Selecting native perennial plants for ecological intensification in Mediterranean greenhouse horticulture

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Abstract

Natural control by predators and parasitoids provides an important and often unnoticed ecosystem service to agricultural landscapes by reducing pest populations in crops. The current model of horticultural intensification in south-eastern Spain produces high yields but has also resulted in a landscape almost completely covered by plastic. Promoting natural areas among greenhouses could enhance biodiversity, by being beneficial insects, and reduce pest pressure outdoors. The first step is to ascertain how pests and their natural enemies (NEs) use Mediterranean vegetation for selecting the best plants for pest suppression outdoors. The abundance of the two major horticultural pests, the tobacco whitefly, *Bemisia tabaci*, and the western flower thrips, *Frankliniella occidentalis*, together with their NEs, were assayed in 22 flowering perennial plants, which were newly planted in an experimental field surrounded by greenhouses. Eight plant species were identified as the most critical species for sustaining pest populations outdoors. A set of five plant species supported a medium level of pests, and another set of ten plant species supported the lowest level of both pests. Tobacco whitefly occurred in a few plants species, whereas western flower thrips occurred on almost all the plant species studied, and was favoured by the presence of flowers in perennial plants. The results suggest that plant diversity may provide relatively few acceptable host plants for tobacco whitefly than for western flower thrips. NEs were generally collected in plants that also supported abundance of pests, indicating that host/prey availability, more than food resources from flowers, was a stronger predictor of NE abundance in perennial plants. Field trials using the plants with the lowest host acceptance by pests are needed in order to ascertain whether pest abundance outdoors is reduced.

Keywords: bottom–up effect, conservation biocontrol, western flower thrips, tobacco whitefly, top–down effect

Introduction

Ecological intensification seeks to increase crop productivity using ecological processes more intensively in a sustainable manner (Bommarco *et al.*, 2013). One way to maximize yield through ecological intensification is to promote biodiversity by maintaining natural habitats next to agricultural lands, thus providing ecosystem regulation such as pest control in the crops (Gaba *et al.*, 2014). For example, implementation of

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off-field measures such as hedgerows may encourage beneficial organisms within agroecosystems because of the resulting high biodiversity (Pollard & Holland, 2006; Hannon & Sisk, 2009; Batary et al., 2010; Moradin & Kremen, 2013; Haenke et al., 2014; Moradin et al., 2014; Park et al., 2015; Dainese et al., 2015, 2016). Biodiversity can enhance the survival of natural enemies (NEs) of pests and thereby improve their efficiency as pest-control agents by top–down effects, providing them with food (pollen, nectar and alternative prey) as well as favourable micro-climates (Landis et al., 2000; Bianchi et al., 2006). Top–down control can lead to a positive relationship between biodiversity and pest control when NEs complement each other (Letourneau et al., 2009). Greater plant species diversity may also be beneficial via a direct bottom–up effect on herbivores' ability to locate their host (Finch & Collier, 2000). However, although there is compelling evidence that diversified agroecosystems benefit pest control and yield (Thies & Tscharntke, 1999; Letourneau et al., 2009; Vandermeer et al., 2010; Burel et al., 2013; Woltz & Landis, 2014; Henri et al., 2015; Gurr et al., 2016), there are also examples where biodiversity fails to support biological pest control in crops. For instance, top–down control can be dampened by intra-guild predation or balanced by functional redundancy (Straub et al., 2008; Snyder & Tylianakis, 2012). In a recent study, Tscharntke et al. (2016) have identified five hypotheses for when and why a more natural habitat does not always lead to more beneficial insects and reduced pest populations. It maintains that some alternative management approaches on local scales (pesticide avoidance, implementing habitat patches, replacing invasive plants with native flora) as well as on a landscape scale (increasing habitat availability and crop diversity) may be bolster biocontrol.

The Mediterranean region of Europe, particularly the province of Almería in south-eastern Spain, has one of the largest concentrations of protected crop production in the world with around 30,000 ha of greenhouse vegetable production. This intensive horticulture creates a landscape characterized by crops under high pressure of pests and diseases (Glass & González, 2012), with non-crop areas dominated by non-native weedy species and little remaining native vegetation (Mendoza et al., 2015). The whitefly Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae), namely tobacco whitefly, and the thrips Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae), commonly known as western flower thrips are the most abundance insect pest species in this horticultural system. They are effective vectors of viruses and this is deemed the direst risk of these pests (Gilbertson et al., 2015). To encourage less insecticide use and promote non-chemical pest-management practices, the EU obliged all Member States to apply the general principles of integrated pest management (IPM) by 2014 (Directive 2009/128/EC). Adoption of IPM has been particularly successful in greenhouse horticulture of Almería, where IPM decreased the need for pesticides considerably through a greater reliance on commercial augmentative biological control, and managing pest pressure through cultural practices (Lozano et al., 2010; Pérez-Mesa & Galdeano-Gómez, 2010; Calvo et al., 2015). Therefore, in the current context of pesticides reduction, promoting specific habitats, with emphasis on planting hedgerows containing native perennial plants among greenhouses, may boost biodiversity, encouraging NEs and thus pest control.

Native perennial vegetation has demonstrated value in horticultural systems by showing less risk for hosting vegetable pests than non-native weedy plants, and by harbouring predators and parasitoids of pests (Rencken, 2006; Stephens et al., 2006; Fiedler & Landis, 2007a, b; Schellhorn et al., 2010; Bianchi et al., 2013). The native flora of Almería is typical of Mediterranean semi-arid environments and is rich in shrubs adapted to the harsh and variable climate (Mendoza et al., 2015). Similarly, terrestrial arthropod fauna in semi-arid areas of SE Spain are highly diverse (Piñero et al., 2011). The most suitable perennial plants for hedgerows among greenhouses have been already selected and include shrubs that have become commercially available. These include nectar- and pollen-rich species with overlapping bloom periods and varied habits (Rodríguez et al., 2012). On the other hand, previous results have demonstrated that the main viruses affecting greenhouse crops in Almería are not found on native perennial plants (Rodríguez et al., 2014). Thus, replacing non-native weeds by perennial plants may decrease the sources of viruses at a farming scale (Schellhorn & Bianchi, 2010). However, although biological control programmes have been successfully implemented in Almería horticulture, and perennial plants host fewer vegetable viruses, it remains unclear whether the selected shrubs for hedgerows may provide benefits to horticulture production in terms of pest suppression (top–down and bottom–up effects). It is unknown how pests and their NEs can use newly planted vegetation in highly simplified settings. Therefore, the aim of this study was to identify which perennial plants may harbour pests (tobacco whitefly and western flower thrips) and their NEs, in a set of Mediterranean shrubs newly planted within the greenhouse landscape. This knowledge is much in demand from growers and local authorities and it is a starting point for horticultural management aimed at natural pest prevention.

Material and methods

Site description

Field surveys were conducted in an experimental field at the Experimental Station 'Las Palmerillas', in the agricultural region of Almería Province, Spain (36°48′N, 2°3′W and ≈155 m a.s.l.). In December 2010, we established a semi-arid shrub patch (17 m × 10 m in size), that was hand weeded during the study, composed of 3-year-old individuals of 22 plant species pooled, belonging to 13 different botanical families. The experimental design included nectar-rich plants (eight species), pollen-rich plants (six species) and pollen- and nectar-rich plants (seven species) (table 1). The design was meant to simulate natural plant species associations in a spatially explicit semi-arid environment. Each plant species was replicated at a different ratio according to its size. This experimental field was located in the centre of the Campo de Dalías, which is the largest region of greenhouses in Europe and an area of year-round intensive horticulture. Since 2008, all the greenhouses in the experimental area were managed under an IPM regimen with emphasis on augmentative biological control, guaranteeing that native plant–arthropod interactions were not affected by the impact of pesticides.

Collecting pests and NEs

After 18 months, when the perennial plants were well established, the insects were sampled monthly in 162 plants from June 2012 to June 2013 at a patch scale (17 m × 10 m in size). The insects were collected by vacuuming each shrub for 40 s (Stihl® SH 85C), time enough to vacuum the entire

Table 1. Shrub species selected and sampled for habitat management in semi-arid Mediterranean greenhouse areas.

Food reward	Species assayed	Common name	Family	Plant code	Number assayed
Pollen	*Ephedra fragilis* Desf.	Joint pine	Ephedraceae	Ef	7
	Genista umbellata Poir.	Bolina	Fabaceae	Gu	7
	Macrochloa tenacissima (L.) Kunth	Alfa grass	Poaceae	Mt	9
	Myrtus communis L.	Myrtle	Myrtaceae	Mc	7
	Olea europaea var. *sylvestris* L.	Wild olive tree	Oleaceae	Oe	3
	Phillyrea angustifolia L.	False olive	Oleaceae	Pha	10
Nectar	*Dorycnium pentaphyllum* Scop.	Prostrate canary Clover	Fabaceae	Dp	6
	Lavandula latifolia Medik.	Spike lavender	Lamiaceae	Li	6
	Lycium intricatum Boiss.	Cambrón	Solanaceae	Li	4
	Phlomis purpurea L.	Purple phlomis	Lamiaceae	Pp	2
	Rosmarinus officinalis L.	Rosemary	Lamiaceae	Ro	25
	Thymus hyemalis Lange.	Winter thyme	Lamiaceae	Th	17
	Thymus vulgaris L.	Thyme	Lamiaceae	Tv	19
	Viburnum tinus L.	Laurustinus	Adoxaceae	Vt	4
Pollen/Nectar	*Anthyllis cytisoides* L.	Albaida	Fabaceae	Ac	2
	Crithmum maritimum L.	Rock samphire	Apiaceae	Cm	6
	Dittrichia viscosa (L.) Greuter	False yellowhead	Asteraceae	Dv	2
	Periploca angustifolia Labill.	Cornical	Asclepiadaceae	Pea	6
	Retama sphaerocarpa (L.) Boiss.	Yellow broom	Fabaceae	Rs	3
	Ricinus communis (L.)	Castor bean	Euphorbiaceae	Rc	1
	Rhamnus lycioides subsp. *lycioides* L.	Mediterranean buckthorn	Rhamnaceae	Rl	10
	Whitania frutescens (L.) Pauquy.	Oroval	Solanaceae	Wf	6

surface area of the shrub (Fiedler & Landis, 2007*a*). Insects from each shrub were collected in a fine mesh bag inserted into the vacuum nozzle. Bags were labelled and kept on ice until identification in the laboratory. Particularly, the pest species identified were the western flower thrips and the tobacco whitefly. As reproduction habitats can be identified by the presence of wingless and less mobile immature stages, and the feeding/resting habitats can be identified by the presence of mobile adults (Bianchi *et al.*, 2013), data from the pests were sorted into immature stages and adults. The major NEs identified included the whitefly parasitoid *Eretmocerus* ssp. (Hymenoptera: Aphelinidae), the whitefly predator *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae), the thrips parasitoid *Ceranisus* ssp. (Hymenoptera: Eulophidae) and the thrips predator *Orius* spp. (Hemiptera: Anthocoridae). Most of these, including *Eretmocerus* ssp., *N. tenuis* and *Orius* spp., are being mass reared and used for augmentative releases in the study area.

To assess whether seasonal abundance of pests in crops (indoors) was similar to that in perennial plants (outdoors), a comparison was made. The data from crops are shown as the percentage of plants damaged by western flower thrips and tobacco whitefly, and were provided by the Andalusia's Alert and Phytosanitary Information Network (RAIF). Particularly, the information used in this study refer to tomato, pepper, eggplant and cucumber grown in greenhouses that surrounded the experimental field during the sampling. A key point in this network is the availability of up-to-date real data, taken in the field on a regular basis by the agricultural technicians of the different associations (http://www.tragsa.es/_layouts/GrupoTragsa/Ficha-Proyecto.aspx?param=ENG.0000000187).

Flowering

To relate the occurrence of pests and NEs with plant-food resources, we assessed the flowering of each native plant each month of the sampling year (from June 2012 to June 2013),

with dates of day before arthropod collection. Flowering was calculated by estimating the overall flower abundance per plant (scale 0–1).

Data analysis

To assess differences in the abundance of the different insects, we first pooled all the data referring to a single plant of each species and then performed a generalized linear model with a Poisson error structure. Next, we analysed the results of the model outputs with a Tukey's *post hoc* evaluation to determine significant differences between the plant species tested. To separate the plants with a higher risk of harbouring pests from plants with a lower risk, we show significant differences from the Tukey's test only for those plants that surpassed the average pest abundance. A set of generalized linear mixed models were built to identify the resource (blooming or host) that best explained the abundance of pests and NEs in each plant species, as appropriate. For the two pests (tobacco whitefly and western flower thrips), we built the models by including as a fixed factor the plant species and their percentage of flowering. Sampling date was included as a random factor. A set of eight models was generated by combining fixed and random factors. For NEs, we built models in the same way as for pests but we included the variable prey representing the abundance of the above-mentioned pest species associated with their NE. Thus, for *N. tenuis* and *Eretmocerus* spp., we used the abundance of tobacco whitefly, and for *Orius* spp. and *Ceranisus* spp., we used the abundance of western flower thrips. Thus, for NEs, we generate 12 models by combining the fixed factors plant species, flowering and prey together with the random factor sampling date. Similarly, only the plants that showed higher abundance than the average established are shown.

We chose the model-selection procedure as an alternative to traditional hypothesis testing (Johnson & Omland, 2004; Canham & Uriarte, 2006). Alternative models were compared using the Akaike information criterion (AIC$_c$) corrected for
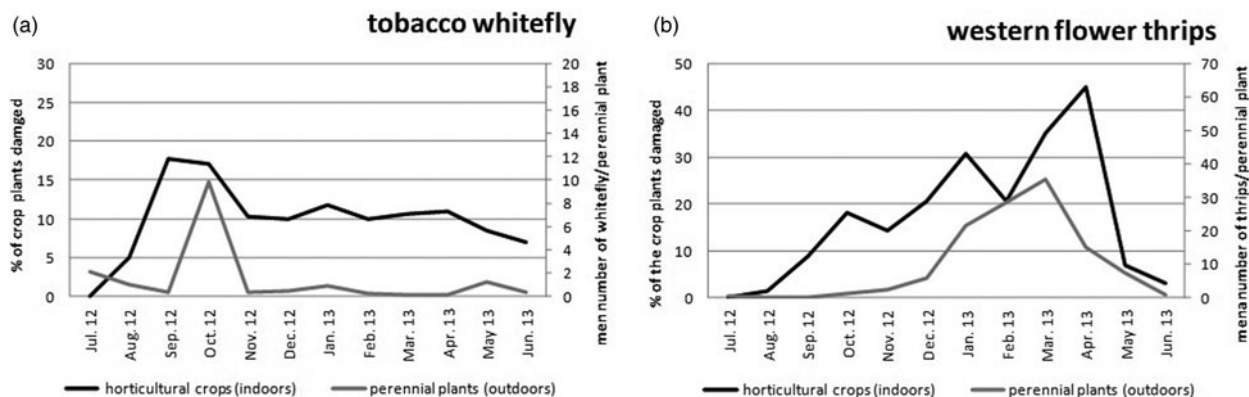
Fig. 1. Monthly mean numbers per perennial plant of the two major horticultural pests: tobacco whitefly (*Bemisia tabaci*) (a) and western flower thrips (*Frankliniella occidentalis*) (b), and percentage of the horticultural crop plants damaged during the growing season 2012/2013 in Almeria (south-eastern Spain).

small sample sizes (Burnham & Anderson, 2002). Models with a difference in $AIC_c > 2$ indicate that the worse model has virtually no support and can be omitted from further consideration. Models were tested for validation by analysing residuals using the DHARMa package (Hartig, 2016). For the best model, we calculated the R^2 to account for the variability supported by the best models. Two components of R^2 can be calculated for generalized linear mixed models: (1) a marginal R_m^2 that takes into account only the variability explained by fixed effects; and (2) a conditional R_c^2 that accounts for the variability supported by both the fixed and random effects (Nakagawa & Schielzeth, 2013). Analyses were made with the packages 'lme4' (Bates *et al.*, 2014) and 'multcomp' (Hothorn *et al.*, 2016) written for the R environment (R Development Core Team, 2014). Based on these two indicators, i.e. R^2 and DHARMa outputs, we chose those response variables to be considered for further discussion, as stated in the following section.

Results

Seasonal distribution of pests in horticultural crops (indoors) and in perennial plants (outdoors)

Tobacco whitefly and western flower thrips showed similar abundance patterns (fig. 1) in horticultural crops within greenhouses (indoors) and in perennial plants (outdoors). Particularly, tobacco whitefly abundance tended to be low in the perennial plants, registering a peak only in October with 9.9 whiteflies per plant. In crops, around 10% of the plants were damaged and the pest reached a peak of abundance with 18% of the plants damaged 1 month earlier than outdoors (fig. 1a). Therefore, the period when tobacco whitefly was present within the greenhouses was longer than outside (fig. 1a). The highest population of whitefly was recorded at 29.9°C indoors and 25.7°C outdoors for temperature, respectively. Western flower thrips gradually increased in abundance outdoors during late January, when temperatures were relatively low (12–13°C), peaking with 35.23 thrips per plant in late March with a considerable population decline throughout April and May. Within the greenhouses, where temperatures were higher than indoors (16–25°C), this pest was active longer than in perennial plants, peaking earlier than outdoors in mid-October (18% of plants damaged), and two sharper spikes

during January and April (31 and 45% of the plants damaged, respectively) (fig. 1b). As with tobacco whitefly, the abundance of western flower thrips was delayed outdoors compared with indoors.

Identifying perennial plants harbouring pests

Model estimation displayed a mean value for tobacco whitefly abundance in perennial plants of 16.6 ± 22.7 whiteflies per plant. This pest was significantly higher on *Dodonaea viscosa*, *Withania frutescens*, *Thymus vulgaris*, *Thymus hyemalis* and *Dorycnium pentaphyllum* (fig. 2a). Particularly, the maximum estimated value for tobacco whitefly exceeded 50 individuals in two cases. However, excepting these five plant species, the estimated whitefly abundance on the perennial plants tested remained below eight, with 7.4 ± 3.6 whiteflies per plant. For immature stages of the pest, the estimated value was below two on all perennial plants (fig. 2b). However, the value of immature pests was significantly higher in some plant species including *D. viscosa* and *T. vulgaris* (with 13.5 and 11.3 15 immature per plant, respectively), followed by *T. hyemalis* and *W. frutescens* (with <3 immature per plant) (fig. 2b). Western flower thrips were found in plant species with an estimated mean value of $101.39 + 105.9$ thrips per plant. This pest reached the highest values in six of those species: *D. pentaphyllum*, *Grimpoteuthis umbellata*, *Rosmarinus officinallis*, *Anthyllis cytisoides*, *W. frutescens* and *T. hyemalis* (fig. 2c). The first two plants exceeded 300 estimated individuals per plant and about 50% of plants tested exceeded 50 individuals of maximum estimated value (fig. 2c). As in the case of whitefly, the plant species that supported higher abundance values of adult stages of western flower thrips also recorded the higher abundance of immature stages of this pest. The highest number of immature pest was found in *Rubus occidentalis* (72 immature/plant), followed by *D. pentaphyllum*, *T. hyemalis* (44 and 41 immature/plant, respectively), *W. frutescens*, *G. umbellata*, *A. cytisoides* (29, 27 and 24 immature/plant, respectively) and *T. vulgaris* (16 immature/plant) (fig. 2d). Next, a set of three plant species, including *Phanera purpurea*, *Lycium intricatum* and *Lavandula latifolia*, supported a lower level of both pests compared with the previous plant species. Finally, a set of ten plant species was identified for supporting the lowest levels of both of the two horticultural pests. These plants were:
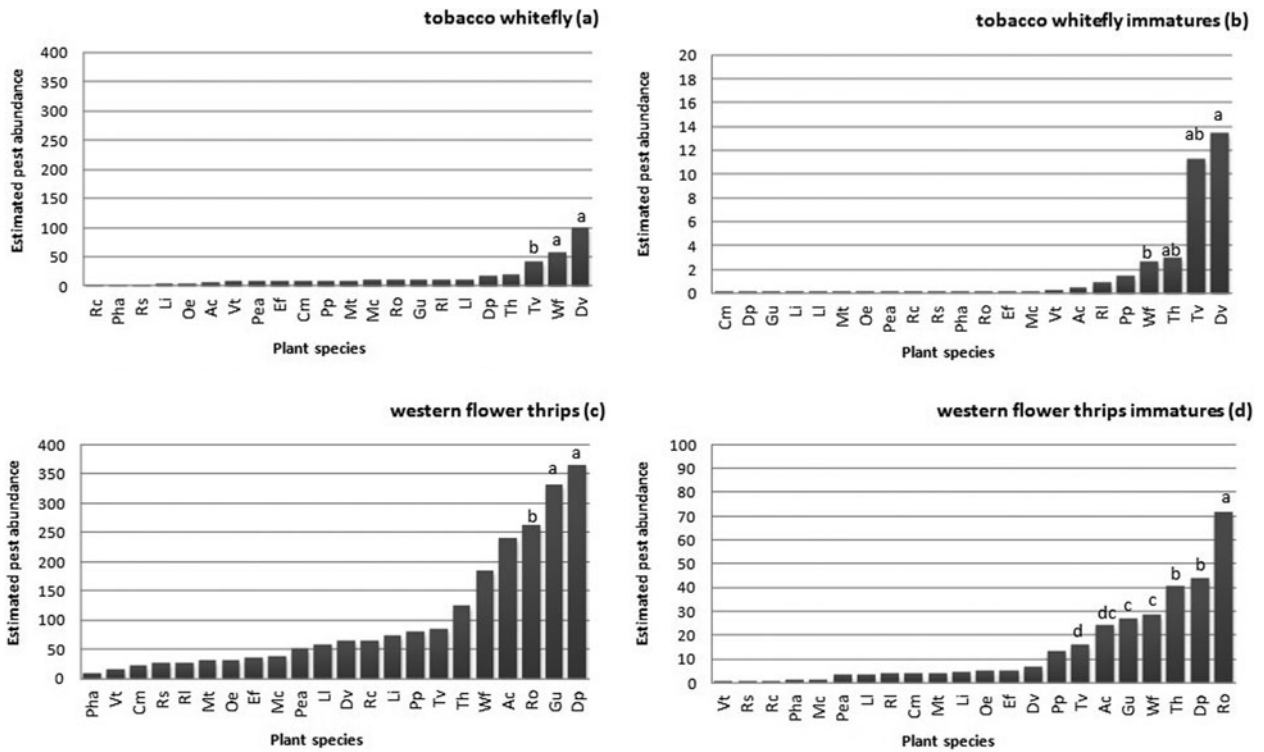
Fig. 2. Estimated abundance value per plant of adults + immature stages of tobacco whitefly (*Bemisia tabaci*) (a), immature of tobacco whitefly (b), adults + immature stages of western flower thrips (*Frankliniella occidentalis*) (c) and immature of western flower thrips (d). Small letters denote significant pairwise Tukey's differences between perennial plants species ($P < 0.05$). Significant differences were shown only when estimated abundance was equal to or higher than the mean of the estimated value. For plant species code, see table 1.

Prunus angustifolia, *Crithmum maritimum*, *Retama sphaerocarpa*, *Rhamnus lyciodes*, *Marsdenia tenacissima*, *Olea europaea var. sylvestris*, *Ephedra fragilis*, *P. angustifolia*, *Macrozamia communis* and *Viburnum tinus* (fig. 2). The lowest values of immature stages were also observed for such plants species.

Pests, NEs and flowering

For both pests, the best model that predicts their occurrence in perennial plants included the plant species and their corresponding flowering period (table 2). In the case of tobacco whitefly, the model predicted that, when *T. vulgaris* was blooming, it supported more whiteflies than other blooming plants such as *T. hyemalis* and *W. frutescens*. However, in *D. viscosa* and *D. pentaphyllum*, no more whiteflies were collected even though abundant flowers were present (fig. 3a). Flowering also significantly influenced the abundance of western flower thrips (fig. 3b). Overall, the model predicted that the bloom period of the solanaceous plant *W. frutescens* coincided with the highest abundance of western flower thrips. However, the abundance of thrips did not necessarily correspond to the availability of floral resource on *G. umbellata*, one of the plants most preferred by this pest.

Regarding NEs, the models indicated that, excepting the parasitoid of thrips *Ceranisus* spp., host/prey availability was better than flowering as a predictor of the occurrence of NEs in perennial plants (table 3). With regard to NEs of tobacco whitefly, two plants species, *D. viscosa* and *P. purpurea*, harboured more predators (*N. tenuis*) and parasitoids

(*Eretmocerus* spp.), respectively, than did other plants (fig. 4). In the case of western flower thrips, the abundance of the predator *Orius* spp. was higher in the aromatic species *T. vulgaris* than in the other plants (fig. 4). In the particular case of the parasitoid *Ceranisus* spp., its occurrence was greater in *D. pentaphylllum* and *R. officinalis* when these plants were in bloom (fig. 4).

Discussion

Despite boosting the abundance of major NEs, native flora also can also reportedly increase the abundance of some potential pest species for nearby crops (Fiedler & Landis, 2007a, b; Danne *et al.*, 2010; Winkler *et al.*, 2010). Thus, the identity of perennial plants and the timing of pest attacks on them have significant relevance for habitat management (Lavandero *et al.*, 2006). In this study, the seasonal distribution of the two pests, tobacco whitefly and western flower thrips, in crops such as tomato, pepper, eggplant and cucumber, as well as in perennial plants proved very similar. Moreover, the pests occurred for less time in perennial plants than in crops, and later outdoors than indoors. The warm conditions and abundant food in a greenhouse is likely to provide a stable environment for pest development. The results indicate that perennial plants did not represent an initial pest source for crops. In this sense, Schellhorn *et al.* (2010) found that crops support higher densities of thrips than do perennial plants, and Bianchi *et al.* (2013) showed that crops usually act as sources of pest species much more than do shrubs.

Table 2. Comparison of alternative models (using AIC$_c$) for the two pests tested in this study (i.e. *Bemisia tabaci and Frankliniella occidentalis*) to identify flowering-dependent effects of pest occurrence in native plants. According to the rule that ∆AIC < 2 suggests the best parsimony in a group of candidate models, only one model (marked in bold) was selected to likely explain the pests' abundance in flowering-native plants. The marginal (m) and conditional (c) R^2 refer to the best model.

| Models | | AIC$_c$ | |
Fixed effect	Random effect	Western flower thrips (*F. occidentalis*)	Tobacco whitefly (*B. tabaci*)
No	No	42,330.19	7391.34
Flowering	No	37,533.32	6925.70
Species	No	40,312.71	6823.69
Flowering × species	No	33,741.41	5874.17
No	Sampling date	16,006.98	4800.29
Flowering	Sampling date	15,182.24	4412.28
Species	Sampling date	13,989.50	4232.65
Flowering × species	Sampling date	11,761.48	3685.38
R^2_m		0.204	0.393
R^2_c		0.964	0.872
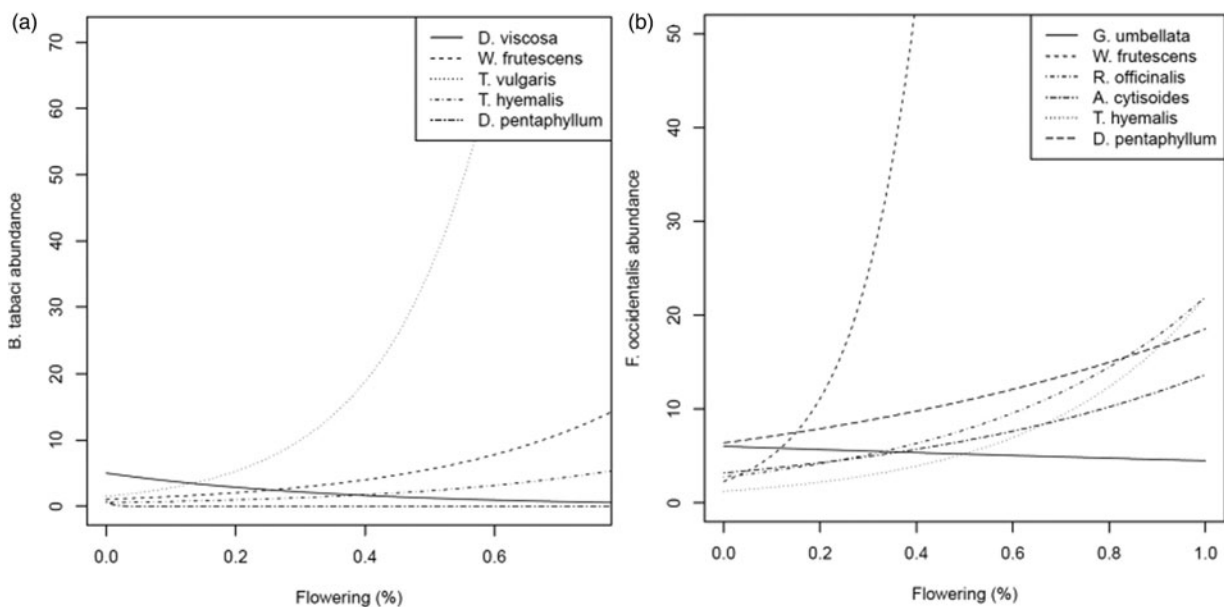
Fig. 3. Model estimations for the best model selected showing the relationship between flowering and abundance of the pests, tobacco whitefly (*Bemisia tabaci*) (a) and western flower thrips (*Frankliniella occidentalis*) (b) in the most preferred perennial plants.

Tobacco whitefly and western flower thrips were collected from all plant species. However, three plant species, *W. frutescens*, *D. pentaphyllum* and *T. hyemalis*, harboured more pests than did all other plants. More specifically, two plant species, *D. viscosa* and *T. vulgaris*, supported more whiteflies, while another three species, *G. umbellata*, *R. officinalis* and *A. citysoides*, had more western flower thrips. In general, adults and immature stages of pests were more abundant in the same set of plant species, indicating that reproduction and feeding took place on the same host plants. However, it should be noted that immature stages of tobacco whitefly were found at low densities in perennial plants, and this could have been influenced by the sampling, which was carried out by vacuum, which likely biased samples towards sessile stages, such as immature stages of tobacco whitefly. This pest is an enormously polyphagous insect associated with almost 600 different species of plants, including cultivated and non-cultivated annuals and perennials worldwide, although it prefers Asteraceae, Cruciferae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Labiatae, Malvaceae and Solanaceae families (Inbar & Gerling, 2008; Shah *et al.*, 2015). In the present study, this pest was more abundant in perennial species from Asteraceae, Labiateae, Fabaceae and Solanaceae. Its abundance was not clearly associated with flowering in all plant species, signifying that floral resources themselves had no strong impact on the occurrence of the pest, though its abundance was higher in some plants when they were in bloom, such as *T. vulgaris*. Similarly, Fiedler & Landis (2007b) found that herbivore abundance in perennial plants, including sap-sucking insects, increased with particular floral traits although the pests responded more weakly to these traits than did the NEs. Our result is difficult to interpret because whiteflies are phloem-feeding insects and do not feed on floral resources; thus, the positive impact of flowering on tobacco

Table 3. Comparison of alternative models (using AIC_c) for the natural enemies tested in this study to identify their occurrence on native plants. According to the rule that $\Delta AIC < 2$ suggests the best parsimony into a group of candidate models, only one model (marked in bold) was selected to likely explain the natural enemies' abundance. The marginal (m) and conditional (c) R^2 refer to the best model.

Models		AIC_c			
Fixed effect	Random effect	*Nesidiocoris tenuis*	*Eretmocerus* spp.	*Orius* spp.	*Ceranisus* spp.
No	No	1176.85	505.36	1639.08	863.59
Flowering	No	1040.19	506.12	1613.24	846.40
Species	No	1142.29	484.48	1572.90	743.01
Prey	No	1077.60	453.00	1603.94	667.11
Flowering × species	No	998.60	479.12	1520.42	717.59
Prey × species	No	960.52	446.98	1512.91	640.95
No	Sampling date	938.45	473.87	1217.98	592.73
Flowering	Sampling date	801.79	474.63	1192.14	575.55
Species	Sampling date	918.64	456.83	1198.92	524.30
Prey	Sampling date	741.93	430.84	1140.85	540.99
Flowering × species	Sampling date	786.25	449.67	1163.44	502.89
Prey × species	Sampling date	608.42	427.69	1103.86	520.66
R^2_m		0.719	0.237	0.105	0.034
R^2_c		0.947	0.392	0.541	0.704

whitefly abundance is probably related to some quality changes linked to blooming of each perennial plant species (Rebek *et al*., 2005). Hence, tobacco whitefly abundance was limited to a very specific, short period of time, and occurred in high abundance only in a few plant species, suggesting that plant diversity may provide relatively few acceptable host plants for this pest. Implications for practice of these results are of relevance, since providing plant diversity among greenhouses may be a promising option to reduce pest pressure outdoors by a bottom–up effect, operating via diversification of the first trophic level (Finch & Collier, 2000; Gurr *et al*., 2003; Aguilar-Fenollosa *et al*., 2011). On the other hand, seasonal abundance of western flower thrips in perennial plants was greater than that of tobacco whitefly, and also western flower thrips were supported by a broad spectrum of perennial plants than tobacco whitefly. Thus, although western flower thrips appear to prefer some plant species over others, it was prevalent on almost all the plant species studied; therefore, the polyphagous nature of these thrips creates a more difficult pest-control situation outdoors. A total of 244 species of plants belonging to 62 different plant families have also been found to host western flower thrips, including open agricultural crops, ornamentals and protected crops (Tommasini & Maini, 1995; Lewis, 1997). Few studies have reported western flower thrips occurrence on non-crop plant species, but our results coincide with some reports from the USA (Cockfield *et al*., 2007; Miliczky & Horton, 2011), Chile (Ripa *et al*., 2009), South Africa (Allsopp, 2010) and South Australia (Schellhorn *et al*., 2010), where this pest is usually collected in large numbers from a number of weed species growing in and around the fields and also from several perennial plants. Furthermore, our results show that flowering positively influenced western flower thrips abundance in perennial plants. Adults of this pest are highly mobile and feed primarily by piercing plant cells but also consume floral parts such as petals and pollen, so that adults are often found in large numbers in flowers of several plants and crops (Tommasini & Maini, 1995; Lewis, 1997). Therefore, the overlapping bloom period of the perennial plant species in the experimental field might also ensure continuous availability of floral (food) resource for western flower thrips adults, this explaining why this pest was more polyphagous and ubiquitous in perennials than was tobacco

whitefly. However, Schellhorn *et al*. (2010) showed that crop proximity influenced the probability of density of western flower thrips in flowers of exotic weeds and native plants species, but the effect appears to be less so when the adjacent vegetation is native. Particularly, our results show that flowers of the solanaceous plant *W. frutescens* were highly attractive to the pest. Strikingly, the flowering of the leguminous plant *G. umbellata*, which supported the highest level of the pest, had a negligible influence on western flower thrips abundance. In this case, pest peak coincided with *G. umbellata* bud break (data not shown), suggesting that the pest was present in pre-bloom inflorescences. The attraction of floral buds to western flower thrips has been reported in plant hosts (Ripa *et al*., 2009; Allsopp, 2010). On this basis, flowering on *W. frutescens* and pre-bloom inflorescences on *G. umbellata* could be significant predictors of western flower thrips occurrence outdoors, this opening the opportunity for researching the use of these perennial plants as traps for controlling this pest outdoors.

Regarding the NEs, the same plants that were hosts for tobacco whitefly and western flower thrips, also hosted their potential predators and parasitoids. Furthermore, results showed that host/prey availability was a stronger predictor of NE abundance on perennial plants than was food (floral parts). Other studies have shown that the abundance of NE on attractive plant species is explained not only by bloom, and that other important attractions include shelter, suitable micro-climate and prey/host availability. These are also essential components for conservation biological control (Rebek *et al*., 2005; Fiedler & Landis, 2007*b*; Witting *et al*., 2007; MacLeod & Winfree, 2011) and are especially relevant in fields that encourage biodiversity with perennial plants (Griffiths *et al*., 2008; Gareau *et al*., 2013). In particular, the whitefly predator *N. tenuis* was abundant in *D. viscosa*. This zoophytophagous predator maintains a close relationship with its host plants by using them not only to feed on, but also as an oviposition substrate. The relationship between this Mediterranean shrub and *N. tenuis* has been previously reported (Sánchez *et al*., 2003; Cano *et al*., 2009), and it has been studied for its potential role as a companion plant to control other important horticultural pests such as *Tuta absoluta* (Lepidoptera: Gelechiidae) in tomato crops (Biondi *et al*., 2016). The whitefly parasitoid *Eretmocerus* spp., collected mainly in *P. purpurea*,
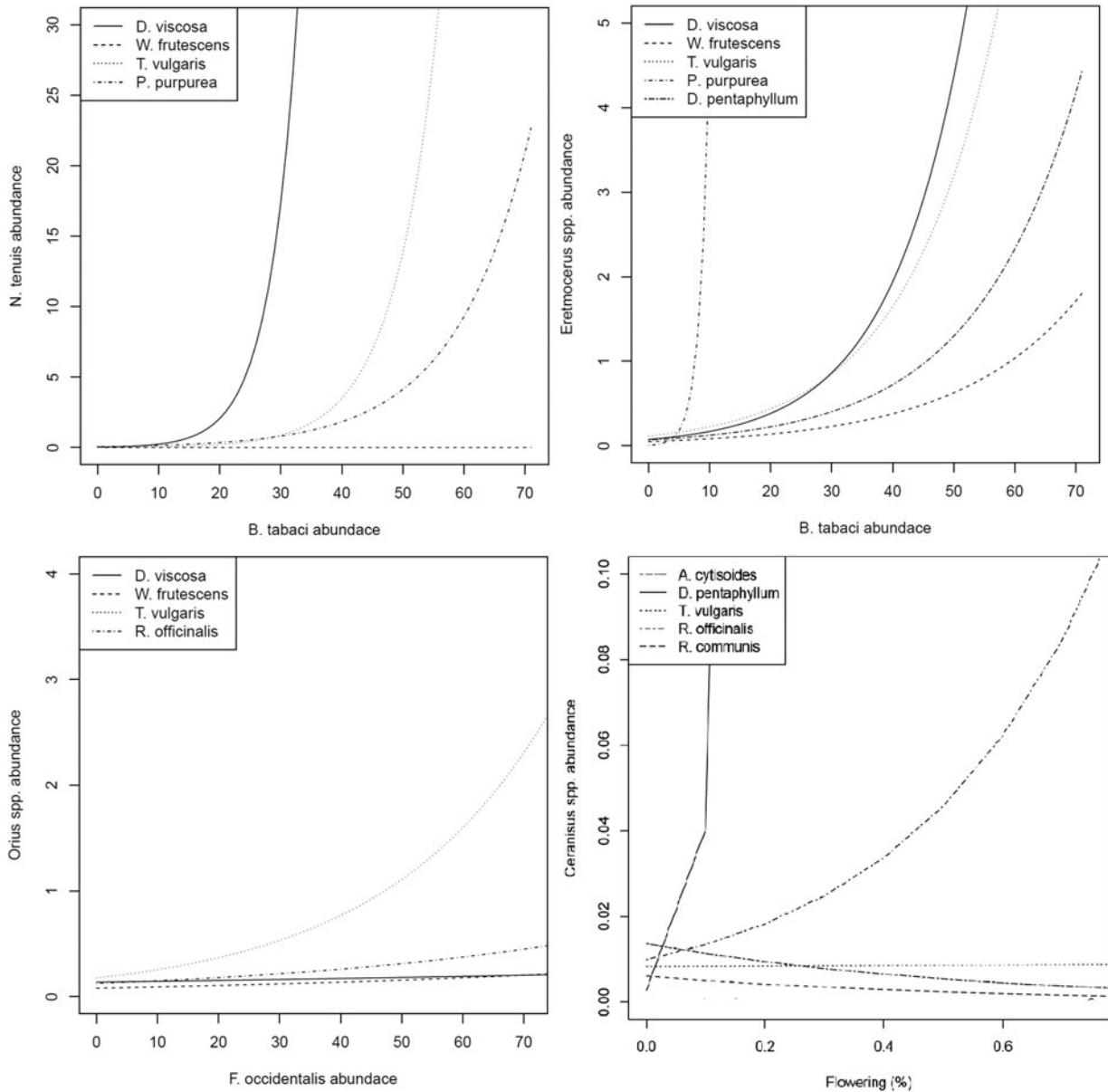
Fig. 4. Model estimations for the best model selected for each of the natural enemies tested in this study showing the relationship between their abundance and the predictors of occurrence (flowering vs. host/prey availability) in different plant species (see table 3).

was also a host for tobacco whitefly. It is known that host plants of tobacco whitefly may notably mediate the activity of parasitoids, since plant species and varieties have foliar attributes such as volatile compounds, presence or absence of pubescence and/or wax, etc., that affect parasitism rates (Inbar & Gerling, 2008; Shah *et al.*, 2015). The pirate bug, *Orius* spp., was found mainly in the aromatic plant *T. vulgaris*. *Orius* spp. is an important predator of thrips and other soft-bodied insects throughout the world (Lewis, 1997). Although they feed chiefly on prey, they also rely on different plant resources such as sap (Lundgren *et al.*, 2008), pollen (Kiman & Yeargan, 1985) and nectar (Bugg, 1987) from several plant species when prey is scarce. Thus, an association with plants species such as *T. vulgaris* could give *Orius* spp. access

to both prey and plant food. The thrips parasitoid *Ceranisus* spp. was collected primarily in flowers of *D. pentaphyllum* and *R. officinalis*. Similarly, Lacasa *et al.* (1996) pointed out *R. officinalis* as a primary plant to collect *Ceranisus* spp., in surveys conducted in wild plants near to greenhouses in 1996, to find potential host plants of this thrips parasitoid.

In conclusion, from all the perennial plants assessed, eight native plants were the most critical species for sustaining pest population outdoors. It has been possible to identify a subset of five plant species that supported less abundance of pests, and other subset of ten plant species that supported a very low level of pests. The tobacco whitefly was more discriminating in selecting host plants than was the western flower thrips, which were supported by a broad spectrum of perennial

plants, and which showed that their abundance was favoured by blooming. NEs generally attained their highest abundance on host plants that also supported high pest abundance, suggesting that floral resource was not a strong predictor of NEs' abundance on native plant species. Consequently, the lower host plant acceptance observed for tobacco whitefly offers a promising option to reduce this pest pressure outdoors by a bottom–up effect, operating via diversification of the first trophic level. All the perennial plants that supported low–medium pest level in the present study could be beneficial choices for conservation biocontrol in surrounding greenhouses because they might provide hosts with parasitoids and predators while not significantly benefiting the pests. Field trials in which these perennial plants can be implemented as hedgerows among greenhouses are needed to ascertain whether pest abundance outdoors is reduced.

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