of herbaceous semi-natural cover at the landscape scale promoted *M. pygmaeus*
39 colonisation; while the use of *C. officinalis* banker plants encouraged *M. pygmaeus* colonisation
40 independently of the landscape context. We identified host plants adjacent to tomato
41 greenhouses that sustain *M. pygmaeus* populations, however, they did not have a major effect on
42 *M. pygmaeus* colonisation compared to larger landscape and banker plant effects. Early
43 colonisation of greenhouses by this predator species also translated into lower accumulated
44 incidence of pests at the end of the sampling period. This study demonstrates the importance of
45 active habitat management practices in promoting the early arrival of *M. pygmaeus* in
46 greenhouses with delayed spontaneous colonisation.

47 **Keywords**

48 Tomato, colonisation, banker plants, landscape, *Macrolophus*, biological control

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51

52 **Introduction**

53 Conservation biological control (CBC) involves manipulation of the environment to enhance the
54 survival, fecundity, longevity, and behaviour of natural enemies to increase their effectiveness
55 in controlling crop pests. The key to an effective CBC is an early colonisation and establishment
56 of natural enemies in a crop, when pest populations are still at low densities (Wiedenmann and
57 Smith 1997; Symondson et al. 2002). This can be particularly complex in the case of ephemeral
58 habitats, like annual crops, as it requires natural enemies to successively disperse between crops
59 and alternative habitats following a seasonal cycle (Wissinger 1997; Tschardt et al. 2007;
60 Schellhorn et al. 2014). Thus, for CBC to become a reliable pest management strategy it is
61 necessary to understand which factors are involved in promoting natural enemy colonisation
62 and early establishment in crops. Early establishment is particularly relevant for spring
63 greenhouse crops as they grow in a climate that is favourable for the fast development of pest
64 populations (Albajes and Alomar, 1999). Alternative host plants within agricultural landscapes
65 provide key resources to natural enemies (such as alternative prey and host, nectar and pollen)
66 and can directly influence native natural enemy population dynamics (Landis et al. 2000; Norris
67 and Kogan 2005; Gurr et al. 2017). Promoting host plants at either the field, the farm
68 (Letourneau et al. 2011) or the landscape level (Bianchi et al. 2006) may therefore foster natural
69 enemy spill over to crops by minimizing the distance between crops and alternative hosts, while
70 maximizing the overlap of host plant resources in time (Wissinger 1997; Schellhorn et al. 2015).

71 Biological control is a key strategy of pest controlling protected tomato crops in the
72 Mediterranean region (Perdikis et al. 2011; Arnó et al. 2018). Pest management strategies on
73 tomato greenhouses have relied for many years on inoculative releases of commercial natural
74 enemies (Messelink et al. 2014). However, the early findings of spontaneous colonisation of
75 unsprayed greenhouses by native natural enemies (see review by Arno et al 2018) led to an
76 increased interest on CBC as a promising tool to increase the sustainability and profitability of
77 protected tomato crops. Among the native natural enemies on tomato crops in the Mediterranean
78 region, polyphagous predatory mirid bugs (Heteroptera: Miridae) of the genera *Macrolophus*,
79 *Dicyphus*, and *Nesidiocoris* have proved very successful in controlling whiteflies and other key
80 tomato pests (Lykouressis et al., 2001; Alomar et al., 2002; Gabarra et al., 2004; Ingegno et al.,
81 2009; Lenteren et al., 2020). Polyphagy has been considered an advantage because it encourages
82 the early establishment of the predators in the crop when the target pest is still at low densities,
83 and it allows predators to sustain their populations in the crop once biological control of the
84 target prey has been achieved (Albajes and Alomar 1999; Symondson et al. 2002; Castañé et al.
85 2016).

86

87 Currently, the predator *Macrolophus pygmaeus* (Rambur) is the focus mirid species in tomato
88 crops in NE Spain and France given the prevalence of their naturally occurring populations
89 relative to other mirid bugs in the region, their persistence in low prey density patches
90 (Montserrat et al. 2004), and more importantly because this species does not produce damages
91 in open tomato greenhouses (Castañé et al. 2011; Arnó et al. 2018). Nevertheless some
92 controversy still exists about its use in other geographical regions (Sanchez et al. 2018). An
93 appropriate management of *M. pygmaeus* populations in tomato greenhouses may save many
94 inoculative releases by sustaining predator populations through the different tomato crop cycles
95 around the year. Several studies have related the presence of adjacent host plants to adequate
96 colonisation of tomato fields by predatory mirids (Alomar et al. 2002; Gabarra et al. 2004;
97 Ingegno et al. 2009). This, however, might not be the only factor, as good levels of colonisation
98 of tomato crops by mirid bugs have also been observed for crops with no adjacent host plants
99 present (<75 m) (Alomar et al. 2002). A likely explanation for these observations is that mirid
100 predators colonise tomato crops both from local host plant sources (field scale), and from more
101 distant sources (farm and landscape scale).

102 The common marigold, *Calendula officinalis* L. (Asteraceae), is one of the main host plants of
103 *M. pygmaeus* and it has been proposed as a banker plant to preserve populations of *M.*
104 *pygmaeus* between crop cycles and/or to provide an on-farm refuge for spontaneous populations
105 (Alomar et al. 2006; Messelink et al. 2014; Balzan 2017). Planting *C. officinalis* strips in crop
106 edges as a banker plant has become a CBC strategy in northern Spain and the south of France
107 (Lambion, 2014; Arnó et al., 2018; Agustí et al., 2020), and this practice has been related to
108 lower tomato leaf damage by Lepidoptera (Balzan 2017). However controversy remains given
109 the potential of *C. officinalis* plants to also sustain the mirid *Nesidiocoris tenuis* (Reuter), which
110 is known to inflict damage to the crop when present at high densities (Castañé et al. 2011).
111 Apart from marigold, other non-crop plants have been identified as overwintering refuges for
112 these predatory mirid bugs (e.g. Lykouressis et al., 2001; Alomar et al., 2002; Ingegno et al.,
113 2009), together with tomato, eggplant and potato crops.

114 To date, only one study to our knowledge has studied the effects of landscape composition and
115 configuration on mirid predator populations in protected tomato crops (Aviron et al. 2016). Key
116 findings showed greater levels of *M. pygmaeus* colonisation in greenhouses embedded in
117 landscapes with larger fallow area, while colonisation was reduced in greenhouses associated
118 with larger orchard area at the landscape scale. Yet, these landscape effects on mirid
119 colonisation were smaller than management practices associated to organic and conventional
120 agriculture. Further research is needed to understand the relative importance of habitat
121 management practices, e.g. presence of banker plants and other crops and non-crop host plants

122 (Thomine et al. 2020), and the landscape context on CBC by mirid predators in protected
123 tomato crops.

124 This study aims to identify which greenhouse characteristics, habitat management practices, and
125 landscape features favour an early colonisation of protected tomato crops by mirid predators and
126 their establishment. We hypothesized that (i) mirid predator colonisation precocity is stable
127 through time for each of the studied greenhouses e.g. showing consistently early vs late
128 colonisation; (ii) larger proportion of semi-natural non-crop cover at the landscape scale
129 enhance mirid colonisation by promoting spillover to tomato crops early in spring, and (iii)
130 greenhouse habitat management practices, using *Calendula* banker plants inside the greenhouse
131 and/or by maintaining diverse host plants at the farm scale, favour early colonisation of tomato
132 greenhouses by mirid bugs.

133

134 **Methods**

135 **Study site and greenhouse selection**

136 The study was carried out in the Maresme county, NE Spain, where protected tomato is a key
137 horticultural crop. The region is located NE of Barcelona following the coastline and between
138 the Litoral mountain range and the sea. Land-use in the area is traditionally agricultural with
139 increased urban pressure over the last 40 years. Natural and semi-natural habitats in the region
140 are comprised of woodland, shrub, herbaceous and ephemeral stream habitats. Twelve
141 greenhouses from a Grower's association (Associació de Defensa Vegetal del Baix Maresme,
142 ADV) and supervised by a plant protection advisor were used for the study. Tomato seedlings
143 were transplanted ranging from mid February to early April. Greenhouses were characterized by
144 their structure (wood/metallic), openings (lateral/zenital), date of transplant (February/March/
145 April), crop diversity (tomato/mixed), number of tomato varieties (one/more), altitude (sea
146 level/>50m), and size (Table 1); together with the use of *Calendula* banker plants inside the
147 greenhouse (5 greenhouses with banker plants and 7 without, Table 2). In 4 out of the 5
148 greenhouses with banker plants, *Calendula* plants were established before the previous tomato
149 spring season (> 1 year before the start of the experiment) while in one of the greenhouses a
150 banker plant margin was established in February just before the tomato transplant. Pest
151 management strategies in the selected greenhouses were based on the recommendations of the
152 plant protection advisor following the IPM rules developed for tomato crops in the area (Arnó et
153 al. 2018).

154

155 **Historical data collection**

156 To confirm previous observations that some greenhouses consistently showed earlier
157 colonisation and pest control than others over the years (Castañé et al. 2004), plant health
158 monitoring data were extracted from the plant protection advisor reports for the same season of
159 our sampling (see next section) and the four previous seasons. For greenhouse H9 data on
160 previous seasons were not available, since that greenhouse was not managed by the ADV at that
161 time. Data extracted were: transplant date; date of the first observation of *M. pygmaeus* adults
162 on tomato plants (colonisation precocity); date of the first observation of *M. pygmaeus* nymphs;
163 and pest/disease control treatments and their dates. All historical data colonisation dates were
164 expressed as Julian days. Julian day is a date expresses as the number of days that have passed
165 since the 1st of January of each year. Meteorological data were retrieved from RuralCat
166 (<https://ruralcat.gencat.cat/agrometeo>, Generalitat de Catalunya). Accumulated rainfall was
167 obtained for the winter-spring period (December-April) and degree-days above 10 °C (DD₁₀)
168 were calculated for the spring period (January-April). The decision to use 10°C for the
169 calculation of DD was based on the lower thermal thresholds for *M. pygmaeus* eggs and
170 nymphal development (Martínez-García et al. 2017).

171 **Arthropod sampling in tomato greenhouses**

172 Tomato greenhouses were sampled every other week with yellow sticky traps from mid-March
173 to mid-June, with the intention to detect the arrival of mirid bugs in each greenhouse and
174 estimate the amount of prey present. Greenhouses were sampled five times during this period,
175 with the exception of two greenhouses that were only sampled four times because of delayed
176 transplanting. Yellow sticky traps (31x21 cm, Entomopraxis, Barcelona, Spain) were attached to
177 wooden sticks and placed between tomato plants along the crop rows. Trap height was adjusted
178 to be at the same level as the top of the plant canopy at the early stages of tomato growth, and at
179 1.20 m in full grown plants. Nine yellow sticky traps were used per greenhouse and sampling
180 date, and were evenly distributed in the greenhouse to cover its surface. Sticky traps were
181 recovered one week later. Traps were then covered by plastic film and placed in a cold climatic
182 chamber (4 °C) until processed. Mirid predator species and key pest groups (whiteflies, aphids,
183 leafmining diptera and thrips) were later identified to taxonomic units and counted. Colonisation
184 precocity was determined as the number of sampling event in which the first mirid was
185 captured, e.g if a mirid predator was first detected on the third sampling event the colonisation
186 precocity of the greenhouse was assigned to 3.

187 **Predatory mirid surveys in adjoining vegetation and *Calendula* banker plants**

188 The abundance and composition of mirid species on plants adjacent to the greenhouse and on
189 banker plants inside the greenhouse was determined three times for early planting greenhouses
190 and two times for late planting greenhouses during the sampling period. The vegetation was
191 sampled every 10 m around the outer perimeter of the tomato greenhouses whenever plants
192 were present. For each sampling point, approximately a 0.5 m² vegetation area was beaten three
193 times with a bat and insects were collected on a white plastic tray (DIN-A4 size). Adult and
194 nymph mirid bugs were collected by means of a mouth aspirator and were placed in tubes in a
195 cooling box to avoid predation. Plants present in each sampling point were identified to genus
196 level in most cases. Whenever a sampling point had more than one plant species, the proportion
197 of each plant species in the mixture was visually estimated. If *Macrolophus* spp. were collected
198 in points with plant mixtures, all plant species present in the mixture were individually re-
199 sampled to be able to relate a particular *Macrolophus* species to the host plant (see next section).
200 *Calendula* banker plants inside the greenhouses were sampled at the same sampling dates and in
201 the same manner than the adjoining vegetation. Back in the laboratory, nymphs were placed in
202 boxes containing a green bean pod, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs
203 and a water supply to complete their development to adults and allow further identification to
204 species level. Adult individuals were morphologically classified as either *Macrolophus* spp.,
205 *Nesidiocoris tenuis*, *Dicyphus bolivari* Lindberg or *Dicyphus errans* (Wolff). As the number of
206 sampling events differed between greenhouses, only the last two samplings of adjacent
207 vegetation were considered (early and late April). Variables related to habitat management
208 (listed in Table 2) were used in further analysis. Among those, the abundance of *Macrolophus*
209 spp., the number of sampling points, and the identified host plant species may indirectly
210 represent a farmer's habitat management practices outside the greenhouse, e.g. herbicide
211 treatments, conservation of weedy margins and active encouragement of plant diversity at the
212 farm scale.

213 ***Macrolophus* spp. molecular identification**

214 Two sympatric *Macrolophus* species present in the area, *M. pygmaeus* and *M. melanotoma*,
215 (Costa) have a great morphological similarity, and have often been confused (Perdikis et al.
216 2003; Martinez-Cascales et al. 2006; Castañé et al. 2013). Yet only *M. pygmaeus* is known to
217 establish on tomato crop; for this reason, we used molecular markers to distinguish the two
218 *Macrolophus* species and to find out to what extent both species coexisted on the sampled non-
219 crop host plants. Subsamples of adult and nymphs of *Macrolophus* spp. specimens collected in
220 each host plant were identified using conventional PCR using the specific primers Mp1F (5'-
221 GTAACATAGATAAAAATCCCATTTTC-3') - Mp4R.2 (5'-
222 CCTAATAATTGTGGTTCTCACAA-3') for *M. pygmaeus*, and Mm1F (5'-

223 CTTCTTGATGCCTTTTATTGTGGC-3') - Mm3R (5'-
224 TTATCATACTATGTAGTCCTTGATT-3') for *M. melanotoma*. These primers were
225 previously described in Castañé et al. (2013), with the exception of Mp4R.2, which is a
226 modification of Mp4R described there. Individual insects were DNA extracted using the
227 SpeedTools Tissue DNA Extraction Kit (BioTools; Madrid, Spain) following the
228 manufacturer's protocol. PCR reactions were conducted as described in Castañé et al. (2013).
229 Target DNA (*M. pygmaeus* and *M. melanotoma*) and water were always included as positive
230 and negative controls, respectively. Resulting PCR products were separated by electrophoresis
231 in 3.5% agarose gels, stained with ethidium bromide and visualised under UV light. The number
232 of individuals analysed per host plant species varied from 9 to 15 (Table 3).

233 **Landscape cover characterization**

234 Land use composition surrounding each greenhouse was quantified using a circular buffer area
235 at two scales (250 and 150 m) with ArcGIS 9.3 (ESRI, 2005). The radius was chosen according
236 to the results reported by previous biological control studies on *M. pygmaeus* (Alomar et al.
237 2002; Aviron et al. 2016). The land use in these landscapes was mapped based on geo-
238 referenced aerial photographs and available data on cover types SIGPAC (Institut Cartogràfic i
239 Geològic de Catalunya, <http://www.icc.cat/vissir3/>). During field inspections, landscape patches
240 were classified as crop (including the three cover classes: protected horticulture, open field
241 agriculture, and olive/vineyard trees) or non-crop (including urban and four semi-natural habitat
242 cover classes: herbaceous, shrub, woodland, and riparian). Land use was verified in the terrain,
243 and corrections were made during the digitalization process. The proportions of all cover classes
244 in each landscape buffer were calculated for all the greenhouses used in the study.

245 **Statistical analysis**

246 Historical data was used to establish the importance of yearly variation and greenhouse identity
247 on predator colonisation precocity, and the relationship of this precocity with their
248 establishment in tomato greenhouses. First, a linear model was fitted with log transformed *M.*
249 *pygmaeus* precocity (expressed as Julian day) as dependent variable; and the year, greenhouse,
250 transplant date and their interaction as independent variables. Then, meteorological variables
251 were used to explore whether they could help explain the yearly variation in colonisation by
252 replacing factor year in the previous model by the variables spring accumulated degree days
253 (DD₁₀) and accumulated winter-spring rainfall. Pair-wise comparisons were evaluated with
254 Tukey's post hoc test with Bonferroni correction. Second, a linear model was fitted with log
255 transformed *M. pygmaeus* nymph detection date as dependent variable and adult *M. pygmaeus*

256 precocity as explanatory variable. In order to do that, data points where nymphs were detected
257 before adults were excluded from analysis.

258 To evaluate whether yellow sticky traps could be reliable in detecting *M. pygmaeus* colonisation
259 of tomato greenhouses for the season when the study was conducted, a linear model was built
260 with the first detection of *M. pygmaeus* adults by yellow traps as dependent variable
261 (approximate Julian day), and the first detection of *M. pygmaeus* adults by plant sampling as an
262 independent variable. As sticky traps were placed twice a month and left in the field for a week,
263 approximate Julian days were calculated.

264 To test whether mirid colonisation precocity and abundance were associated with greenhouse
265 characteristics (Table 1), habitat management (Table 2) or landscape composition, models were
266 fitted with mirid captures on yellow sticky traps as the dependent variable. Analyses of mirid
267 precocity and abundance were focused on *M. pygmaeus*, given that *D. bolivari* adults were only
268 detected in two of the 12 greenhouses at the end of the sampling period. Linear models were
269 used for *M. pygmaeus* colonisation precocity, and generalized linear models following a
270 negative binomial distribution and log link were used for abundance to account for over-
271 dispersion of the data. First, in order to establish the importance of a given predictor variable for
272 explaining colonisation or population abundance, separate models were fitted for each landscape
273 composition variable at two spatial scales (150m and 250m from the greenhouse, landscape
274 cover class variables are described in previous section and listed in the Supplementary material
275 Fig S1 and Fig S.2), and for each greenhouse habitat management variable (*Calendula* banker
276 plant presence and other numerical variables obtained by adjoining vegetation sampling and
277 listed in Supplementary material Fig S3) and greenhouse characteristics (all variables in Table
278 1). In the case of mirid abundance models, the variable mirid colonisation precocity was also
279 used as an explanatory variable. As multicollinearity can influence the interpretation of models
280 results Spearman coefficients between each set of numerical variables were calculated to
281 establish the relationship between them (Supplementary material Fig. S1, Fig. S2 and Fig. S3).
282 Numerical adjoining vegetation variables were highly correlated (>0.7, Supplementary material
283 Fig. S3) so only the total *M. pygmaeus* abundance in adjoining vegetation (variable Mp, Fig S3)
284 was selected together with the categorical variable *Calendula* banker plants (Cal,
285 presence/absence) as habitat management variables in further analyses. Then, mirid precocity
286 and abundance were modelled using the best landscape predictors in interaction with each of the
287 greenhouse characteristics and habitat management variables. This approach was followed to
288 avoid a priori selection of the explanatory variables included in the analysis. All explanatory
289 variables were standardized (mean = 0, SD = 1) which allowed the comparison of effect sizes
290 between predictors.

291 Finally, in order to evaluate the effects of *M. pygmaeus* time of colonisation on pest abundance,
292 a composite pest abundance index per greenhouse was used. This global pest abundance index
293 was built by standardizing (0-1) the accumulated abundances of each pest taxon (whiteflies,
294 thrips, aphids and leafminers) and adding their values (all pests had the same weight in the
295 index). The composite pest abundance index, ranging between 0 and 4, is thus an aggregate
296 measurement of pest pressure. This index was calculated for two times during the season: t_c
297 time of detection of the first *M. pygmaeus* and t_f time of final sampling. A linear model was then
298 fitted to evaluate whether colonisation precocity by *M. pygmaeus* and pest abundance index at
299 time of colonisation (t_c) explained pest abundance index at the end of the sampling period (t_f).
300 Pest abundance index at t_f was log-transformed to achieve model assumptions.

301 All models were evaluated according to their performance based on Akaike's Information
302 Criterion for small samples sizes (AICc) following Burnham & Anderson (2002). Briefly, the
303 best model with the lowest AICc value was identified together with any competing model with
304 $\Delta AICc < 2$ that was considered as receiving equal support from the data (including the null
305 model). For all models R^2_{adj} (linear model) or D^2_{adj} (glm negative binomial model, Guisan &
306 Zimmermann, 2000), predictor estimates, and their interval of confidence (95%) were
307 calculated. Assumptions of linearity and homogeneity of variances on residuals from the best
308 models were checked graphically. No spatial autocorrelation was detected for the residuals of
309 the best models (Moran's I statistic, Ape package; Paradis & Schliep, 2019). All statistical
310 analyses were performed using R version 3.5.2 (R Core Team, 2018) and figures were produced
311 using the package ggplot2 (Wickham 2009).

312

313 **Results**

314 **Historical mirid colonisation and establishment**

315 The main mirid predator species colonizing spring tomato protected crops in the study area was
316 *M. pygmaeus*. In only two occasions in a five-year period, *M. pygmaeus* adults were not
317 detected in tomato crops, and in both cases the farmer had sprayed insecticides (spinosad and
318 flubendiamide, as stated by the plant protection advisor report). In general, only *Bacillus*
319 *thuringensis* Berliner (Bt) based insecticides were applied before colonisation by *M. pygmaeus*
320 when infestation levels of tomato plants by the leafminer *Tuta absoluta* (Meyrick) were high.

321 Linear models showed that greenhouse identity ($F_{10,41}=4.66$, $p<0.0001$) was the main effect
322 accounting for early colonisation of tomato crops by *M. pygmaeus* together with DD_{10}
323 ($F_{1,39}=4.94$, $p=0.02$) and accumulated spring rainfall ($F_{1,39}=3.74$, $p=0.03$), with a $R^2_{adj}=0.51$ and

324 lowest AICc (-14.96). Models including tomato transplant date had greater AICc values and
325 were less parsimonious. The combination of the meteorological predictors explained better the
326 seasonal variation in predatory mirid colonisation than the factor year. Colonisation precocity
327 by *M. pygmaeus* differed between greenhouses (Fig. 1A), with greenhouses H3 and H10
328 representing the early (mid March) and late (mid May) colonisation extremes respectively. In
329 general, years with warm and wet winter and spring seasons showed earlier colonisation of
330 protected tomato crops by *M. pygmaeus* than colder and drier years.

331 The detection of the first nymphs of *M. pygmaeus* in greenhouses was correlated with the
332 detection of the first adults ($R^2_{\text{adj}} = 0.57$, Fig. 1B), indicating that the establishment of this
333 predator in a tomato greenhouse depended on the time of arrival of the first colonisers. On
334 average the first nymphs were detected four weeks after the first adult detection.

335 **Predatory mirid surveys in adjoining field margins and *Calendula* banker plants**

336 A total of 435 *Macrolophus* spp. and 60 *Dicyphus* spp. specimens were collected from the
337 vegetation adjoining the tomato greenhouses (Table 2), while 740 *Macrolophus* spp. and 43
338 *Dicyphus* spp. were collected from *Calendula* banker plants located inside the tomato
339 greenhouses. Some individuals of *N. tenuis* were collected on *Calendula* banker plants in the
340 two greenhouses where this species had been released years earlier as part of a crop protection
341 strategy (H12 historical data, and H10 personal communication from the farmer), and one
342 nymph was captured in H1 (Table 2). Few individuals were also collected on *C. officinalis*
343 plants adjoining two of the greenhouses with no known history of *N. tenuis* releases (Table 2).

344 Almost all *Macrolophus* spp. specimens sampled from beat sheet sampling were identified as
345 *M. pygmaeus* by molecular analysis (Table 3). In eight of the plant species surveyed, both adults
346 and nymphs of *M. pygmaeus* were detected, which indicates the ability of this predator to
347 reproduce and feed on those plants and can therefore be considered confirmed host plants.
348 Confirmed host plants for *M. pygmaeus* comprise both ornamental plants (and therefore
349 intentionally or unintentionally part of the farm habitat management practices) and weeds. The
350 number of host plant taxa around to each greenhouse ranged from 0 to 9 (Table 2, mirid host
351 plant species breakdown for each greenhouse can be found in Supplementary material Table
352 S1). Overall *C. officinalis* plants harboured the largest *M. pygmaeus* populations in comparison
353 with the other seven host plants. Aromatic ornamentals *Lavandula* spp. and *Salvia* spp., and
354 other ornamentals like *Dimorphotheca ecklonis* (DC.), sustained considerable populations of *M.*
355 *pygmaeus* (Table 3). Weeds like *Erodium* spp., *C. arvensis*, *P. officinalis* and *Borago* spp. were
356 also identified as hosts for *M. pygmaeus*. The cryptic *M. melanotoma* was only detected in two
357 host plants in very low numbers: *D. viscosa* (2 adults) and *Lavandula* spp. (1 nymph) (Table 3).

358 Landscape and greenhouse management effects on mirid colonisation and pest abundance

359 Data recorded with the two sampling techniques for one year, visual sampling and yellow sticky
360 traps, associated with each other with an acceptable reliability ($R^2 = 0.46$, Fig. 1C). Given that
361 sampling took place twice a month for both sampling methods and sticky traps were left in the
362 greenhouse for 1 week, a mismatch of ± 15 days between methods was to be expected.

363 Colonisation precocity by *M. pygmaeus* was dependent on both the amount of herbaceous semi-
364 natural cover at the 250m buffer around greenhouses (PS_{250}) and the presence of *Calendula*
365 banker plants (Cal) inside the greenhouses, as shown by the interaction of the two predictors
366 (Table 4). In general greater amounts of herbaceous semi-natural cover favoured early
367 colonisation of tomato greenhouses by *M. pygmaeus*; while the use of *Calendula* banker plants
368 inside the greenhouses attenuated the negative effects of the low proportion of surrounding
369 favourable habitats by promoting early colonisation of the tomato crop (Fig. 2). Landscape
370 variables at 150m performed worse than those at 250m and hence were not included in the best
371 or competing models. Likewise no other greenhouse characteristics or habitat management
372 variables, apart from *Calendula* banker plant presence (Cal), were included in the best or
373 competing models.

374 Accumulated abundance of *M. pygmaeus* adults at the end of the sampling period was explained
375 by its colonisation precocity (Table 4): greenhouses with earlier colonisation had a greater
376 number of predator adults than those with late colonisation. Pest abundance index at the end of
377 the sampling period was explained jointly by *M. pygmaeus* colonisation precocity and the co-
378 variable pest abundance index at the time of *M. pygmaeus* colonisation t_c (Table 4), indicating a
379 negative relationship between pest index and *M. pygmaeus* precocity.

380

381 Discussion

382 This study aimed at understanding how greenhouse characteristics, habitat management
383 practices and landscape features favour early colonisation of protected tomato crops by mirid
384 predators and their establishment. Historical data collected by the plant protection adviser
385 showed that the identity of a greenhouse was central in determining time of colonisation by the
386 most common predator, *M. pygmaeus*. This effect of greenhouse identity on colonisation
387 precocity was further explored as a combination of 1) greenhouse characteristics, 2) habitat
388 management, and 3) landscape composition. Results show that the key factors determining
389 precocity in the colonisation of tomato crops by *M. pygmaeus* are landscape composition and
390 habitat management by use of *Calendula* banker plants inside greenhouses. In general, greater

391 amounts of herbaceous semi-natural cover at the landscape scale promoted *M. pygmaeus*
392 colonisation of tomato greenhouses; however, the use of *Calendula* banker plants encouraged
393 *M. pygmaeus* colonisation independently of the abundance of herbaceous semi-natural cover.
394 Early colonisation of greenhouses by mirid predators also translated into lower accumulated
395 incidence of pests, and therefore potentially into a lower likelihood of pesticide application later
396 in the season (Li et al. 2020). These findings encourage the use of banker plants as a key
397 element for CBC in tomato protected crops in NE Spain.

398 Historical data confirmed that the main predator observed in the 5-year records was *M.*
399 *pygmaeus* as it is usual in the area (e.g Castañé *et al.*, 2004). While meteorological factors -
400 accumulated degree days above 10 °C (DD₁₀) and winter rainfall - partly explained yearly
401 patterns in colonisation, it was the identity of the greenhouse that explained most of the
402 variation in colonisation precocity by *M. pygmaeus*. Data sustained the idea that colonisation
403 precocity of a particular greenhouse was consistent across years. Overall models showed no
404 significant effects of greenhouse characteristics on *M. pygmaeus* colonisation precocity,
405 whereas Aviron *et al.* (2016) detected strong effects of greenhouse crop management. This
406 suggests that the greenhouses in the current study had relatively homogeneous crop practices
407 resulting from the recommendations of a unique plant protection advisor, using practically no
408 pesticides before mirid colonisation, while the former work compared greenhouses following a
409 broad spectrum of practices grouped into organic vs. conventional. In addition, while the
410 present study focused mainly on the first detection of predators in the crop as a proxy for
411 colonisation, Aviron *et al.* (2016) focused on accumulated abundance which would potentially
412 reflect in turn the cumulative crop protection practices in each greenhouse.

413 Colonisation precocity by *M. pygmaeus* in a greenhouse was best explained by the interactive
414 effect of herbaceous semi-natural cover at the landscape scale and the use of *Calendula* as
415 banker plant inside the greenhouses. Herbaceous cover enhanced the early arrival of *M.*
416 *pygmaeus* adults to tomato crops in greenhouses without banker plants. These results are
417 consistent with the study in SE France where greater abundances of this mirid species were
418 observed in those greenhouses associated with greater fallow area (Aviron et al. 2016). The
419 habitat cover type categorized as herbaceous semi-natural in this work comprises the continuum
420 between semi-natural vegetation to non-cultivated former agricultural fields where ruderal
421 vegetation predominates. When *Calendula* banker plants were used, the colonisation precocity
422 of *M. pygmaeus* was independent of the abundance of herbaceous semi-natural cover at the
423 landscape scale. This was a result of banker plants encouraging early colonisation in those
424 greenhouses associated to small amounts of herbaceous semi-natural habitat. These findings
425 agree with previous work in open agriculture and flower strip planting that indicate that

426 landscapes which have experienced greater damage from agricultural intensification have more
427 to gain from habitat management practices (Thies and Tschardtke 1999; Haenke et al. 2009;
428 Jonsson et al. 2015).

429 Banker plants can potentially be as effective as inoculative releases in delivering *M. pygmaeus*
430 to tomato crops. Predatory *M. pygmaeus* have been reported to move from *Calendula* banker
431 plants to tomato in a continuous flux of individuals 1.6 adults/m² every 3 days at an average
432 planting of 4 tomatoes/m² (Agustí *et al.*, 2020). This represents densities consistent with the
433 ranges of recommended commercial releases (0.25-0.5 adults/m² every 1-2 weeks for a total of
434 2-4 releases) (Moerkens et al. 2017). Promising results about the colonisation of tomato
435 greenhouses by *M. pygmaeus* were also obtained using *Ballota hirsuta* Benth (Lamiaceae) as
436 banker plants in SE Spain (Sanchez et al. 2020). In this study, the highest colonisation of tomato
437 greenhouses by *M. pygmaeus* and pest control was obtained when *B. hirsuta* plants were
438 deployed for 30 days as opposed to 1 day, as greater amount of founder *M. pygmaeus*
439 individuals in tomato contributed to greater predator growth rates (Sanchez et al. 2020).
440 Collectively these results indicate that the permanent establishment of banker plants in tomato
441 greenhouses actively promotes early colonisation of the crop by *M. pygmaeus*, and this effect
442 will be more notorious in greenhouses with limited spontaneous colonisation e.g. embedded in
443 landscapes with small amount of herbaceous semi-natural habitat.

444 Another important aspect to be considered when studying the establishment of mirid bugs in a
445 greenhouse is the distribution of colonisation sources within a greenhouse (e.g openings and
446 banker plants) and how do predators distribute in the crop (Alomar et al. 2002; Gabarra et al.
447 2004). In a field study, Alomar *et al.*, (2002) showed that adult *M. pygmaeus* were more
448 abundant in outer tomato rows, particularly in fields with close predator host plant sources;
449 while later in the season predator nymphs were distributed following adult predator or prey
450 spatial pattern. The dispersal of commercial *M. pygmaeus* adults within a tomato greenhouse
451 has been estimated to be <3 m from the release plant (Moerkens et al. 2017). Therefore, *M.*
452 *pygmaeus* seem to exhibit a limited dispersal within the crop despite their ability to colonise
453 tomato from semi-natural habitats present at < 300 m (this study; Aviron *et al.*, 2016), which
454 can be related to their ability to persist in low prey patches (Montserrat et al. 2004). In order to
455 overcome this limitation and ensure a quick and even distribution of this predator in a
456 greenhouse, banker plants should be ideally placed evenly spaced between tomato rows at 5m
457 intervals (Moerkens *et al.*, 2017; Agustí *et al.*, 2020). However some caution is needed in the
458 use of *C. officinalis* as a banker plant, since they are also hosts of *N. tenuis*, which has been
459 shown to produce damage to tomato plants in some circumstances (Sanchez 2008; Calvo et al.
460 2009; Arnó et al. 2010). Given that the relative abundance of *N. tenuis* over *M. pygmaeus* has

461 increased in tomato crops in the area of study in the last years (RG, JA, J. Riudavets
462 unpublished data), banker plants should be closely monitored during the season, and plant
463 protection decisions on *Calendula* banker plant management will need to be taken on a per-
464 greenhouse basis.

465 Apart from *C. officinalis*, other host plant species identified in this work and previous research
466 (Alomar et al. 2002; Ingegno et al. 2009, 2011; Lambion 2014) can be favoured at the farm
467 scale to sustain mirid populations through their life cycle. Although results reported in this work
468 show that adjacent vegetation does not seem to be a major factor on *M. pygmaeus* colonisation
469 in tomato greenhouses compared to stronger landscape and banker plant effects, host plant
470 species richness can potentially provide insurance habitats to natural enemies at the farm scale
471 (Tscharrntke et al. 2007). For example these plants could constitute a refuge for mirid predators
472 in agricultural intensive landscapes where crops with a high pressure of chemical sprayings, like
473 orchards, are common (Aviron et al. 2016; Ricci et al. 2019; Clemente-Orta et al. 2020); and
474 could act as a host “stepping stone” after the spring crop and contribute predators to adjacent
475 open tomato crops later in the season.

476 Our findings provide insight into the local and landscape factors driving mirid colonisation in
477 tomato greenhouses in NE Spain. This study demonstrates the importance of herbaceous semi-
478 natural habitats and the use of *Calendula* banker plants in promoting *M. pygmaeus* colonisation.
479 Most importantly, results show that farmers with greenhouses surrounded by lower proportion
480 of herbaceous semi-natural habitats can promote early *M. pygmaeus* colonisation of tomato
481 through active habitat management by using banker plants. The use of banker plants in a farm is
482 in control of the producer, as opposed to landscape management, and therefore it has the
483 potential to become a key CBC strategy for protected tomato crops. Yet, both habitat
484 management in farms by means of host plants and the conservation of semi-natural habitats
485 beyond those individual farms might be needed to ensure that natural enemies persist over time
486 (Schellhorn et al. 2015; Tooker et al. 2020), and for CBC to become a reliable crop protection
487 strategy. Further research is needed to test how host plant conservation strategies can be used at
488 the farm scale to facilitate timely colonisation of tomato and other crops by natural enemies
489 through the farm’s crop cycles.

490

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631

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638 **Conflicts of interest/Competing interests**

639 None

640 **Ethics approval**

641 Not applicable

642 **Availability of data and material**

643 Available from corresponding author and available in Dryad id manuscript is accepted.

644 **Code availability**

645 Not applicable

646 **Authors' contributions**

647 AA, RG, RA, JA and OA conceived and designed research. NA optimized molecular
648 identification of *Macrolophus* species. AA and MF conducted experiments. MM contributed
649 with historical data collected as plant protection adviser and facilitated AA and MF access to
650 commercial greenhouses. RG supervised MF's Master Thesis. AA extracted historical data,
651 analysed data. AA wrote the first draft of this paper and edited it based on significant comments
652 from RA, JA, OA, NA and RG. All authors read, improved and approved the manuscript.

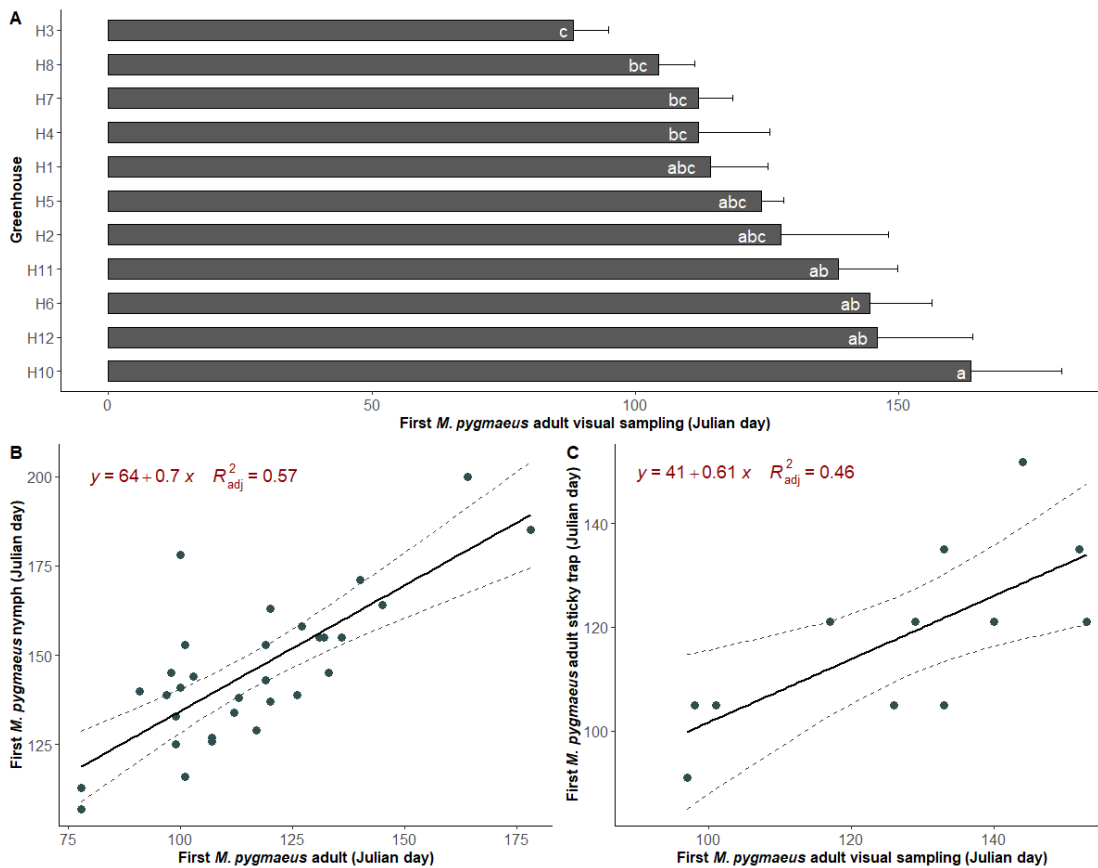
653

654 Table 1. Characteristics of the 12 greenhouses sampled to study mirid colonization in tomato
 655 crops.

ID	Structure	Openings	Transplant	Crop diversity	Tomato varieties	Altitude	Area (m²)
H1	metal	zenital	8/2	tomato	one	>50m	4198
H2	wood	zenital/lateral	15/2	mixed	one	sea level	3846
H3	metal	zenital/lateral	25/2	mixed	more	>50m	2491
H4	wood	lateral	3/3	mixed	more	sea level	1729
H5	wood	lateral	1/3	tomato	more	sea level	1323
H6	metal	zenital	3/4	mixed	more	>50m	3266
H7	metal	zenital/lateral	8/3	mixed	more	>50m	3079
H8	metal	zenital	6/3	mixed	one	sea level	1570
H9	metal	zenital	1/3	tomato	more	sea level	5972
H10	wood	lateral	11/2	tomato	one	sea level	1608
H11	wood	lateral	15/3	tomato	one	>50m	1985
H12	metal	zenital	23/2	tomato	one	sea level	2387

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659 Fig 1. A) Day of the first *M. pygmaeus* adult detected (+SE) on tomato greenhouses in 5 consecutive
 660 seasons. Different letters indicate significant differences between groups (Tukey post-hoc test with
 661 Bonferroni correction, $P < 0.05$). B) Relationship between the day of the first *M. pygmaeus* nymph
 662 detection with the day of the first adult detection by visual sampling. Data in which nymphs were
 663 recorded before or on the same day as adults have been removed. C) Relationship between the first
 664 detection of *M. pygmaeus* in the greenhouse when two different sampling methodologies were used in
 665 one sampling season: visual sampling and yellow sticky trap sampling. In all cases the first detection of
 666 *M. pygmaeus* is expressed as Julian days. The dashed lines represent 95% confidence limits.

Table 2. Summary of the number of mirids recovered from beat sheet sampling in (a) vegetation adjoining tomato greenhouses and (b) *Calendula* banker plants inside the greenhouses (when present). Greenhouses are numbered according to the total *Macrolophus* spp. recovered from the adjoining vegetation. In (a) *Macrolophus* spp. are divided into those recovered from *C. officinalis* and from other host plants. A plant taxa is considered as host when both adults and nymphs of a mirid species were recovered (includes host plants from all mirid species). The list of host plants adjacent to each of the greenhouses can be found in Supplementary material Table S1. Also in (a), the mirid host plant richness and their abundance in the adjoining vegetation is shown. Richness refers to the number of host plant species present in the adjacent vegetation of each greenhouse. Points with host plant presence refers to the number of sampling points with confirmed host plants around the greenhouse perimeter. Potential points refers to the potential sampling points at 10m intervals based on the greenhouse perimeter. *Data on *Dicyphus* spp. includes *D. bolivari* and *D. errans*.

		Greenhouse ID											
a) Adjoining vegetation		H1	H2	H3	H4	H5	H6	H7	H8	H9	H10	H11	H12
Macrolophus spp.	Total	175	145	52	28	12	12	7	3	1	0	0	0
	<i>C. officinalis</i>	150	145	0	0	0	0	0	0	0	0	0	0
	Other host plants	25	0	52	28	12	12	7	3	1	0	0	0
Other mirids	<i>Dicyphus</i> spp.*	15	9	28	0	1	7	0	0	0	0	0	0
	<i>N. tenuis</i>	0	3	0	0	0	0	0	0	0	8	0	0
Host plant (HP)	Richness	8	2	9	3	2	3	5	7	2	0	0	0
	Points with HP presence	9	17	23	18	4	16	6	9	1	0	0	0
	Potential points	36	31	32	25	22	30	28	23	41	22	26	28
b) Banker plants													
Macrolophus spp.	Total	157	177					324				52	25
Other mirids	<i>Dicyphus</i> spp.*							4				38	1

N. tenuis

1

0

0

15

6

Table 3. Total number of *Macrolophus* spp. and *Dicyphus bolivari* individuals per host plant taxa obtained from beat sheet samples in vegetation surrounding tomato greenhouses. The total number of *M. pygmaeus* and *M. melanotoma* identified by PCR from subsamples of each host plant is also shown. n = number of greenhouses with the host plant present in the adjoining vegetation.

Host plant	<i>Macrolophus</i> spp.					<i>Dicyphus bolivari</i>		
	n	Adults	Nymphs	<i>M. pygmaeus</i> (PCR)	<i>M. melanotoma</i> (PCR)	n	Adults	Nymphs
<i>Borago officinalis</i>	2	8	1	9		1		1
<i>Calendula arvensis</i>	3	7	5	10				
<i>Calendula officinalis</i>	5	122	255	15		4	5	30
<i>Dimorphoteca ecklonis</i>	1	4	18	9				
<i>Dittrichia viscosa</i>	1		2		2			
<i>Erodium</i> spp.	3	21	11	9		3	5	15
<i>Gallium</i> spp.	1	1						
<i>Lavandula</i> spp.	2	4	29	12	1			
<i>Leucanthemum</i> spp.						1		1
<i>Malva</i> spp.	1	1				2	5	4
<i>Parietaria</i> spp.	7	37	39	10		3	1	5
<i>Salvia officinalis</i>	1	8	29	10		1		2
<i>Sonchus</i> spp.	2	1	1					

Table 4. Estimates, confidence intervals (CI), AICc and model fit for the best models (with lowest AICc) with (a) colonization precocity and (b) abundance of *M. pygmaeus* in tomato greenhouses, and (c) the pest index at the end of the sampling period as dependent variables. All selected variables in the models are relevant as their CI do not overlap with 0. Colonization precocity is expressed as the sampling event in which the first *M. pygmaeus* adults were detected in each greenhouse by means of yellow traps, with smaller values representing early colonization.

	Selected Variables	Estimate	CI (2.5%)	CI (97.5%)	AICc	R²_{adj}/D²_a
					32.7	
a) Colonization precocity	Intercept	4.24	3.8	4.68	1	0.796
	PS250	-1.21	-1.66	-0.76		
	Cal	-0.87	-1.55	-0.19		
	PS250 × Cal	0.90	0.18	1.61		
					72.5	
b) Abundance	Intercept	1.42	0.84	1.98	6	0.712
	Precocity	-1.57	-2.23	-1.02		
					31.9	
c) Pest index tr	Intercept	-0.47	-0.85	-0.08	9	0.622
	Pest index t _c	1.12	0.55	1.7		
	Precocity	-0.65	-1.22	-0.07		

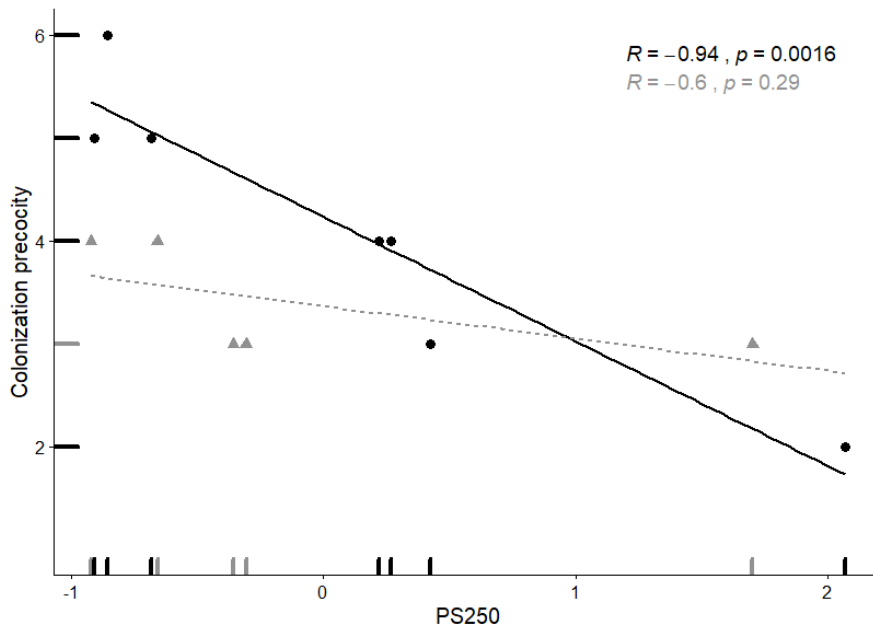


Fig. 2. Tomato greenhouse colonization precocity of the predator *M. pygmaeus* in relation to the herbaceous semi-natural cover at 250m scale (PS250). Colonization precocity is expressed as the sampling event in which the first *M. pygmaeus* adults were detected in each greenhouse by means of yellow traps, with smaller values representing early colonization. The grey dashed line represents the fit for greenhouses with *Calendula* banker plants (triangles); the black solid line represents the fit for those greenhouses without banker plants (circles). For both regressions, R represents the correlation between colonization precocity and herbaceous semi-natural vegetation at 250m scale, and p is the p-value of the correlation.

Supplementary material

Table S1. List of the host plant species of mirid predators adjoining to tomato greenhouses and their presence in the greenhouses sampled in this study. Two greenhouses (H10 and H11) are not included the identified host plants were not present in their surroundings. Greenhouses are ordered according to the number of host plants present, ranging from 10 (H3) to 1 (H12). * is only hosting *M. melanotoma* (Table 3). ^ is a potential host plant of *Macrolophus* spp. (molecular identification was not performed on those individuals).

Host plant species	Family	Type	Habit	H3	H1	H8	H7	H4	H6	H2	H5	H9	H12
<i>Borago officinalis</i>	Boraginaceae	Weed	annual	X	X		X						
<i>Calendula arvensis</i>	Asteraceae	Weed	annual		X		X		X				
<i>Calendula officinalis</i>	Asteraceae	Ornamental	perennial		X						X		
<i>Dimorphoteca ecklonis</i>	Asteraceae	Ornamental	perennial	X									
<i>Dittrichia viscosa</i> *	Asteraceae	Weed	perennial	X									
<i>Erodium</i> spp.	Geraniaceae	Weed	annual	X	X	X	X						
<i>Gallium</i> spp.	Rubiaceae	Weed	annual	X		X							
<i>Lavandula</i> spp.	Lamiaceae	Ornamental	perennial	X									
<i>Malva</i> spp.	Malvaceae	Weed	annual	X	X	X		X					
<i>Leucanthemum</i> spp.	Asteraceae	Ornamental	perennial			X							
<i>Parietaria</i> spp.	Urticaceae	Weed	perennial	X	X	X	X	X	X		X	X	
<i>Salvia officinalis</i>	Lamiaceae	Ornamental	perennial	X									
<i>Sonchus</i> spp.^	Asteraceae	Weed	annual	X	X	X		X	X	X	X	X	X

Fig S.1 Spearman correlations between landscape cover variables at the 250 m scale. IV: protected horticulture, CROP: open field agriculture, AG: riparian a, FO: forest semi-natural; PR: shrub semi-natural, PS: herbaceous semi-natural, URBAN: urban, SN: sum of all semi-natural covers (FO, PR, PS). Circle size and colour represent Spearman correlations with blue representing positive correlations and red negative correlations, all with $p < 0.05$ are highlighted with a *.

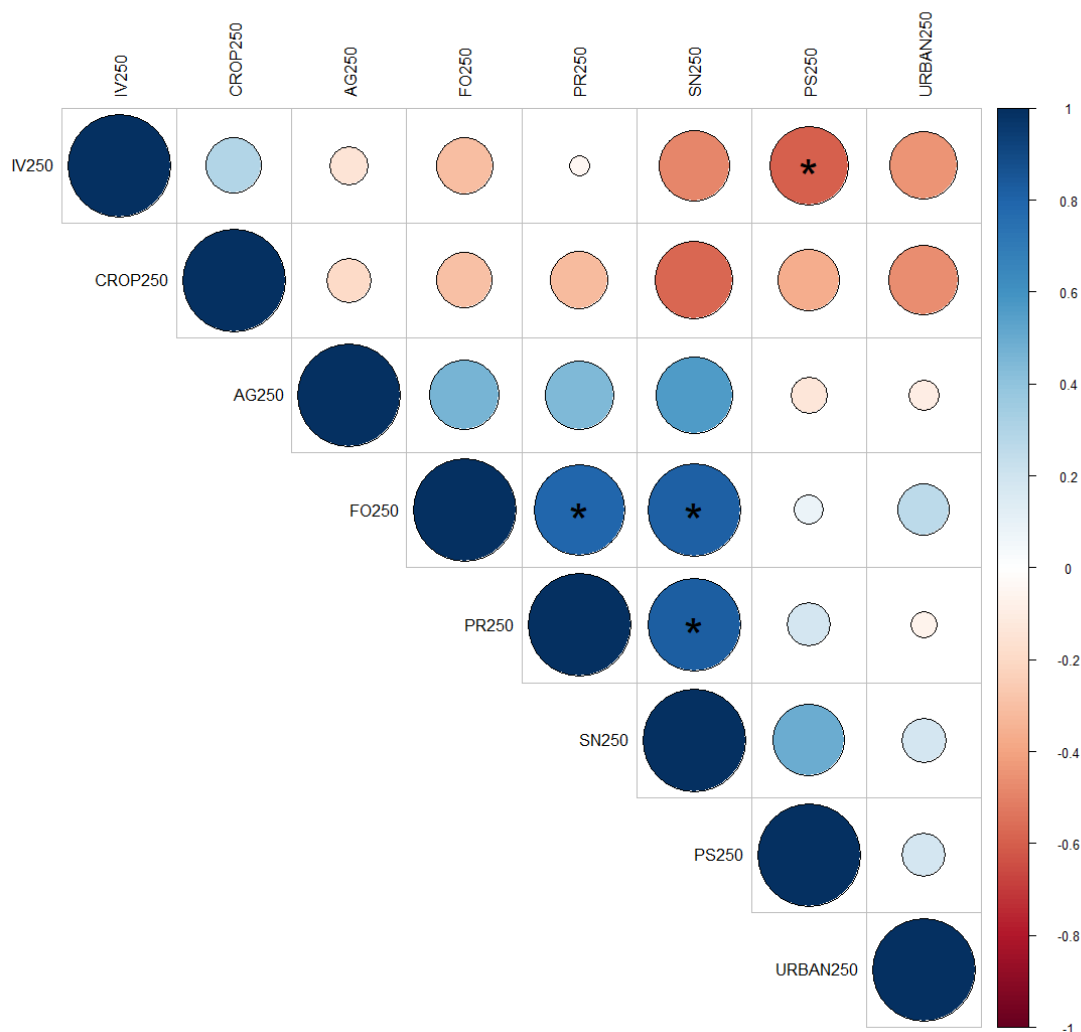


Fig S.2 Spearman correlations between landscape cover variables at the 150 m scale. IV: protected horticulture, CROP: open field agriculture, AG: riparian a, FO: forest semi-natural; PR: shrub semi-natural, PS: herbaceous semi-natural, URBAN: urban, SN: sum of all semi-natural covers (FO, PR, PS). Circle size and colour represent Spearman correlations with blue representing positive correlations and red negative correlations, all with $p < 0.05$ are highlighted with a *.

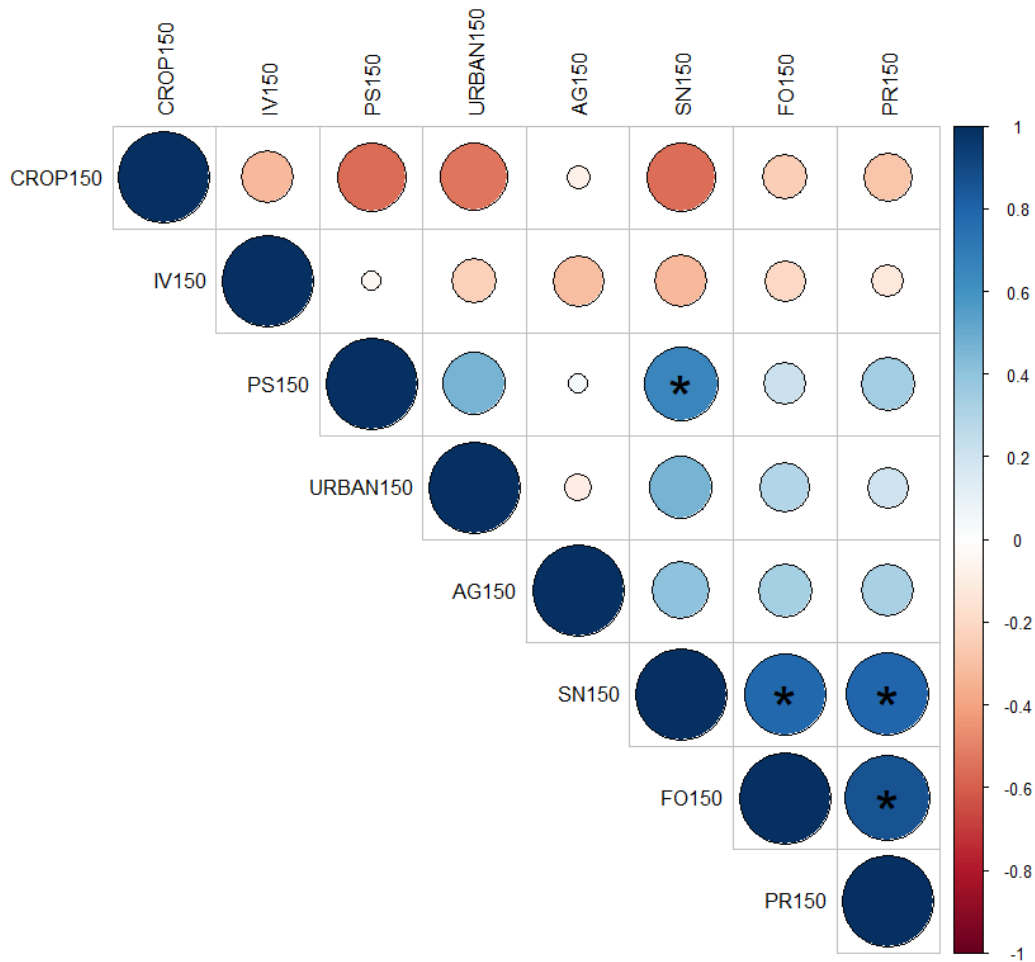


Fig S.3. Spearman correlations between numerical habitat management variables. These variables were obtained by adjoining vegetation sampling in each greenhouse (Table 2). Mp: number of *M. pygmaeus* captures in adjacent vegetation, Mp_noCal: number of *M. pygmaeus* captures in adjacent vegetation excluding *Calendula officinalis* plants, Nt: number of *N. tenuis* captures in adjacent vegetation, Dt: number of *D. bolivari* captures in adjacent vegetation, Total_points: number of points of adjacent vegetation sampled in 10 m intervals surrounding the greenhouse, HostR: mirid host plant richness in adjacent vegetation, Points_HostPI: Points with host plant presence, refers to the number of sampling points with confirmed host plants around the greenhouse perimeter. Circle size and colour represent Spearman correlations with blue representing positive correlations and red negative correlations, all with $p < 0.05$ are highlighted with a *.

