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4  
5 **Preconditioning of the generalist herbivore *Trialeurodes***  
6 ***vaporariorum* to greenhouse monocultures and its subsequent**  
7 **performance on wild polycultures**

8  
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22 **Short title:** *Preconditioning of greenhouse whitefly*

23  
24 *Key words:* host plant preference, host plant experience, preconditioning, cucumber, tomato,  
25 poinsettia, weeds, whitefly, Hemiptera, Aleyrodidae

26  
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1 **Abstract**

2 Generalist herbivores can face many challenges when choosing their host plant. This can be  
3 particularly difficult if their choice and performance are affected by host experience.  
4 Greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae), is an  
5 invasive generalist herbivore, which has established in year-round greenhouses at northern  
6 latitudes where it cannot overwinter outdoors. It mainly uses crops such as cucumber  
7 (*Cucumis sativus* L.), tomato (*Solanum lycopersicum* L.), and ornamentals as host plants.  
8 However, every summer the insect escapes greenhouses and is exposed to natural vegetation.  
9 We evaluated the performance of *T. vaporariorum* on diverse vegetation outside greenhouses  
10 after prolonged experience of greenhouse crops. First, we surveyed the vegetation near  
11 infested greenhouses. Development success of the insect differed among wild hosts. We  
12 identified five new hosts among 12 plant species that bore pupae and were thus considered  
13 suitable as the insect's host plants. Members of the Urticaceae and Onagraceae were the most  
14 preferred and frequently inhabited by all insect life stages. The highest abundance of insects  
15 occurred in plots with low plant species richness, independent of plant family in these  
16 habitats. We then studied experimentally the impact of 1 year of preconditioning to one of  
17 three common greenhouse crops, cucumber, tomato, or poinsettia (*Euphorbia pulcherrima*  
18 Willd. ex Klotzsch), on the performance of the preconditioned adults and their progeny on  
19 four wild plants. Adults from tomato and poinsettia preferred the novel host species over the  
20 species to which they were preconditioned. The whitefly population preconditioned to  
21 cucumber was the most fecund on all offered hosts. We conclude that generalist herbivores  
22 can have large variation in performance, despite polyphagy, on novel hosts as shown by the  
23 variable abundance of *T. vaporariorum* pupae among outdoor hosts. Furthermore,  
24 performance of whiteflies on natural vegetation was affected by experience on greenhouse  
25 crops. Based on our observations, we provide insights and recommendations for pest  
26 management.

27

## 1 **Introduction**

2 Generalist herbivores are characterized by a large niche breadth and are considered to have an  
3 advantage over specialist species in their ability to adapt to ongoing global changes such as  
4 habitat and climate disturbances, and are therefore rapidly expanding their ranges and  
5 replacing specialist species (McKinney & Lockwood, 1999; Vázquez, 2006; Clavel et al.,  
6 2011). Generalist species have a greater resource availability, which is considered to be  
7 universally beneficial. They also have the possibility of mixing foods to improve nutrient  
8 balance or to reduce exposure to high levels of particular allelochemicals (Bernays &  
9 Minkenberg, 1997). Specialist herbivores, for their part, are more effective in making a  
10 choice among plants of variable quality in terms of increased speed of host finding,  
11 recognition, and discrimination owing to, e.g., sensory focusing that provides advantages in  
12 terms of information acquisition and processing in complex environments (Bernays &  
13 Wcislo, 1994; Bernays, 2001). On the other hand, generalist herbivores must possess flexible  
14 means of ensuring shifting attentiveness to environmental cues that are biologically relevant  
15 in resource finding (Bernays & Wcislo, 1994). Generalist herbivores are also influenced by  
16 the chemistry and morphology of their hosts; as a consequence, they display variation in  
17 performance on different host plant species (Via, 1990). Some generalist herbivores (e.g.,  
18 some Orthoptera) have a higher growth rate when feeding on mixtures of host plants  
19 compared to a uniform diet, whereas others (e.g., some Hemiptera) are more selective when  
20 making a choice among host plants of variable quality and have higher growth and  
21 development rates on a particular host species than on a mixture of hosts (Bernays &  
22 Minkenberg, 1997). Although both types of generalist herbivores remain polyphagous, long-  
23 term survival of their progenies on novel hosts differs, at least during the initial stages of host  
24 adaptation (Thompson, 1988; Via, 1990; Bernays, 2001). The term ‘novel’ here refers to  
25 situations where the herbivore population has been feeding on a particular host plant species  
26 over several generations and then switches to another host species.

27 Preference and performance of herbivores on novel hosts depends not only on their  
28 inherent diet breadths but also on their host experience. Preconditioning or long-term  
29 experience of a host might in some cases lead to changes of host preference that can be either  
30 cumulative or reversible (Papaj & Prokopy, 1989), whereas in other cases preconditioning  
31 has no effect on insect performance (Lee et al., 2010). Preconditioning may cause differences  
32 in insect performance in terms of fecundity, survival, and development time on experienced  
33 compared to novel hosts (Thomas, 1993; Coyle et al., 2011). Ultimately, on an evolutionary

1 time scale, such differences could lead to speciation through host races (Drès & Mallet,  
2 2002). Adaptation to plant chemistry allows increasing insect abundance over time, resulting  
3 in outbreaks of insect pests in monocultures (Altieri & Nicholls, 2004), whereas in  
4 polycultures the majority of herbivorous arthropods is not able to reach high abundance due  
5 to plant stand or plant life-history characteristics (Andow, 1991; Altieri, 1999). Theoretically,  
6 prolonged experience on a single host-plant species in commercial greenhouses could change  
7 the performance of herbivorous insects on novel hosts in outdoor habitats. Temperate year-  
8 round greenhouses provide an environment that facilitates prolonged preconditioning of  
9 herbivorous insects on one plant species over several generations during the autumn and  
10 winter time. In the spring and summer, the herbivores have access to mixtures or monoculture  
11 stands of novel host plant species outside the greenhouses. The insects reach the outdoor  
12 environment from within the greenhouses either by voluntary migration through vents or via  
13 plant parts that are removed from the greenhouse. Our previous findings suggested that  
14 prolonged experience on a particular host plant species in the greenhouse contributes to  
15 genetic differences between *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae)  
16 populations collected from year-round tomato (*Solanum lycopersicum* L.) and cucumber  
17 (*Cucumis sativus* L.) greenhouses (Ovčarenko et al., 2014a). This may be partly explained by  
18 adaptation to the monoculture hosts in question. The ability of generalist herbivores to  
19 achieve pest status in enclosed greenhouse monocultures, coupled with their temporal access  
20 to outdoor polycultures, offers a chance to study the resource use of generalist herbivores.

21 The whiteflies *T. vaporariorum* and *Bemisia tabaci* (Gennadius) are polyphagous  
22 species feeding on herbaceous plants. Both generalist whitefly species can develop a  
23 preference for and better performance on certain hosts with a prolonged period of host  
24 experience (Roditakis, 1990; Byrne & Bellows, 1991; Bernays & Minkenberg, 1997; Lei et  
25 al., 1998; Bezerra, 2004; Ma et al., 2005). The time that is required for preference to develop  
26 depends on the plant species: it can be 50 whitefly generations on some plants (Thomas,  
27 1993) or only three on others (Greenberg et al., 2009). Observations of *T. vaporariorum* host  
28 races were reported from sweet pepper cultivars in Hungary, whereas preconditioning of  
29 other populations to this host have never resulted in the same insect performance (Thomas,  
30 1993). Preconditioning may also result in lower performance on novel hosts, e.g., the first  
31 generation of *B. tabaci* on a novel host had a shorter life span and lower fecundity than on  
32 hosts they had had experience with (Hu et al., 2011). Therefore, host experience can affect  
33 preference and performance of polyphagous herbivores in several different ways, depending  
34 on the combination of the pest and host-plant species.

1           Although more than 200 plants have been described as hosts of *T. vaporariorum*  
2 (Lloyd, 1922; Bodenstein, 1952; Mound & Halsey, 1978; Roditakis, 1990), these reports are  
3 often limited to economically important crops and rarely describe whether the insect is able to  
4 complete its life cycle, i.e., the reproductive suitability of the host. *Trialeurodes*  
5 *vaporariorum* has been reported on plants growing in the vicinities of greenhouses in Crete  
6 (Roditakis, 1990), The Netherlands (van Dorst et al., 1983), and even in Kola peninsula in  
7 northern Russia (Rak & Litvinova, 2010). However, records of *T. vaporariorum* host species  
8 in the boreal environment and the description of its reproductive behaviour are practically  
9 non-existent.

10           In general, host-plant selection by *T. vaporariorum* adults positively correlates with the  
11 insect's reproductive success on the host, but on some plant species high mortality may occur  
12 in the egg and first and second instars (Castane & Albajes, 1994). Once *T. vaporariorum*  
13 females select the host for egg laying, further movement of progeny is restricted. The first  
14 instars are able to move only within the leaf of their emergence (Lei et al., 1996; Bird &  
15 Krüger, 2007), whereas the second, third, and fourth nymphal stages and eventually the pupal  
16 stage remain sessile (for discussion of whitefly life-stage terminology see Byrne & Bellows,  
17 1991). Adults and sessile sap-feeding life stages may induce plant defence against herbivores  
18 and release of toxic compounds into the sap, causing mortality of instars (Inbar & Gerling,  
19 2008). As whitefly immatures stop feeding upon development into pupae, the presence of  
20 pupal stages on host plants can be used as an indicator of the host plant's suitability for  
21 whitefly reproduction and development (Byrne & Bellows, 1991; Lei et al., 1996).

22           In this study, we examined the performance of the generalist herbivore *T. vaporariorum*  
23 on diverse flora in two ways. First, we conducted a survey of hosts, where we examined the  
24 insect's ability to utilize host plant species in the immediate vicinity of commercial  
25 greenhouses in relation to habitat diversity. We hypothesized that the occurrence of pupae  
26 would be low in outdoor plant communities of higher compared to lower species richness,  
27 due to poor performance of generalist herbivores in polycultures and/or due to insect  
28 preconditioning to greenhouse monocultures over 8-9 generations during the preceding  
29 winter months. Second, we conducted a host choice experiment, in which we analysed the  
30 ability of adults preconditioned to one of three common crop plant species to utilize novel  
31 hosts and the reproductive suitability of the hosts chosen for oviposition. We hypothesized  
32 that the insects from any population should have a preference for cucumber, as it is the most  
33 preferred crop plant among several studied species (van Lenteren & Noldus, 1990), and have  
34 better performance on hosts that they had experienced.

1

## 2 **Materials and methods**

### 3 **Host plant survey**

4 *Study area.* Greenhouses in western Finland have been year-round habitats of *T.*  
5 *vaporariorum* since the 1980s (TIKE & OSF, 2014), serving as spots of high insect propagule  
6 pressure. However, due to subzero temperatures in winter, adaptation to local flora in natural  
7 ecosystems outside greenhouses has been temporally restricted to the warmer seasons. The  
8 average length of the growing season (when average daily temperature exceeds 5 °C) is up to  
9 175 days, from the end of April to late October or early November in southern and central  
10 Finland (Finnish Meteorological Institute, 2014). Thus, the time suitable for *T. vaporariorum*  
11 to persist outdoors in Finland is from mid-May to late October, as the temperature below  
12 which development of *T. vaporariorum* ceases is 8.3 °C (Osborne, 1982). However, studies  
13 of cold tolerance of local populations are needed to confirm this threshold. Because egg to  
14 adult development time varies from 20 to 50 days (Park et al., 2011), the insect can produce a  
15 maximum of 4-5 generations per year in outdoor conditions in Finland. At the time of the  
16 survey period, July-August 2010, *T. vaporariorum* was at the stage of second-third  
17 generation on outdoor hosts. Owing to an exceptionally early spring (Finnish Meteorological  
18 Institute, 2011) the outdoor hosts were possibly available for oviposition already in April.  
19 Thus, adults of the first generation emerged in May, those of the second in June, and those of  
20 the third in July. Considering variation of insect development times among hosts, the insects  
21 probably were in the second or third generation during the 2-week sampling period, which  
22 took place in July-August, 2010.

23 We surveyed the surroundings of three infested year-round greenhouses, two producing  
24 tomato and one cucumber, where *T. vaporariorum* persisted during 2010-2011 (Ovčarenko et  
25 al., 2014a). The greenhouses were located in three villages separated from each other by a  
26 distance of 20-40 km. Persistence of the same whitefly population in each sampled location  
27 over a period of 2 years was documented earlier (populations NR3, TJ1, and PR in  
28 Ovčarenko et al., 2014a). Persistence in the greenhouse, which has a crop production break  
29 and complete eradication of the indoor crop plants during the summer, is possible only if  
30 whiteflies are able to utilize outdoor wild plants as refugia and re-infest the new crop in  
31 autumn. Whiteflies sampled on outdoor hosts originated from nearby monoculture  
32 greenhouses during the same warm season, as most of the outdoor vegetation decays during  
33 winter in Finland.

1  
2 *Survey protocol.* During the 2 weeks of sampling in July-August, 2010 plants were inspected  
3 for the presence of *T. vaporariorum* within 1 m distance from greenhouses. The 1 m<sup>2</sup>  
4 vegetation plots were selected based on the following criteria: each plot contained at least one  
5 infested plant, and an attempt was made to document abundance of *T. vaporariorum* on as  
6 many plant species as possible. Five to 10 leaves per plant species in a plot were inspected for  
7 the highest abundance of *T. vaporariorum* (adults, pupae, nymphs, and eggs) using ×5  
8 magnification lenses. Maximum abundance was assigned to three classes: (1) absence of *T.*  
9 *vaporariorum*, (2) 1-4 individuals per leaf, or (3) five or more individuals per leaf. Host  
10 suitability for the insect was determined on the basis of the rate of occurrence of pupae or  
11 their exuviae on the plants. As many overlapping generations were often observed on the  
12 leaves, several life stages were often recorded from the same plant species. The majority of  
13 the plants were identified to species level but vegetative or seedling stages were identified  
14 only to genus level (e.g., *Geranium* sp.) (Mossberg & Stenberg, 2003). Grasses were  
15 identified only as members of Poaceae, as no life stage of *T. vaporariorum* was found on  
16 them during the survey. Two infested host plants were not identified due to decayed foliage.

17

18 *Characteristics of plots.* Three 1 m<sup>2</sup> vegetation plots were inspected from each cardinal  
19 direction – north, south, east, and west of the greenhouse –, resulting in 12 plots per  
20 greenhouse and 36 plots in total. Overall, the plots consisted of 50 plant species. The most  
21 common plants found in the studied plots were grasses, as 94% of plots contained Poaceae,  
22 followed by dandelion, *Taraxacum officinale* F.H. Wigg (64%), yarrow, *Achillea millefolium*  
23 L. (55%), nettle, *Urtica dioica* L. (53%), fall dandelion, *Leontodon autumnalis* L. (42%), and  
24 fireweed, *Chamerion angustifolium* (L.) Holub (39%). Identified plants consisted for 70% of  
25 perennial species (Table 1). Plant species characterized by early flowering (beginning in May  
26 or June) comprised 40% of the identified plants, and 29% of the early flowering species had  
27 pupae on them. The majority of species flowered in July/August and 44% of them had pupae.  
28 The proportion of plant species coverage per plot was estimated visually by recording the  
29 percentage of the spatial area taken by each plant species in 1 m<sup>2</sup>. Plant richness was  
30 estimated by counting the number of plant species in each plot. Mean (± SD) plant species  
31 cover was 11.92 ± 15.23% and varied from 1 to 90% in a plot. Mean (± SD) plant species  
32 richness was 8.25 ± 3.40 species and varied from 3 to 15 species per plot. For all analyses,  
33 plant richness was transformed into a categorical variable by assigning values into categories:  
34 1 = 1-7, 2 = 8-11, and 3 = 12-15 plant species per plot.

1  
2 *Statistical analysis.* Due to the categorical nature of response variables (insect abundance  
3 levels) preliminary tests were performed using cross tables (Proc FREQ) implemented in  
4 SAS software v.9.3 (SAS Institute, Cary, NC, USA) and Cochran-Mantel-Haenszel statistics  
5 (based on table scores). Likelihood of insect occurrence was estimated using generalized  
6 linear mixed models based on logit link function (Proc GLIMMIX) implemented in SAS. The  
7 latter procedure allowed us to take into account several random and fixed effects and their  
8 interactions, as data were collected in situ in uncontrolled environmental settings. To simplify  
9 and meet the convergence criterion of the model, the response variables (adult, egg, nymph  
10 and pupal abundance levels) were transformed into binary data (0 = absence, 1 = one or more  
11 insect individuals) and host plant families (variable ‘family’), instead of species, were used in  
12 the model. Furthermore, to enhance the level of reliability of the data we followed Peduzzi et  
13 al.’s (1996) recommendation for minimum sample size of logistic regression analysis and  
14 only plant families that had at least 10 presence/absence observations of *T. vaporariorum* life  
15 stages (adults, eggs, nymphs, or pupae) were used in the model to analyse the likelihood of  
16 the occurrence of the corresponding life stage. Proportion of plant coverage in the plot was  
17 log-transformed to meet the assumptions of the parametric analysis. Models consisted of the  
18 same input variables initially and several combinations of fixed and random effects  
19 assignments were tested. Non-significant effects and/or their interactions were eliminated  
20 based on type III tests of fixed effects and tests of covariance parameters, resulting in an  
21 individual statistical model for each response variable. Insignificant or marginally significant  
22 variables and/or their interactions were kept in the model only if the P-values of fixed effects  
23 were not affected by their presence. These statistical models produced mean estimates and  
24 odds of insect occurrence likelihood on plant families, representing the ability of *T.*  
25 *vaporariorum* to utilize outdoor hosts. To compare odds for insect occurrence, odds ratio  
26 (OR) was calculated for each category of host family (Figure 1), cardinal direction (Figure 2)  
27 and plant richness (Figure 3), by dividing odds of one category over the other used in the  
28 comparison. Significance ( $\alpha = 0.05$ ) of OR comparisons was estimated by Tukey-Kramer  
29 adjusted P-values for multiple comparisons.

30

### 31 **Host choice experiment**

32 *Whitefly populations.* *Trialeurodes vaporariorum* was originally collected from indoor crops  
33 (roses, in Honkajoki, Finland) in 2007 and since then has been maintained on poinsettia  
34 (*Euphorbia pulcherrima* Willd. ex Klotzsch). To test for the effect of host plant experience

1 on host choice, we divided this population into three by transferring 100 adults of mixed sex  
2 into separate Plexiglas cages with either tomato (cv. Encore), cucumber (cv. Eminentia), or  
3 poinsettia (cv. Allegra by Lazzeri) – three major crops in Finland. These three *T.*  
4 *vaporariorum* populations were then maintained in the greenhouses of Natural Resources  
5 Institute Finland (Luke) in Jokioinen for 1 year before the start of the choice experiment in  
6 2012. The requirement of *T. vaporariorum* for a minimum period of adjustment on the novel  
7 host for three generations (Greenberg et al., 2009) was fulfilled for all populations.

8  
9 *Plant cultures.* The plant species offered in the choice experiment included both commonly  
10 cultivated and wild plant species. The cultivated plant species and cultivars were the same as  
11 used for whitefly populations: cucumber, tomato, or poinsettia. The wild plant species were  
12 chosen on the basis of the host plant survey and they were nettle, fireweed, dandelion, and  
13 red clover (*Trifolium pratense* L.). The wild plant species were grown from seeds purchased  
14 from Herbiseed (Reading, UK). All host plants used in the experiments were grown in a pest-  
15 free greenhouse prior to the experiments. The pots contained peat and were watered daily  
16 with the same fertilizer solution of NP<sub>2</sub>O<sub>3</sub>-K<sub>2</sub>O(MgO) 14-5-21(2) (Ferticare KOMBI1; Yara,  
17 Helsinki, Finland). The greenhouse climatic settings throughout the experiment were as  
18 follows: 20-24 °C and L16:D8 photoperiod maintained by high-pressure sodium lamps (200  
19 W; Philips, Amsterdam, The Netherlands).

20  
21 *Characteristics of plants offered.* In the choice experiment, *T. vaporariorum* from each of the  
22 original host plants were allowed to feed and lay eggs by choosing among seven plant  
23 species. The seven host plant species were each represented by up to three specimens,  
24 arranged as a group and positioned in a circle with diameter of 1 m. Plants with smaller  
25 leaves consisted of up to three pots to partially compensate for differences in leaf areas. The  
26 distance among groups of plant species was about 20 cm. Plants used in the experiments  
27 differed in age and canopy sizes at the time of *T. vaporariorum* release, as the seven host  
28 plant species have different seedling development times. Thus, before each experiment we  
29 measured plant height (maximum height within plant species) and canopy width (maximum  
30 distance occupied by individuals of plant species), and counted the leaves (belonging to  
31 different leaf sizes) per plant species. Leaf areas were measured from pictures taken before  
32 the experiment. Only leaves representing the most commonly occurring leaf sizes were  
33 pictured. The area of each pictured leaf was calculated by dividing the total pixel number in  
34 leaf area by the pixel number in 1 cm<sup>2</sup> of known size object with Gimp software v.2.8.0

1 (Mattis & Kimball, 1995). The estimate of total leaf area of plant species was calculated by  
2 multiplying the areas of leaves by the number of leaves of the plant species. To take into  
3 account the variation of light intensity near every plant during *T. vaporariorum* release, the  
4 plants were randomly placed and average light intensity ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) near every plant  
5 species was measured before each whitefly release by positioning a light sensor (SKP200  
6 display meter with SKP217 sensor; Skye Instruments, Powys, UK) on the table surface to the  
7 closest shadowless spot near each plant.

8

9 *Experimental protocol.* The release of *T. vaporariorum* populations was performed in three  
10 separate greenhouse compartments ( $l \times w \times h = 8.5 \times 2.8 \times 6$  m) and repeated 3× for each  
11 population, each time randomizing location (greenhouse room) and arrangement of the  
12 plants. Whiteflies of mixed age were collected individually in glass vials from Plexiglas  
13 cages containing host plant and whitefly culture. The glass vials were sealed with cotton and  
14 briefly chilled on ice. The sex of immobilized insects was determined under stereo  
15 microscope based on the shape of the abdomen and presence of ovipositor in females, as  
16 opposed to claspers and aedeagus in males (Gerling, 1990). Females were aspirated from  
17 glass vials to the container, which was positioned in the centre of the plant circle, i.e., at a 50-  
18 cm distance from the plants. The container contained 230 females during each release into a  
19 greenhouse compartment. The container with *T. vaporariorum* females and the pots with  
20 seven host plants were of the same height (15 cm) to provide equal access opportunity.

21 *Trialeurodes vaporariorum* was released before dusk on the day of collection. Host selection  
22 was recorded by counting the *T. vaporariorum* females on every host plant species at 1 and  
23 48 h after release, to avoid bias regarding host preference by adults due to random landing.  
24 Before the last adult counting, the containers were checked to confirm the absence of dead or  
25 live insects. After 48 h, females were collected from all plants by a mouth aspirator and the  
26 plants were moved into a separate clean greenhouse ( $9.3 \times 4.3 \times 6$  m) to monitor egg  
27 development. Females of *T. vaporariorum* are able to lay fertilised eggs for over a month  
28 after coitus and to reproduce by arrthenotokous parthenogenesis (Lloyd, 1922; Aahman &  
29 Ekbohm, 1981). Fecundity was estimated by counting *T. vaporariorum* eggs after 6 days from  
30 the start of the experiment, when they became darker and more easily visible, using  $\times 10$   
31 magnification lenses. Plant species suitability was estimated by counting pupal exuviae of  
32 hatched *T. vaporariorum* adults. Plants were checked on a daily basis and pupal exuviae were  
33 counted when full development was observed on plant species based on personal  
34 observations of maximum adult emergence rates. Therefore, pupal exuviae were recorded

1 after 35 days from the start of the experiment on tomato, cucumber, dandelion, and fireweed  
2 and after 42 days from the start of the experiment on poinsettia, red clover, and nettle.  
3 Whitefly releases and counting of eggs and pupal exuviae were carried out from October to  
4 mid-December, 2012.

5  
6 *Statistical analysis.* The choices made by *T. vaporariorum* were estimated by a mixed linear  
7 model (Proc MIXED) for each continuous dependent variable: abundance of adults at 1 and  
8 48 h, as well as abundance of eggs and pupal exuviae. The model employed restricted  
9 (residual) maximum likelihood estimation method. SAS Enterprise Guide software v.5.1 was  
10 used for this purpose (SAS Institute, Cary, NC, USA). The abundance data were  $\log(x+1)$   
11 transformed to meet the assumptions of the parametric analysis. The significance of fixed and  
12 random effects, covariates, and their interaction was estimated using type III tests within  
13 regression model. In case of significance of fixed effects or their interaction, post-hoc  
14 analyses were carried out using differences in estimates of least-squares means. The release  
15 of each preconditioned population was repeated 3 $\times$ , each time in a different compartment  
16 (repeat number). The effects consisted of two categorical independent variables – host plants  
17 offered (host) and the original host plants used for preconditioning (origin) – and several  
18 explanatory variables: plant height, canopy width, and total leaf area of plant species during  
19 the releases of females, as well as light intensity near every plant species. We assigned host,  
20 origin, and their interaction as the main fixed effects, repeat number and its interaction with  
21 origin as random effects, and initial leaf area of the whole plant as a covariate in every model  
22 to correct for differences in plant sizes. All explanatory variables were tested as covariates,  
23 but non-significant covariates were excluded from the final models. As plant height  
24 correlated with leaf area (Pearson:  $r = 0.31$ ,  $P = 0.013$ ;  $n = 63$ ) it was eliminated from the  
25 model. This resulted in the following model:  $\log(\text{abundance}+1) = \text{fixed} (\text{origin} + \text{host} +$   
26  $\text{origin}*\text{host}) + \text{covariate} (\text{leaf area}) + \text{random} (\text{repeat number} + \text{origin}*\text{repeat number})$ . A  
27 contrasting method employing t-tests within the above-mentioned regression model was  
28 employed to compare *T. vaporariorum* population abundance on original familiar host  
29 against abundance on six other hosts.

30 To evaluate differences in host preference 1 and 48 h after female release, *T.*  
31 *vaporariorum* abundances after 1 and 48 h were combined into one variable and a new  
32 variable indicating observation hour (time) was introduced to the regression model with  
33 above-mentioned variables. This resulted in the model:  $\log(\text{abundance}+1) = \text{fixed} (\text{time} +$   
34  $\text{time}*\text{origin} + \text{time}*\text{host} + \text{time}*\text{origin}*\text{host}) + \text{covariate} (\text{leaf area}) + \text{random}$

1 (origin\*host\*repeat number + time\*repeat number + time\*origin\*repeat number).

2

### 3 **Results**

#### 4 **Host plant survey**

5 We hypothesized that the insect would have low development success (occurrence of pupae)  
6 on outdoor hosts and would be prevalent in low diversity plots occurring in less windy areas.  
7 In contrast to our expectations, eggs were detected on as many as 25 plant species, and eggs  
8 developed into pupae on 12 plant species. Five new plant species were identified as hosts  
9 supporting a full reproduction cycle of *T. vaporariorum* (Table 1).

10 *Trialeurodes vaporariorum* was often found on nettle and fireweed, infesting them in  
11 95 and 100% of the plots where these plants were present, respectively. Nettle and fireweed  
12 were also the best reproductive hosts, as pupae were recorded on them in 53 and 86% of plots  
13 where they were present, respectively. Analysis of cross tables indicated that the highest level  
14 of adult and pupal abundance was recorded more frequently on Onagraceae ( $\chi^2 = 49.377$ , d.f.  
15 = 6) and Urticaceae ( $\chi^2 = 59.646$ , d.f. = 4, both  $P < 0.001$ ), compared to other plant families  
16 (the family names refer only to the species outlined in Table 1). When dandelion and red  
17 clover were present they had high *T. vaporariorum* abundance in some plots, but whiteflies  
18 occupied them only in 50% of cases and pupae occurred in 17 and 33% of plots, respectively.  
19 Overall, host plant family was an important predictor of adult, egg, and nymph occurrence in  
20 regression models (Table 2). Variation in the occurrence of pupae among five plant families  
21 with at least 10 presence/absence observations of pupae was not significant (Table 2). The  
22 Onagraceae (*C. angustifolium* and *E. montanum*) and Urticaceae (*U. dioica*) tended to have  
23 higher counts of all *T. vaporariorum* life stages than other hosts (Figure 1). However, only  
24 few significant differences among families were detected (Figure 1).

25 Plant cover, plant richness, and cardinal direction played an important role for *T.*  
26 *vaporariorum* habitat choice (Table 2). Odds for the occurrence of *T. vaporariorum* adult,  
27 egg, and pupa were higher with increasing percentage of plant cover in the plots.  
28 Furthermore, plant cover interacted with plant richness and both variables had a cumulative  
29 positive effect for egg occurrence. Interactions of plant family and plant cover or family and  
30 richness were not significant for either of the dependent variables. Thus, insect occurrence on  
31 these families was not related to plant abundance, and insect occurrence in less diverse plots  
32 was not related to family occurrence in these habitats. Similarly, there were no significant  
33 interactions between cardinal direction and other fixed or random effects, indicating that

1 insect occurrence in either direction is independent of plant occurrence data. Results of cross  
2 table analyses were similar to those of regression models. Adults occurred more frequently in  
3 the east than in the west ( $\chi^2 = 11.510$ , d.f. = 3,  $P = 0.009$ ; OR = 7.018,  $t = 2.99$ , d.f. = 149,  $P =$   
4 0.017), whereas pupae occurred more frequently in the north than in the west (OR = 11.398,  $t$   
5 = 2.61, d.f. = 126,  $P = 0.049$ ; Figure 2). According to results of cross table analysis, the  
6 highest level of adult and pupal abundance was observed less frequently in plots with high  
7 plant richness (adult:  $\chi^2 = 3.829$ , d.f. = 1,  $P = 0.050$ ; pupa:  $\chi^2 = 7.616$ , d.f. = 1,  $P = 0.006$ ).  
8 However, this result was only partially supported in regression models. Plant richness  
9 significantly affected egg and nymph occurrence (Table 2) and the latter tended to  
10 accumulate in plots with low rather than with high richness (OR= 5.318,  $t = 2.51$ , d.f. = 147,  
11  $P = 0.035$ ; Figure 3).

12

### 13 **Host choice experiment**

14 We hypothesized that differences among selected plants will be higher in at 48 h than  
15 in at 1 h after release, as since both visual and olfactory cues will be utilized by insects in the  
16 longer time period (van Lenteren & Noldus, 1990). Furthermore, insects from any population  
17 should develop a preference towards cucumber, since as it is the most preferred crop plant  
18 (van Lanteren Lenteren and & Noldus, 1990). We were also expecting preference for nettle  
19 and fireweed, based on survey results.

20 Host preference estimated at 1 and 48 h after release differed significantly ( $F_{12,35} = 2.09$ ,  $P =$   
21 0.044; Figure 4). Whitefly adults were less selective at the beginning (1 h:  $F_{6,35} = 2.19$ ,  $P =$   
22 0.067) than at the end (48 h:  $F_{6,35} = 2.76$ ,  $P = 0.026$ ) of the observation period in the host  
23 choice experiment (Table 3). Of the total of 230 females released initially, after 1 h on  
24 average 43% was counted on the seven hosts (range: 30-60%) and 69% after 48 h (60-90%).  
25 Thus, mean *T. vaporariorum* abundance on seven hosts increased by 26% (2-38%) at 48 h  
26 compared to 1 h, suggesting a delay of settlement onto the plants. The highest increase in  
27 preference at 48 h was observed for cucumber and the lowest for tomato (Figure 4). Even  
28 though the increase of adult abundance from 1 to 48 h was significant on tomato and nettle  
29 (Figure 4), these hosts as well as poinsettia had the lowest abundance of eggs and pupal  
30 exuviae (Figure 5).

31 Adult preference for cucumber, dandelion, and fireweed tended to be higher than for  
32 other hosts at 48 h (Figure 4). Female fecundity and host suitability as estimated by the  
33 abundance of eggs and pupal exuviae, respectively, differed similarly among host plant  
34 species (Table 3, Figure 5). Whiteflies laid most eggs on fireweed followed by dandelion,

1 whereas the most suitable host as estimated by the pupal exuviae was fireweed followed by  
2 cucumber and dandelion (Figure 5).

3 The origin of *T. vaporariorum* was not important for preference at 1 and 48 h ( $F_{2,4} =$   
4 1.04 and 1.69, respectively; both  $P > 0.05$ ) and it had marginal significance for the abundance  
5 of eggs ( $F_{2,4} = 5.33$ ,  $P = 0.074$ ), as well as for pupal exuviae ( $F_{2,4} = 4.45$ ,  $P = 0.096$ ) (Table  
6 3), indicating possible differences in fecundity and progeny development among *T.*  
7 *vaporariorum* populations. Females preconditioned to cucumber were more fecund, i.e., laid  
8 significantly more eggs on all plant species than females preconditioned to poinsettia ( $t =$   
9 3.23, d.f. = 4,  $P = 0.032$ ). This resulted in marginally higher progeny emergence rates of  
10 populations preconditioned to cucumber (abundance of pupal exuviae) than of populations  
11 preconditioned to poinsettia ( $t = 2.57$ , d.f. = 4,  $P = 0.062$ ) or tomato ( $t = 2.60$ , d.f. = 4,  $P =$   
12 0.060) on all plant species. Host preference of these three *T. vaporariorum* populations was  
13 not different, as interaction of population origin with the host was not significant in any of the  
14 four models (i.e., for adult abundance after 1 h, 48 h, and abundance of eggs and pupal  
15 exuviae; Table 3). Thus, no post-hoc analyses were carried out using differences in estimates  
16 of least-squares means for pairwise comparisons and preference by each population for each  
17 of seven hosts offered is not described. The t-test revealed that overall populations preferred  
18 novel hosts at 1 h from insect release (Figure 6). Adults preconditioned to tomato had  
19 significantly lower abundance on the original, i.e., familiar hosts at 1 h from release.  
20 Although the differences were not statistically significant, overall estimates of cucumber  
21 whitefly population adult abundance at 48 h, as well as the abundance of their eggs and pupal  
22 exuviae on cucumber were positive, whereas for poinsettia and tomato whitefly populations,  
23 the estimates on original host were negative, indicating a tendency of higher cucumber  
24 attractiveness as a host for cucumber whitefly population (Figure 6). Poinsettia was the least  
25 suitable as a host for the poinsettia whitefly population compared to the other six host plant  
26 species, as indicated by significantly negative estimates of abundance of pupal exuviae  
27 (Figure 6).

## 29 Discussion

30 Polyphagy of the species does not guarantee a successful progeny development on novel host.  
31 In this study polyphagy of *T. vaporariorum* was frequently followed by egg laying but  
32 resulted in successful development into pupae on only 12 outdoor hosts out of 30 host species  
33 inhabited by adults in the survey. Five new host plant species of the greenhouse whitefly

1 were identified in the host survey. Preference and performance of the insect was affected by  
2 host experience in the host-choice experiment.

3 Performance of the generalist herbivore *T. vaporariorum* was affected by host plant  
4 availability and diversity. The whitefly displayed preference for the most common hosts:  
5 fireweed and *E. montanum* (Onagraceae) and nettle (Urticaceae), as these hosts tended to  
6 contain higher numbers of all *T. vaporariorum* life stages than others in the host survey. Plots  
7 with low and intermediate plant richness were most often occupied by *T. vaporariorum*.  
8 Nymphs occurred more frequently in the less than in the more diverse plots. Preference for  
9 less diverse habitats might be related to poor insect performance in polycultures. For  
10 example, *B. tabaci* has poor oviposition performance in mixtures of host plant species  
11 (Bernays, 1999). Although insect occurrence in less diverse plots coincided with presence of  
12 most preferred hosts in these habitats (68% of Onagraceae and 63% of Urticaceae occurrence  
13 was recorded in less diverse plots), the interaction of plant family and richness was not  
14 significant for either of the dependent variables in the model. Frequent insect occurrence on  
15 members of Onagraceae and Urticaceae might be related to their high nitrogen content  
16 (Jauset et al., 1998), as both fireweed and nettle are nitrophilic plants (Rosnitschek-  
17 Schimmel, 1985; Nams et al., 1993). Alternatively, these hosts may have been preferred due  
18 to their common occurrence. Fireweeds and nettle are widespread species and abundant  
19 and/or commonly occurring host plants have been documented before as preferred hosts for  
20 some herbivores (Agrawal et al., 2006). Onagraceae and Urticaceae plants were frequently  
21 found in the studied plots – both were encountered in 53% of all plots. Although nettle and  
22 fireweed covered on average 12% of the plot, the vertical component was not taken into  
23 account and both species were often the highest species, thereby providing abundant habitats  
24 for insects. Both fireweed and nettle are present in the assumed native areas of European *T.*  
25 *vaporariorum* populations. In the southwest of North America, where fireweeds and nettles  
26 are common, the insect's morphological diversity is high, indicating potential origin of *T.*  
27 *vaporariorum* (Russell, 1948; NatureGate, 2013; USDA & NRCS, 2013). Alternatively, if the  
28 insect population in Europe originated from a single introduction event, the insect may have  
29 come from South America, where pupae were observed on Urticaceae (*U. urens*) (Westwood,  
30 1856; Gonsebatt et al., 2012). Thus, *T. vaporariorum* most likely encountered both fireweed  
31 and nettle during its evolution.

32 Not only are greenhouses sources of *T. vaporariorum* escaping and encountering  
33 common outdoor plants, they also function as shelters from prevailing winds. The occupation  
34 of plots in the east, rather than west by adult whiteflies suggests that the insects may avoid

1 prevailing winds from the Baltic Sea in the surveyed area and this may indicate the location  
2 of initial pest infestation. That pupal numbers were higher on plants in the north rather than in  
3 the west may be explained from the fact that the northern side exits of all three studied  
4 greenhouses are used to bring out old infested plant material at the beginning of the spring  
5 season. Thus, occurrence of pupae in the less windy northern locations indicates the oldest  
6 and initial pest settlement. The avoidance of windy locations outside greenhouses by  
7 whiteflies was observed also around greenhouses in Spain (Gabarra et al., 2004). The  
8 presence of any type of shelter is of vital importance for whiteflies, as adults are only about  
9 1.5 mm long (Martin, 1999). Most of the plants with fewer records of adults in the host  
10 survey have small (*Polygonum aviculare* L. and clover) or pinnately compound leaves  
11 [*Anthriscus sylvestris* (L.) Hoffm.] and thus may provide poor hiding places under windy  
12 conditions (Castane & Albajes, 1992, 1994) or less protection from UV radiation (Ohtsuka &  
13 Osakabe, 2009). Larger host leaves were reported as an attractive characteristic for adults  
14 (Castané & Albajes, 1992). Furthermore, in the choice experiment, total leaf area of a plant  
15 contributed significantly to differences of adult abundance among the hosts. From these  
16 results we can conclude that shelter function is an important characteristic of indoor and  
17 outdoor habitats for such small insects as whiteflies.

18 In the choice experiment, there were clear differences among the seven plants offered  
19 in number of adults after 48 h, as well as in subsequent number of eggs and pupae. The  
20 highest numbers of adults were found on dandelion, whereas most eggs and pupae were  
21 found on fireweed, dandelion, and cucumber. These results suggest that the whiteflies  
22 inherently prefer some native plants over the greenhouse crop species to which they were  
23 preconditioned. In general, occurrence of eggs was more frequent than nymphs or pupae.  
24 This is in concordance with findings of Castané & Albajes (1994) and Greenberg et al.  
25 (2009), who reported that mortality on novel hosts was highest in the egg stage, leading to  
26 lower pupal than egg abundance. The senescence of some leaves before the immature insects  
27 completed their development might be the cause of higher abundance of eggs but fewer pupal  
28 exuviae on fireweeds and dandelions in the choice experiment, as several leaves with eggs on  
29 both hosts decayed during their development (I Ovčarenko, pers. obs.). Reduced whitefly  
30 abundance on nettles in the experiment compared to frequent occurrence on nettles in the host  
31 survey might be associated with different age of plants under natural and experimental  
32 conditions. It has been noticed that whiteflies prefer feeding on younger leaves that are more  
33 nutritious (Martin, 1999); also in nettle younger leaves are more nutritious than older leaves  
34 (Pullin, 1986).

1           Preconditioning to greenhouse crop plants either facilitated *T. vaporariorum* selection  
2 of alternative novel hosts or increased its fecundity on the familiar hosts. Adults of the  
3 whitefly population from tomato preferred alternative hosts more than whiteflies that  
4 originated from cucumber or poinsettia. Preference of a novel rather than a familiar host was  
5 also observed by Shah & Liu (2013). Whiteflies originating from cucumber had higher  
6 fecundity on all hosts than those originating from poinsettia. It has been reported by Yun et  
7 al. (2006) that, at 22-24 °C, development from egg to adult is shortest on cucumber (25 days),  
8 followed by tomato (30 days) and poinsettia (40 days). Fast development usually positively  
9 correlates with high egg abundance on the same host (Greenberg et al., 2009). But host  
10 experience and host switching in general may lead to increased fecundity on novel hosts as  
11 well, as was observed in *B. tabaci* (Carabali et al., 2005). Thus, experience of cucumber host  
12 has resulted in high fecundity of *T. vaporariorum* on other hosts.

13           Results of this study correspond to the host plant ranking for *T. vaporariorum* proposed  
14 by van Lenteren & Noldus (1990). Van Lenteren & Noldus (1990) established host suitability  
15 ranks of *T. vaporariorum* based on mortality and fecundity on several commercial host plants  
16 as follows: eggplant (Solanaceae) > gherkin (Cucurbitaceae) > cucumber (Cucurbitaceae) >  
17 gerbera (Asteraceae) > melon (Cucurbitaceae) > tomato (Solanaceae) > sweet pepper  
18 (Solanaceae). *Trialeurodes vaporariorum* also have a higher preference for eggplant over  
19 poinsettia (Lee et al., 2009, 2010). In the present choice study cucumber had higher adult and  
20 egg abundance than poinsettia and tomato, and higher abundance of pupal exuviae than  
21 poinsettia. Preconditioning to tomato and poinsettia for more than three generations did not  
22 increase attractiveness of these hosts. Thus, we propose a host suitability ranking (in  
23 decreasing order) as follows: cucumber, tomato, and poinsettia. However, further tests are  
24 needed to determine performance of *T. vaporariorum* on poinsettia compared to other plants  
25 in the ranking proposed by van Lenteren & Noldus (1990) that were not used in this study.

26           In the current climatic conditions, live plant material and enclosed environments are  
27 essential for *T. vaporariorum* overwintering in the temperate and boreal latitudes. Adult  
28 whiteflies die from starvation and desiccation within 35 h without host availability (Nauen et  
29 al., 1998). The genus has originated in the Palaeotropics (Boykin et al., 2013), whereas  
30 European populations of *T. vaporariorum* have been suggested to originate from Mexico  
31 (Westwood, 1856). The species lacks a dormant overwintering stage (Stenseth, 1983).  
32 However, frequent occurrence of *T. vaporariorum* on the two common hosts, fireweed and  
33 nettle, may increase its overwintering possibilities if winters get milder. The chances of  
34 overwintering on perennial vegetation, which currently decays in the winter in the boreal

1 climate zone, may increase in the mild winter scenarios due to climate change (Peltonen-  
2 Sainio et al., 2009) that would facilitate the prolonged occurrence of such plants in late  
3 autumn and winter. The mean winter temperature in southern Finland is predicted to rise to 0  
4 °C and mean snow depth to decrease by 80% by the end of this century (Jylhä et al., 2009).  
5 The most frequently inhabited hosts of *T. vaporariorum* among the Onagraceae and  
6 Urticaceae families are characterized by late occurrence in the autumn. Pupae of *T.*  
7 *vaporariorum* were found on both species until the beginning of October in 2010 and 2011,  
8 i.e., until the first frosts killed the plants (J Granfors, pers. obs.) In the British Isles, *T.*  
9 *vaporariorum* has been able to overwinter outside greenhouses on *U. dioica* and *Lamium*  
10 spec. with eggs and adults being the most cold resistant (Lloyd, 1922). In Germany the  
11 greenhouse whitefly has been noticed on evergreen plants like *Stellaria* spec. and *Urtica*  
12 spec. after frosts in October, and was spotted flying outside greenhouses on warm days in  
13 January (Bodenstein, 1952). Some populations have demonstrated cold resistance elsewhere,  
14 provided of course that they have access to host plants. In England and the Channel Islands,  
15 flying *T. vaporariorum* adults have been observed after snowfall and at -5 °C (Lloyd, 1922).  
16 *Trialeurodes vaporariorum* exposure to +2 °C for 12 days did not cease the development of  
17 45% of its eggs and red-eyed nymphs, and 80% of its adults survived for 7 days at the same  
18 temperature (Cui et al., 2007).

19 Another common plant species, dandelion, was less preferred as a host in the survey but  
20 was one of the most preferred in the experiment. It may have even higher potential to serve as  
21 overwintering habitat for *T. vaporariorum* than fireweed or nettle. Survival of whiteflies  
22 during winter may also be possible due to the development of a behavioural strategy, such as  
23 aggregation in microhabitats (e.g., wall cracks and leaf litter) creating a microclimate to avoid  
24 exposure to temperature extremes (Berkvens et al., 2010). Greenhouses that are heated during  
25 the whole winter may also form such microhabitats for some host plants of the whitefly,  
26 which needs a live plant to survive extended periods. Green leaves of dandelion have been  
27 observed in snowless plots near greenhouses and under the snow cover in mild winters in  
28 South West Finland (J Granfors, pers. obs.). Thus, dandelions could offer a possibility for the  
29 greenhouse whitefly eggs and adults to stay alive over the winter months under outdoor  
30 conditions in the absence of prolonged exposure to subzero temperatures.

31 The insect's overwintering under current conditions in Scandinavia would require the  
32 acquisition of cold hardy traits. Under repetitive exposure to subzero temperatures many  
33 insects are able to develop various strategies of cold hardiness (Danks, 1996). *Trialeurodes*  
34 *vaporariorum* has persisted in Finland since 1920 (Linnaniemi, 1921); however, its cold

1 tolerance in the boreal zone remains unexplored.

2

### 3 **Implications for whitefly pest management**

4 *Trialeurodes vaporariorum* is a pest currently present in Finland only in greenhouses. Its  
5 main host plants are cucumber and tomato, which are the most common greenhouse crops in  
6 Finland (TIKE & OSF, 2014). Prolonged experience of highly preferred cucumber may  
7 facilitate development of large pest populations indoors. Subsequent high fecundity on  
8 outdoor plant species may facilitate naturalization of this generalist herbivore. Similarly, an  
9 ability to utilize native flora together with the preference of whiteflies from tomato or  
10 poinsettia populations for native flora may also contribute to the invasion potential of this  
11 greenhouse pest. It should be considered in pest management plans that large leaf areas of  
12 cucumber and tomato have the potential to support high whitefly abundance and pose bigger  
13 challenges to whitefly management compared to small potted ornamental crops, such as  
14 poinsettia. Such challenges have recently been addressed in the greenhouse aggregation,  
15 where the current study's host plant survey was performed (Vänninen et al., 2015). The key  
16 issue is to move away from whitefly management based on short-term decision making in  
17 individual greenhouses. Instead, plant producers should favour strategies that consider the  
18 movement of the pest between greenhouses of different production forms (year-round vs.  
19 seasonal greenhouses and their connections, greenhouses with different crop plant species)  
20 (Ovčarenko et al., 2014a). Collective pest management strategies could also reduce the  
21 spreading of individuals that carry genes coding for insecticide resistance (Naranjo &  
22 Ellsworth, 2009; Ovčarenko et al., 2014b).

23 Populations that have lived for 3-4 generations on outdoor hosts may show  
24 differential performance on crop plants upon returning to the greenhouses in the autumn to  
25 overwinter in warm conditions. This differential performance may affect the ability of  
26 biocontrol agents to regulate the pest and, thus, the success of biological control. Biological  
27 control is problematic in the winter months in year-round crops (Vänninen et al., 2010;  
28 Johansen et al., 2011). Even under less challenging conditions, on plant species that are good  
29 hosts for the whitefly, it is crucial that the pest be controlled successfully from the very  
30 beginning of the infestation when pest densities are low (van Lenteren et al., 1996). Future  
31 studies are needed to evaluate (1) the performance of first generations of the pest that moves  
32 from outdoor host species to crop plants, and (2) the cold tolerance of local populations.

33 The best practical strategy to reduce pest pressure on greenhouses from outdoors in  
34 the autumn is to have grass surrounding greenhouses, in which the pest cannot survive. We

1 have shown previously that whiteflies collected from individual greenhouses, both isolated  
2 and near each other, were often genetically similar in consecutive years (Ovčarenko et al.,  
3 2014a). This indicates that individual greenhouses are mostly circulating their own  
4 greenhouse whiteflies between the indoor and outdoor environments. Although fireweed can  
5 form extensive stands in the study area, we could not find whiteflies on stands that were  
6 located  $\geq 5$  m from greenhouses, even if the pest was very abundant on plants growing in the  
7 immediate vicinity of the greenhouse (I Ovčarenko & I Vänninen, pers. obs.). Upon arriving  
8 outdoors, the pest seems to prefer to stay on the nearest potential host plants. Some weedy  
9 plants growing in the immediate vicinity of the greenhouses are an important source of  
10 propagules that re-enter crops in the autumn and should therefore be eliminated. Some  
11 greenhouse producers follow this practice already, whereas others do not. The challenge is to  
12 convince all producers that what happens within the nearest few meters from their  
13 greenhouse is important not only for the health of their own greenhouse crops, but most likely  
14 also for the general plant health in the whole area in the long term.

15

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23

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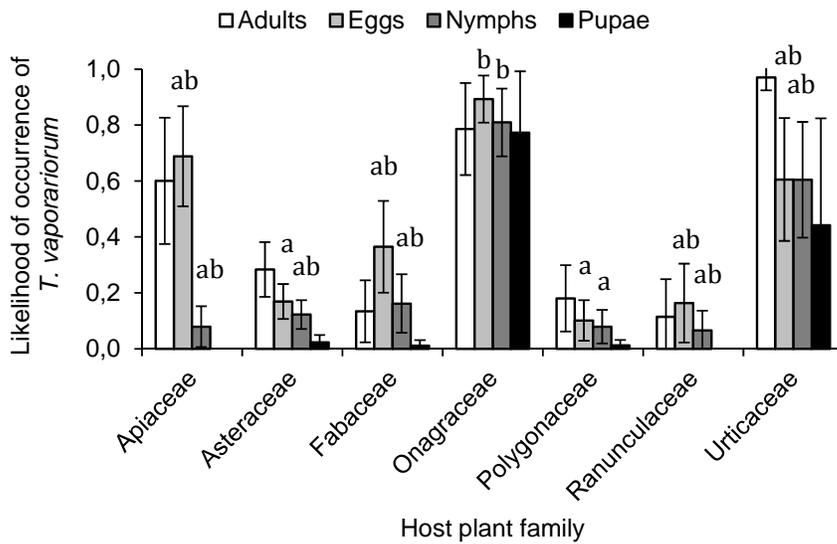
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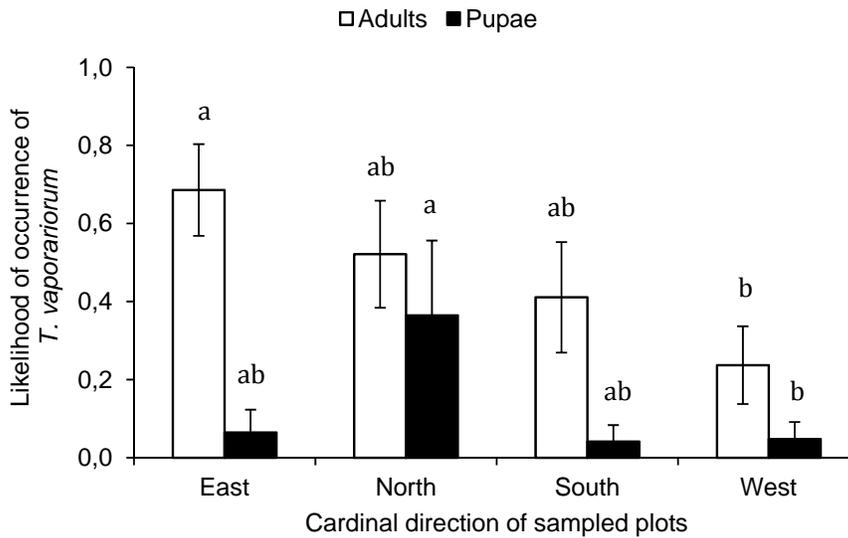
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1 **Figures**



2

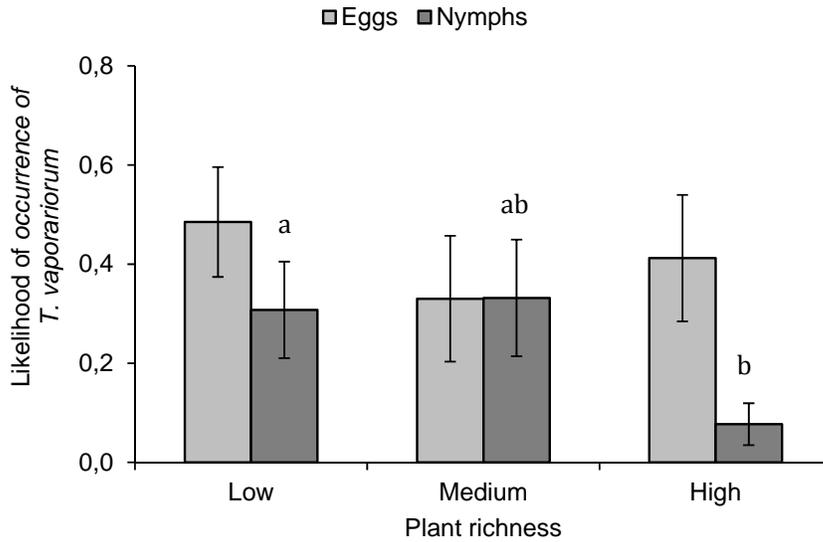
3 **Figure 1** Mean ( $\pm$  SE) estimates of the likelihood of occurrence of *Trialeurodes*  
 4 *vaporariorum* on host plant families (family names refer only to the species outlined in Table  
 5 1). Means within a development stage capped with different letters are significantly different  
 6 among plant families (Tukey-Kramer adjusted  $P < 0.05$ ). Note that family effect in the pupal  
 7 model has marginal significance ( $P = 0.080$ ), but categories of this effect (host families) were  
 8 included in the figure to show the trend.



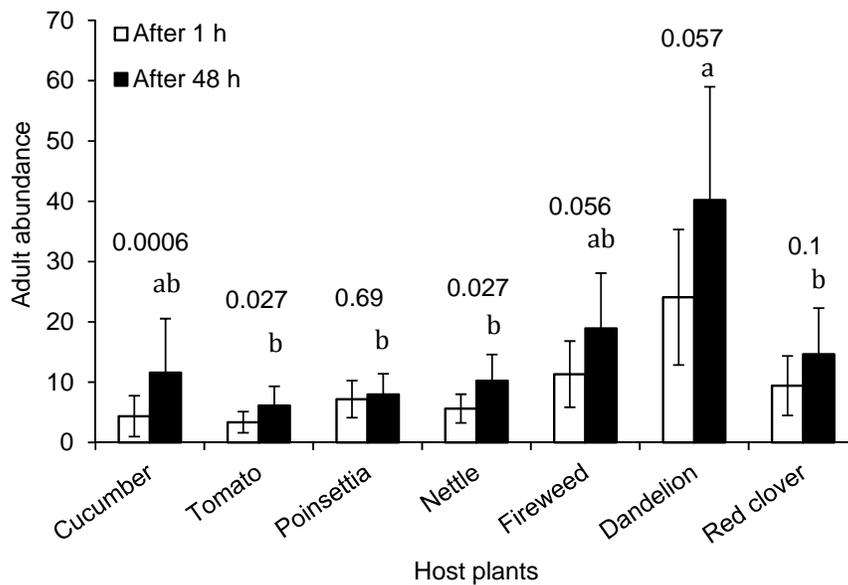
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10 **Figure 2** Mean ( $\pm$  SE) estimates of the likelihood of occurrence of *Trialeurodes*  
 11 *vaporariorum* in cardinal directions of the surveyed plots. Only variables with significant  
 12 cardinal direction effect (Table 2) are displayed. Means within a development stage

1 capped with different letters are significantly different among cardinal directions (Tukey-  
 2 Kramer adjusted  $P < 0.05$ ).



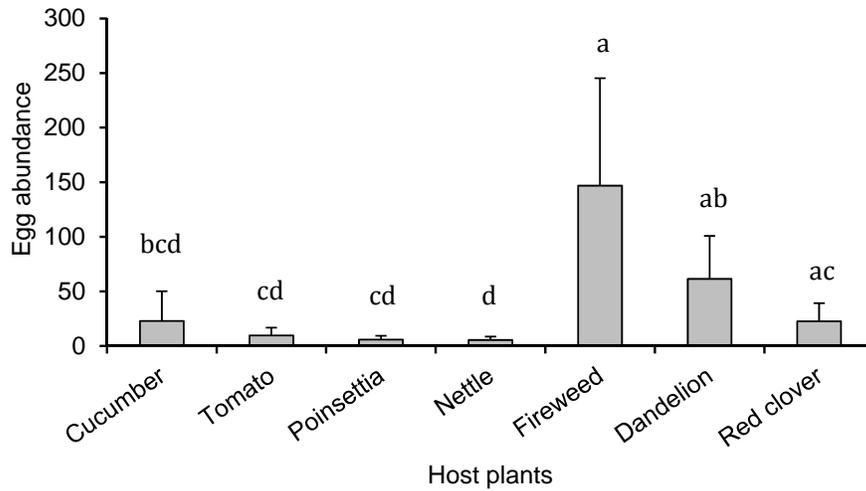
3  
 4 **Figure 3** Mean ( $\pm$  SE) estimates of the likelihood of occurrence of *Trialeurodes*  
 5 *vaporariorum* in surveyed plots consisting of low, medium, and highly rich flora. Only  
 6 variables with significant (Table 2) plant diversity effect are displayed. Means capped with  
 7 different letters are significantly different (Tukey-Kramer adjusted  $P < 0.05$ ).



8  
 9 **Figure 4** Mean ( $\pm$  SE) estimates of abundance of *Trialeurodes vaporariorum* adults after 1 h  
 10 vs. 48 h on seven offered hosts. The numbers above the various host plants indicate P-values  
 11 based on pairwise comparisons of abundance after 1 vs. 48 h (estimated by differences of  
 12 least-squares means). Mean abundances after 48 h capped with different letters are

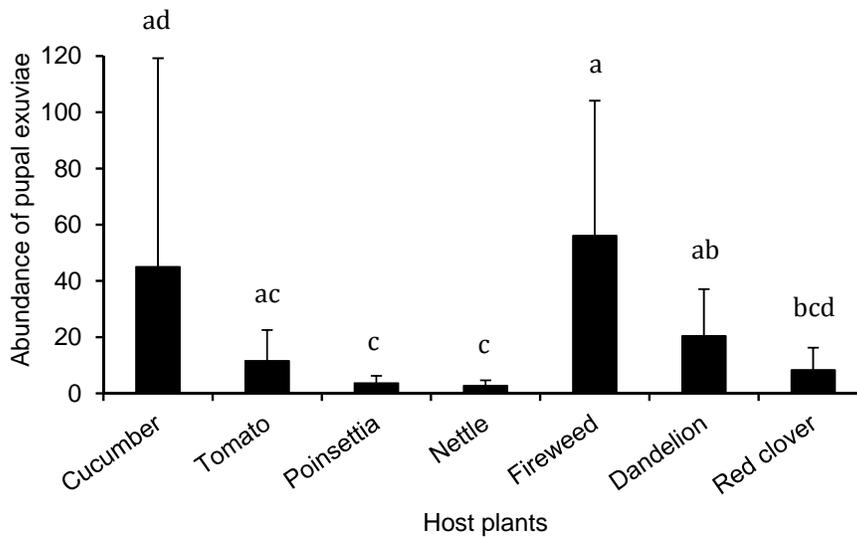
1 significantly different among hosts (Tukey-Kramer adjusted  $P < 0.05$ ).

A



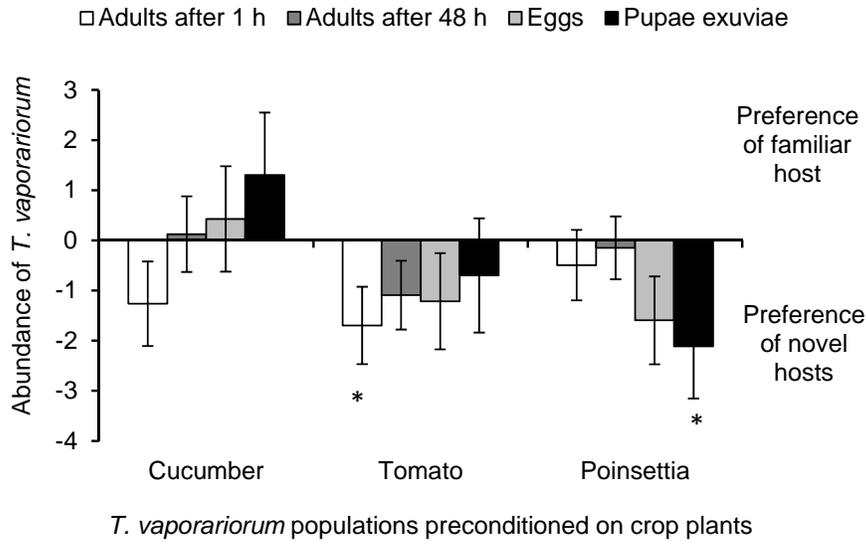
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B



3

4 **Figure 5** Mean (+ SE) estimates of abundance of *Trialeurodes vaporariorum* (A) eggs and  
5 (B) pupal exuviae on the seven offered hosts. Means within a panel capped with different  
6 letters are significantly different (Tukey-Kramer adjusted  $P < 0.05$ ).



1

2 **Figure 6** Mean ( $\pm$  SE) estimates of preference of *Trialeurodes vaporariorum* of original host  
 3 used for preconditioning vs. six other host plants, based on abundance of adults after 1 h and  
 4 48 h, eggs, and pupal exuviae. When an estimate is positive, the original host used for  
 5 preconditioning has higher abundance than the other six offered plants; if negative, the  
 6 abundance is lower. Asterisks indicate significant differences between estimates of least-  
 7 squares means ( $P < 0.05$ ) of abundance on original vs. the six other hosts (comparison made  
 8 within each variable separately).

9

1 **Table 1** Outdoor plants infested by *Trialeurodes vaporariorum*. Suitable hosts are indicated by presence of pupae. Absence of reference denotes  
 2 host novelty and is indicated in bold. Flowering time in Finland and life span were taken from NatureGate (2013). Flowering time and life span  
 3 of plants species that were not identified to species levels are shown for the whole family. All plant species are native but not endemic to  
 4 Finland, commonly occurring in the boreal zone (LNT, 2014)

Family	Host plants	Life span	Flowering time in Finland	Life stages found in survey	References	
					Genus	Species
Amaranthaceae	<i>Chenopodium album</i> L.	Annual	June–September	Adults	B,R	R
Apiaceae	<i>Aegopodium podagraria</i> L.	Perennial	June–August	Adults, eggs, nymphs		
	<i>Angelica sylvestris</i> L.	Perennial	July–August	Adults, eggs		
	<i>Anthriscus sylvestris</i> (L.) Hoffm.	Perennial	June–July	Adults, eggs		
	<i>Heracleum sphondylium</i> L.	Perennial	July–August	Adults, eggs		
Asteraceae	<i>Achillea millefolium</i> L.	Perennial	July–September	Adults, eggs	B	B
	<i>Artemisia vulgaris</i> L.	Perennial	August–October	Adults, eggs, nymphs, pupae	B,M	B,M
	<i>Carduus crispus</i> L.	Biennial	July–September	Adults, eggs, nymphs, pupae		
	<i>Cirsium heterophyllum</i> L.	Perennial	July–September	Adults	B	
	<i>Leontodon autumnalis</i> L.	Perennial	July–September	Adults		
	<i>Senecio viscosus</i> L.	Annual	July–September	Adults, eggs, nymphs, pupae	B	
	<i>Sonchus arvensis</i> L.	Perennial	July–August	Adults, eggs, nymphs, pupae	B,M,R	B,M
	<i>Tanacetum vulgare</i> L.	Perennial	July–September	Adults, eggs, nymphs	B	B
	<i>Taraxacum officinale</i> F.H. Wigg .	Perennial	May–July	Adults, eggs, nymphs, pupae	B,M,R	B
Fabaceae	<i>Trifolium pratense</i> L.	Perennial	June–August	Adults, eggs, nymphs, pupae	B,L,M,R	B,L,M,R
	<i>Trifolium repens</i> L.	Perennial	June–August	Eggs, nymphs	B,R	R
	<i>Vicia cracca</i> L.	Perennial	June–August	Adults, eggs, nymphs	B,M,R	B
Geraniaceae	<i>Geranium</i> spec.	Annual/perennial	June–September	Adults, eggs, nymphs, pupae	M,R	

Lamiaceae	<i>Galeopsis bifida</i> Boenn	Annual	July–September	Adults, eggs		
	<i>Galeopsis spec.</i>	Annual	May–October	Eggs		
Onagraceae	<i>Chamerion angustifolium</i> (L.) Holub	Perennial	July–August	Adults, eggs, nymphs, pupae	M	
	<i>Epilobium montanum</i> L.	Perennial	July–August	Adults, eggs, nymphs, pupae	M	
Polygonaceae	<i>Persicaria maculosa</i> Gray	Annual	July–September	Adults, eggs, nymphs, pupae	B	B
	<i>Polygonum aviculare</i> L.	Annual	July–September	Adults, eggs, nymphs	M,B	B,M
	<i>Rumex acetosa</i> L.	Perennial	May–July	Adults, eggs	B	
	<i>Rumex acetosella</i> L.	Perennial	June–August	Adults, eggs, nymphs	B	
	<i>Rumex longifolius</i> DC.	Perennial	July–September	Adults	B	
	<i>Rumex spec.</i>	Perennial	July–September	Adults	B	
Ranunculaceae	<i>Ranunculus repens</i> L.	Perennial	June–July	Adults, eggs, nymphs		
Rosaceae	<i>Filipendula ulmaria</i> L.	Perennial	June–August	Adults		
	<i>Rubus idaeus</i> L.	Biennial	June–July	Adults, eggs, nymphs, pupae	M	
Urticaceae	<i>Urtica dioica</i> L.	Perennial	July–September	Adults, eggs, nymphs, pupae	B,L,M,R	B,L,M

1 L, Lloyd, 1922; B, Bodenstern, 1952; M, Mound & Halsey, 1978; R, Roditakis, 1990

2

1 **Table 2** Estimates of the likelihood of occurrence of *Trialeurodes vaporariorum* adult, egg,  
 2 and pupae in a host-plant survey. Only significant effects are presented based on type III  
 3 estimation methods for variance components. P-value is based on a mixture of chi-squares.

Variable	Effects		F, $\chi^2$	P
Adult occurrence likelihood	Fixed	Family	$F_{6,149} = 2.32$	0.036
		Species cover	$F_{1,149} = 16.35$	<0.0001
		Cardinal direction	$F_{3,149} = 3.18$	0.026
	Random	Plant species*greenhouse	$\chi^2 = 9.69$	0.001
Egg occurrence likelihood	Fixed	Family	$F_{6,143} = 3.32$	0.004
		Species cover	$F_{1,143} = 12.55$	0.001
		Plant richness	$F_{2,143} = 3.35$	0.038
		Species cover*plant richness	$F_{2,143} = 4.17$	0.017
		Cardinal direction	$F_{3,143} = 1.54$	0.21
	Random	Plant species	$\chi^2 = 1.33$	0.12
		Plot number	$\chi^2 = 1.26$	0.13
Nymph occurrence likelihood	Fixed	Family	$F_{6,147} = 3.42$	0.003
		Species cover	$F_{1,147} = 3.55$	0.062
		Plant richness	$F_{2,147} = 3.48$	0.033
		Cardinal direction	$F_{3,147} = 1.87$	0.14
	Random	Plant species	$\chi^2 = 3.82$	0.025
Pupae occurrence likelihood	Fixed	Family	$F_{4,126} = 2.14$	0.080
		Species cover	$F_{1,126} = 6.48$	0.012
		Cardinal direction	$F_{3,126} = 3.22$	0.025
	Random	Plant species*Greenhouse	$\chi^2 = 7.13$	0.004

4

1 **Table 3** Estimates of *Trialeurodes vaporariorum* adult abundance at 1 and 48 h, egg and pupae exuviae abundance, as well as *T. vaporariorum*  
 2 abundance on original vs. six other hosts in a choice experiment based on type III estimation methods for variance components

Variable	Fixed effect	F	P	Random effect	Z	P
Adult abundance after 1 h	Origin	$F_{2,4} = 1.04$	0.43	Repeat number	0.44	0.33
	Host	$F_{6,35} = 2.19$	0.067	Origin*repeat number	0	–
	Origin*host	$F_{12,35} = 1.48$	0.18	Residual	4.41	<0.001
	Leaf area	$F_{1,35} = 7.14$	0.011			
Adult abundance after 48 h	Origin	$F_{2,4} = 1.69$	0.30	Repeat number	0.8	0.21
	Host	$F_{6,35} = 2.76$	0.026	Origin*repeat number	0	–
	Origin*host	$F_{12,35} = 1.74$	0.10	Residual	4.42	<0.001
	Leaf area	$F_{1,35} = 3.33$	0.077			
Egg abundance	Origin	$F_{2,4} = 5.33$	0.074	Repeat number	0	–
	Host	$F_{6,35} = 6.57$	0.001	Origin*repeat number	0.61	0.27
	Origin*host	$F_{12,35} = 1.05$	0.43	Residual	4.18	<0.001
	Leaf area	$F_{1,35} = 2.96$	0.094			
Pupae exuviae abundance	Origin	$F_{2,4} = 4.45$	0.096	Repeat number	0	–
	Host	$F_{6,35} = 4.35$	0.002	Origin*repeat number	0.57	0.28
	Origin*host	$F_{12,35} = 0.73$	0.71	Residual	4.17	<0.001
	Leaf area	$F_{1,35} = 1.1$	0.30			
1 vs. 48 h adult abundance	Time	$F_{1,2} = 7.66$	0.11	Origin*host*repeat number	3.94	<0.001
	Time*origin	$F_{4,4} = 0.94$	0.52	Time*repeat number	0.53	0.30

Time*host	$F_{12,35} = 2.09$	0.044	Time*origin*repeat number	0.83	0.20
Time*origin*host	$F_{24,35} = 1.7$	0.074	Residual	4.24	<0.001
Leaf area	$F_{1,35} = 4.74$	0.036			

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1

2