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

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

Keywords Tomato · Colonisation · Banker plants · Landscape · *Macrolophus* · Biological control

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

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

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

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

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

To date, only one study to our knowledge has studied the effects of landscape composition and configuration on mirid predator populations in protected tomato crops (Aviron et al. 2016). Key findings showed greater levels of M. pygmaeus colonisation in greenhouses embedded in landscapes with larger fallow area, while colonisation was reduced in greenhouses associated with larger orchard area at the landscape scale. Yet, these landscape effects on mirid colonisation were smaller than management practices associated with organic and conventional agriculture. Further research is needed to understand the relative importance of habitat management practices, e.g. presence of banker plants and other crops and non-crop host plants (Thomine et al. 2020), and the landscape context on CBC by mirid predators in protected tomato crops.

This study aims to identify which greenhouse characteristics, habitat management practices and landscape features favour an early colonisation of protected tomato crops by mirid predators and their establishment. We hypothesised that (1) mirid predator colonisation precocity is stable through time for each of the studied greenhouses, e.g. showing consistently early vs late colonisation; (2) larger proportion of semi-natural non-crop cover at the landscape scale enhance mirid colonisation by promoting spillover to tomato crops early in spring; and (3) greenhouse habitat
management practices, using *Calendula* banker plants inside the greenhouse and/or by maintaining diverse host plants at the farm scale, favour early colonisation of tomato greenhouses by mirid bugs.

### Methods

#### Study site and greenhouse selection

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

#### Historical data collection

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

#### Arthropod sampling in tomato greenhouses

Tomato greenhouses were sampled every other week with yellow sticky traps from mid-March to mid-June, with the intention to detect the arrival of mirid bugs in each greenhouse and estimate the amount of prey present.

| ID | Structure | Openings | Transplant | Crop diversity | Tomato varieties | Altitude | Area (m²) |
|----|-----------|----------|------------|----------------|------------------|----------|-----------|
| H1 | Metal     | Zenital  | 8/2        | Tomato         | One              | > 50 m   | 4198      |
| H2 | Wood      | Zenital/lateral | 15/2 | Mixed | One | Sea level | 3846 |
| H3 | Metal     | Zenital/lateral | 25/2 | Mixed | More | > 50 m | 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             | > 50 m   | 3266 |
| H7 | Metal     | Zenital/lateral | 8/3 | Mixed | More | > 50 m | 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              | > 50 m   | 1985 |
| H12| Metal     | Zenital  | 23/2       | Tomato         | One              | Sea level | 2387 |
Greenhouses were sampled five times during this period, with the exception of two greenhouses that were only sampled four times because of delayed transplanting. Yellow sticky traps (31 × 21 cm, Entomopraxis, Barcelona, Spain) were attached to wooden sticks and placed between tomato plants along the crop rows. Trap height was adjusted to be at the same level as the top of the plant canopy at the early stages of tomato growth, and at 1.20 m in full grown plants. Nine yellow sticky traps were used per greenhouse and sampling date and were evenly distributed in the greenhouse to cover its surface. Sticky traps were recovered one week later. Traps were then covered by plastic film and placed in a cold climatic chamber (4 ºC) until processed. Mirid predator species and key pest groups (whiteflies, aphids, leafmining Diptera and thrips) were later identified to taxonomic units and counted. Colonisation precocity was determined as the number of sampling event in which the first mirid was captured, e.g. if a mirid predator was first detected on the third sampling event the colonisation precocity of the greenhouse was assigned to three.

| Greenhouse ID | H1 | H2 | H3 | H4 | H5 | H6 | H7 | H8 | H9 | H10 | H11 | H12 |
|---------------|----|----|----|----|----|----|----|----|----|-----|-----|-----|
| (a) Adjoining vegetation | | | | | | | | | | | | |
| _Macrolophus_ spp. | 175 | 145 | 52 | 28 | 12 | 12 | 7 | 3 | 1 | 0 | 0 | 0 |
| Total | 150 | 145 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| C. officinalis | 25 | 0 | 52 | 28 | 12 | 12 | 7 | 3 | 1 | 0 | 0 | 0 |
| Other host plants | 15 | 9 | 28 | 0 | 1 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| Host plant (HP) | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 |
| 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. | 157 | 177 | | | | | | 324 | 52 | 25 |
| Total | 4 | 38 | 1 | | | | | | | |
| _Dicophus_ spp.* | 1 | 0 | | | | | | 0 | 15 | 6 |
| _N. tenuis_ | | | | | | | | | | | | |

*Data on _Dicyphus_ spp. include _D. bolivari_ and _D. errans_

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

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

**Macrolophus** spp. molecular identification

Two sympatric *Macrolophus* species present in the area, *M. pygmaeus* and *M. melanotoma*, (Costa) have a great morphological similarity and have often been confused (Perdikis et al. 2003; Martinez-Cascales et al. 2006; Castañé et al. 2013). Yet only *M. pygmaeus* is known to establish on tomato crop; for this reason, we used molecular markers to distinguish the two *Macrolophus* species and to find out to what extent both species coexisted on the sampled non-crop host plants. Subsamples of adult and nymphs of *Macrolophus* spp. specimens collected in each host plant were identified using conventional PCR using the specific primers Mp1F (5′-GTAACAATAGATAAATCCCATTTC-3′)—Mp4R.2 (5′-CCTAATAATTGGTTCTCACA-3′) for *M. pygmaeus*, and Mm1F (5′-CTTCTTGATGCCCTTTATTTGTGCC-3′)—Mm3R (5′-TTATCCTACTATGTAGTCTCGTTA TT-3′) for *M. melanotoma*. These primers were previously described in Castañé et al. (2013), with the exception of Mp4R.2, which is a modification of Mp4R described there. Individual insects were DNA extracted using the SpeedTools Tissue DNA Extraction Kit (BioTools; Madrid, Spain) following the manufacturer’s protocol. PCRs were conducted as described in Castañé et al. (2013). Target DNA (*M. pygmaeus* and *M. melanotoma*) and water were always included as positive and negative controls, respectively. Resulting PCR products were separated by electrophoresis in 3.5% agarose gels, stained with ethidium bromide and visualised under UV light. The number of individuals analysed per host plant species varied from 9 to 15 (Table 3).

**Landscape cover characterisation**

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

**Statistical analysis**

Historical data were used to establish the importance of yearly variation and greenhouse identity on predator colonisation precocity, and the relationship of this precocity with their establishment in tomato greenhouses. First, a linear model was fitted with log-transformed *M. pygmaeus* precocity (expressed as Julian day) as dependent variable and the year, greenhouse, transplant date and their interaction as independent variables. Then, meteorological variables were used to explore whether they could help explain the yearly variation in colonisation by replacing factor year in the previous model by the variables spring accumulated degree days (DD10) and accumulated winter–spring rainfall. Pair-wise comparisons were evaluated with Tukey’s post hoc test with Bonferroni correction. Second, a linear model was fitted with log-transformed *M. pygmaeus* nymph detection date as dependent variable and adult *M. pygmaeus* precocity as explanatory variable. In order to do that, data points where nymphs were detected before adults were excluded from analysis.

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

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

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

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

Results

Historical mirid colonisation and establishment

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

Linear models showed that greenhouse identity ($F_{10,41} = 4.66, p < 0.0001$) was the main effect accounting for early colonisation of tomato crops by *M. pygmaeus* together with DD$_{10}$ ($F_{1,39} = 4.94, p = 0.02$) and accumulated spring rainfall ($F_{1,39} = 3.74, p = 0.03$), with a $R^2_{\text{adj}} = 0.51$ and lowest AICc (−14.96). Models including estimated tomato transplant date had greater AICc values and were less parsimonious. The combination of the meteorological predictors explained better the seasonal variation in predatory mirid colonisation than the factor year. Colonisation precocity by *M. pygmaeus* differed between greenhouses (Fig. 1a), with greenhouses H3 and H10 representing the early (mid-March) and late (mid-May) colonisation extremes, respectively. In general, years with warm and wet winter and spring seasons showed earlier colonisation of protected tomato crops by *M. pygmaeus* than colder and drier years.

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

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

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

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

Landscape and greenhouse management effects on mirid colonisation and pest abundance

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

Colonisation precocity by *M. pygmaeus* was dependent on both the amount of herbaceous semi-natural cover at the 250 m buffer around greenhouses (PS250) and the presence of *Calendula* banker plants (Cal) inside the greenhouses, as shown by the interaction of the two predictors (Table 4). In general, greater amounts of herbaceous semi-natural cover favoured early colonisation of tomato greenhouses by *M. pygmaeus*; while the use of *Calendula* banker plants inside the greenhouses attenuated the negative effects of the low proportion of surrounding favourable habitats by promoting early colonisation of the tomato crop (Fig. 2). Landscape variables at 150 m performed worse than those at 250 m and hence were not included in the best or competing models. Likewise, no other greenhouse characteristics or habitat management variables, apart from *Calendula* banker plant presence (Cal), were included in the best or competing models.

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

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**Fig. 1** a Day of the first *M. pygmaeus* adult detected (+ SE) on tomato greenhouses in five consecutive seasons. Different letters indicate significant differences between groups (Tukey post hoc test with Bonferroni correction, $P<0.05$). b Relationship between the day of the first *M. pygmaeus* nymph detection and the day of the first adult detection by visual sampling. Data in which nymphs were recorded before or on the same day as adults have been removed. c Relationship between the first detection of *M. pygmaeus* in the greenhouse when two different sampling methodologies were used in one sampling season: visual sampling and yellow sticky trap sampling. In all cases, the first detection of *M. pygmaeus* is expressed as Julian days. The dashed lines represent 95% confidence limits.
indicating a negative relationship between pest index and M. pygmaeus precocity.

**Discussion**

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

| Selected variables | Estimate | CI (2.5%) | CI (97.5%) | AICc | $R^2_{adj}/D^2_{adj}$ |
|-------------------|----------|-----------|------------|------|------------------------|
| a) Colonisation precocity | | | | | |
| Intercept | 4.24 | 3.8 | 4.68 | 32.71 | 0.796 |
| PS250 | −1.21 | −1.66 | −0.76 | | |
| Cal | −0.87 | −1.55 | −0.19 | | |
| PS250 × Cal | 0.90 | 0.18 | 1.61 | | |
| b) Abundance | | | | | |
| Intercept | 1.42 | 0.84 | 1.98 | 72.56 | 0.712 |
| Precocity | −1.57 | −2.23 | −1.02 | | |
| c) Pest index $t_c$ | | | | | |
| Intercept | −0.47 | −0.85 | −0.08 | 31.99 | 0.622 |
| Pest index $t_c$ | 1.12 | 0.55 | 1.7 | | |
| Precocity | −0.65 | −1.22 | −0.07 | | |
general, greater amounts of herbaceous semi-natural cover at
the landscape scale promoted *M. pygmaeus* colonisation of
tomato greenhouses; however, the use of *Calendula* banker
plants encouraged *M. pygmaeus* colonisation independently
of the abundance of herbaceous semi-natural cover. Early
colonisation of greenhouses by mirid predators also trans-
lated into lower accumulated incidence of pests and there-
fore potentially into a lower likelihood of pesticide appli-
cation later in the season (Li et al. 2020). These findings
encourage the use of banker plants as a key element for CBC
in tomato-protected crops in NE Spain.

Historical data confirmed that the main predator observed
in the 5-year records was *M. pygmaeus* as it is usual in the
area (e.g. Castañé et al. 2004). While meteorological fac-
tors—accumulated degree days above 10 °C (DD_{10}) and
winter rainfall—partly explained yearly patterns in coloni-
sation, it was the identity of the greenhouse that explained
most of the variation in colonisation precocity by *M. pyg-
maeus*. Data sustained the idea that colonisation precocity of
a particular greenhouse was consistent across years. Overall,
models showed no significant effects of greenhouse charac-
teristics on *M. pygmaeus* colonisation precocity, whereas
Aviron et al. (2016) detected strong effects of greenhouse
crop management. This suggests that the greenhouses in the
current study had relatively homogeneous crop practices
resulting from the recommendations of a unique plant pro-
tection advisor, using practically no pesticides before mirid
colonisation, while the former work compared greenhouses
following a broad spectrum of practices grouped into organic
vs. conventional. In addition, while the present study focused
mainly on the first detection of predators in the crop as a
proxy for colonisation, Aviron et al. (2016) focused on ac-
cumulated abundance which would potentially reflect in turn
the cumulative crop protection practices in each greenhouse.

Colonisation precocity by *M. pygmaeus* in a greenhouse
was best explained by the interactive effect of herbaceous
semi-natural cover at the landscape scale and the use of
*Calendula* as banker plant inside the greenhouses. Herba-
ceous cover enhanced the early arrival of *M. pygmaeus* adults
to tomato crops in greenhouses without banker plants. These
results are consistent with the study in SE France where
greater abundances of this mirid species were observed in
those greenhouses associated with greater fallow area (Avi-
ron et al. 2016). The habitat cover type categorised as her-
baceous semi-natural in this work comprises the continuum
between semi-natural vegetation to non-cultivated former
agricultural fields where ruderal vegetation predominates.
When *Calendula* banker plants were used, the colonisation
precocity of *M. pygmaeus* was independent of the abundance
of herbaceous semi-natural cover at the landscape scale. This
was a result of banker plants encouraging early colonisa-
tion in those greenhouses associated with small amounts of
herbaceous semi-natural habitat. These findings agree with
previous work in open agriculture and flower strip planting
that indicate that landscapes which have experienced greater
damage from agricultural intensification have more to gain
from habitat management practices (Thies and Tscharntke
1999; Haenke et al. 2009; Jonsson et al. 2015).

Banker plants can potentially be as effective as inocula-
tion releases in delivering *M. pygmaeus* to tomato crops.
Predatory *M. pygmaeus* have been reported to move from
*Calendula* banker plants to tomato in a continuous flux of
individuals 1.6 adults/m² every 3 days at an average plant-
ing of four tomatoes/m² (Agustí et al. 2020). This repre-
sents densities consistent with the ranges of recommended
commercial releases (0.25–0.5 adults/m² every 1–2 weeks
for a total of 2–4 releases) (Moerkens et al. 2017). Prom-
is ing results about the colonisation of tomato greenhouses
by *M. pygmaeus* were also obtained using *Ballota hirsuta*
Benth (Lamiaceae) as banker plants in SE Spain (Sanchez
et al. 2020). In this study, the highest colonisation of tomato
greenhouses by *M. pygmaeus* and pest control was obtained
when *B. hirsuta* plants were deployed for 30 days as opposed
to 1 day, as greater amount of founder *M. pygmaeus*
individuals in tomato contributed to greater predator growth
rates (Sanchez et al. 2020). Collectively these results indi-
cate that the permanent establishment of banker plants in
tomato greenhouses actively promotes early colonisation of
the crop by *M. pygmaeus*, and this effect will be more notori-
ous in greenhouses with limited spontaneous colonisation,
e.g. embedded in landscapes with small amount of herba-
ceous semi-natural habitat.

Another important aspect to be considered when studying
the establishment of mirid bugs in a greenhouse is the distribu-
tion of colonisation sources within a greenhouse (e.g. open-
ings and banker plants) and how do predators distribute in the
crop (Alomar et al. 2002; Gabarra et al. 2004). In a field study,
Alomar et al. (2002) showed that adult *M. pygmaeus* were more
abundant in outer tomato rows, particularly in fields with close
predator host plant sources, while later in the season predator
nymphs were distributed following adult predator or prey spa-
tial pattern. The dispersal of commercial *M. pygmaeus* adults
within a tomato greenhouse has been estimated to be <3 m
from the release plant (Moerkens et al. 2017). Therefore,
*M. pygmaeus* seem to exhibit a limited dispersal within the crop
despite their ability to colonise tomato from semi-natural habi-
tats present at <300 m (this study; Aviron et al. 2016), which
can be related to their ability to persist in low prey patches
(Montserrat et al. 2004). In order to overcome this limitation
and ensure a quick and even distribution of this predator in a
greenhouse, banker plants should be ideally placed evenly
spaced between tomato rows at 5-m intervals (Moerkens et al.
2017; Agustí et al. 2020). However, some caution is needed in
the use of *C. officinalis* as a banker plant, since they are also
hosts of *N. tenuis*, which has been shown to produce dam-
age to tomato plants in some circumstances (Sanchez 2008;
Calvo et al. 2009; Arnó et al. 2010). Given that the relative abundance of *N. tenuis* over *M. pygmaeus* has increased in tomato crops in the area of study in the last years (RG, JA, J. Riudavets unpublished data), banker plants should be closely monitored during the season, and plant protection decisions on *Calendula* banker plant management will need to be taken on a per-greenhouse basis.

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

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

**Authors’ contributions**

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

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**Declarations**

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