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

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Abstract

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

Introduction

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

Preference and performance of herbivores on novel hosts depends not only on their inherent diet breadths but also on their host experience. Preconditioning or long-term experience of a host might in some cases lead to changes of host preference that can be either cumulative or reversible (Papaj & Prokopy, 1989), whereas in other cases preconditioning has no effect on insect performance (Lee et al., 2010). Preconditioning may cause differences in insect performance in terms of fecundity, survival, and development time on experienced compared to novel hosts (Thomas, 1993; Coyle et al., 2011). Ultimately, on an evolutionary time scale, such differences could lead to speciation through host races (Drès & Mallet, 2002). Adaptation to plant chemistry allows increasing insect abundance over time, resulting in outbreaks of insect pests in monocultures (Altieri & Nicholls, 2004), whereas in polycultures the majority of herbivorous arthropods is not able to reach high abundance due to plant stand or plant life-history characteristics (Andow, 1991; Altieri, 1999). Theoretically, prolonged experience on a single host-plant species in commercial greenhouses could change the performance of herbivorous insects on novel hosts in outdoor habitats. Temperate year-round greenhouses provide an environment that facilitates prolonged preconditioning of herbivorous insects on one plant species over several generations during the autumn and winter time. In the spring and summer, the herbivores have access to mixtures or monoculture stands of novel host plant species outside the greenhouses. The insects reach the outdoor environment from within the greenhouses either by voluntary migration through vents or via plant parts that are removed from the greenhouse. Our previous findings suggested that prolonged experience on a particular host plant species in the greenhouse contributes to genetic differences between *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) populations collected from year-round tomato (*Solanum lycopersicum* L.) and cucumber (*Cucumis sativus* L.) greenhouses (Ovčarenko et al., 2014a). This may be partly explained by adaptation to the monoculture hosts in question. The ability of generalist herbivores to achieve pest status in enclosed greenhouse monocultures, coupled with their temporal access to outdoor polycultures, offers a chance to study the resource use of generalist herbivores.

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

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

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

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

Materials and methods

Host plant survey

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

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

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

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

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

Host choice experiment

Whitefly populations. Trialeurodes vaporariorum was originally collected from indoor crops (roses, in Honkajoki, Finland) in 2007 and since then has been maintained on poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch). To test for the effect of host plant experience on host choice, we divided this population into three by transferring 100 adults of mixed sex into separate Plexiglas cages with either tomato (cv. Encore), cucumber (cv. Eminentia), or poinsettia (cv. Allegra by Lazzeri) – three major crops in Finland. These three *T. vaporariorum* populations were then maintained in the greenhouses of Natural Resources Institute Finland (Luke) in Jokioinen for 1 year before the start of the choice experiment in 2012. The requirement of *T. vaporariorum* for a minimum period of adjustment on the novel host for three generations (Greenberg et al., 2009) was fulfilled for all populations.

Plant cultures. The plant species offered in the choice experiment included both commonly cultivated and wild plant species. The cultivated plant species and cultivars were the same as used for whitefly populations: cucumber, tomato, or poinsettia. The wild plant species were chosen on the basis of the host plant survey and they were nettle, fireweed, dandelion, and red clover (*Trifolium pratense* L.). The wild plant species were grown from seeds purchased from Herbiseed (Reading, UK). All host plants used in the experiments were grown in a pest-free greenhouse prior to the experiments. The pots contained peat and were watered daily with the same fertilizer solution of NP_2O_3-$K_2O(MgO)$ 14-5-21(2) (Ferticare KOMBI1; Yara, Helsinki, Finland). The greenhouse climatic settings throughout the experiment were as follows: 20-24 °C and L16:D8 photoperiod maintained by high-pressure sodium lamps (200 W; Philips, Amsterdam, The Netherlands).

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

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

Experimental protocol. The release of *T. vaporariorum* populations was performed in three separate greenhouse compartments (l × w × h = 8.5 × 2.8 × 6 m) and repeated 3× for each population, each time randomizing location (greenhouse room) and arrangement of the plants. Whiteflies of mixed age were collected individually in glass vials from Plexiglas cages containing host plant and whitefly culture. The glass vials were sealed with cotton and briefly chilled on ice. The sex of immobilized insects was determined under stereo microscope based on the shape of the abdomen and presence of ovipositor in females, as opposed to claspers and aedeagus in males (Gerling, 1990). Females were aspirated from glass vials to the container, which was positioned in the centre of the plant circle, i.e., at a 50-cm distance from the plants. The container contained 230 females during each release into a greenhouse compartment. The container with *T. vaporariorum* females and the pots with seven host plants were of the same height (15 cm) to provide equal access opportunity. *Trialeurodes vaporariorum* was released before dusk on the day of collection. Host selection was recorded by counting the *T. vaporariorum* females on every host plant species at 1 and 48 h after release, to avoid bias regarding host preference by adults due to random landing. Before the last adult counting, the containers were checked to confirm the absence of dead or live insects. After 48 h, females were collected from all plants by a mouth aspirator and the plants were moved into a separate clean greenhouse (9.3 × 4.3 × 6 m) to monitor egg development. Females of *T. vaporariorum* are able to lay fertilised eggs for over a month after coitus and to reproduce by arrthenotokous parthenogenesis (Lloyd, 1922; Aahman & Ekbom, 1981). Fecundity was estimated by counting *T. vaporariorum* eggs after 6 days from the start of the experiment, when they became darker and more easily visible, using ×10 magnification lenses. Plant species suitability was estimated by counting pupal exuviae of hatched *T. vaporariorum* adults. Plants were checked on a daily basis and pupal exuviae were counted when full development was observed on plant species based on personal observations of maximum adult emergence rates. Therefore, pupal exuviae were recorded after 35 days from the start of the experiment on tomato, cucumber, dandelion, and fireweed and after 42 days from the start of the experiment on poinsettia, red clover, and nettle. Whitefly releases and counting of eggs and pupal exuviae were carried out from October to mid-December, 2012.

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

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

Results

Host plant survey

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

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

Plant cover, plant richness, and cardinal direction played an important role for *T. vaporariorum* habitat choice (Table 2). Odds for the occurrence of *T. vaporariorum* adult, egg, and pupa were higher with increasing percentage of plant cover in the plots. Furthermore, plant cover interacted with plant richness and both variables had a cumulative positive effect for egg occurrence. Interactions of plant family and plant cover or family and richness were not significant for either of the dependent variables. Thus, insect occurrence on these families was not related to plant abundance, and insect occurrence in less diverse plots was not related to family occurrence in these habitats. Similarly, there were no significant interactions between cardinal direction and other fixed or random effects, indicating that insect occurrence in either direction is independent of plant occurrence data. Results of cross table analyses were similar to those of regression models. Adults occurred more frequently in the east than in the west (χ^2 = 11.510, d.f. = 3, P = 0.009; OR = 7.018, t = 2.99, d.f. = 149, P = 0.017), whereas pupae occurred more frequently in the north than in the west (OR = 11.398, t = 2.61, d.f. = 126, P = 0.049; Figure 2). According to results of cross table analysis, the highest level of adult and pupal abundance was observed less frequently in plots with high plant richness (adult: χ^2 = 3.829, d.f. = 1, P = 0.050; pupa: χ^2 = 7.616, d.f. = 1, P = 0.006). However, this result was only partially supported in regression models. Plant richness significantly affected egg and nymph occurrence (Table 2) and the latter tended to accumulate in plots with low rather than with high richness (OR= 5.318, t = 2.51, d.f. = 147, P = 0.035; Figure 3).

Host choice experiment

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

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

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

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

Discussion

Polyphagy of the species does not guarantee a successful progeny development on novel host. In this study polyphagy of *T. vaporariorum* was frequently followed by egg laying but resulted in successful development into pupae on only 12 outdoor hosts out of 30 host species inhabited by adults in the survey. Five new host plant species of the greenhouse whitefly were identified in the host survey. Preference and performance of the insect was affected by host experience in the host-choice experiment.

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

Not only are greenhouses sources of *T. vaporariorum* escaping and encountering common outdoor plants, they also function as shelters from prevailing winds. The occupation of plots in the east, rather than west by adult whiteflies suggests that the insects may avoid prevailing winds from the Baltic Sea in the surveyed area and this may indicate the location of initial pest infestation. That pupal numbers were higher on plants in the north rather than in the west may be explained from the fact that the northern side exits of all three studied greenhouses are used to bring out old infested plant material at the beginning of the spring season. Thus, occurrence of pupae in the less windy northern locations indicates the oldest and initial pest settlement. The avoidance of windy locations outside greenhouses by whiteflies was observed also around greenhouses in Spain (Gabarra et al., 2004). The presence of any type of shelter is of vital importance for whiteflies, as adults are only about 1.5 mm long (Martin, 1999). Most of the plants with fewer records of adults in the host survey have small (*Polygonum aviculare* L. and clover) or pinnately compound leaves [*Anthriscus sylvestris* (L.) Hoffm.] and thus may provide poor hiding places under windy conditions (Castane & Albajes, 1992, 1994) or less protection from UV radiation (Ohtsuka & Osakabe, 2009). Larger host leaves were reported as an attractive characteristic for adults (Castané & Albajes, 1992). Furthermore, in the choice experiment, total leaf area of a plant contributed significantly to differences of adult abundance among the hosts. From these results we can conclude that shelter function is an important characteristic of indoor and outdoor habitats for such small insects as whiteflies.

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

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

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

In the current climatic conditions, live plant material and enclosed environments are essential for *T. vaporariorum* overwintering in the temperate and boreal latitudes. Adult whiteflies die from starvation and desiccation within 35 h without host availability (Nauen et al., 1998). The genus has originated in the Palaeotropics (Boykin et al., 2013), whereas European populations of *T. vaporariorum* have been suggested to originate from Mexico (Westwood, 1856). The species lacks a dormant overwintering stage (Stenseth, 1983). However, frequent occurrence of *T. vaporariorum* on the two common hosts, fireweed and nettle, may increase its overwintering possibilities if winters get milder. The chances of overwintering on perennial vegetation, which currently decays in the winter in the boreal climate zone, may increase in the mild winter scenarios due to climate change (Peltonen-Sainio et al., 2009) that would facilitate the prolonged occurrence of such plants in late autumn and winter. The mean winter temperature in southern Finland is predicted to rise to 0 °C and mean snow depth to decrease by 80% by the end of this century (Jylhä et al., 2009). The most frequently inhabited hosts of *T. vaporariorum* among the Onagraceae and Urticaceae families are characterized by late occurrence in the autumn. Pupae of *T. vaporariorum* were found on both species until the beginning of October in 2010 and 2011, i.e., until the first frosts killed the plants (J Granfors, pers. obs.) In the British Isles, *T. vaporariorum* has been able to overwinter outside greenhouses on *U. dioica* and *Lamium* spec. with eggs and adults being the most cold resistant (Lloyd, 1922). In Germany the greenhouse whitefly has been noticed on evergreen plants like *Stellaria* spec. and *Urtica* spec. after frosts in October, and was spotted flying outside greenhouses on warm days in January (Bodenstein, 1952). Some populations have demonstrated cold resistance elsewhere, provided of course that they have access to host plants. In England and the Channel Islands, flying *T. vaporariorum* adults have been observed after snowfall and at -5 °C (Lloyd, 1922). *Trialeurodes vaporariorum* exposure to +2 ºC for 12 days did not cease the development of 45% of its eggs and red-eyed nymphs, and 80% of its adults survived for 7 days at the same temperature (Cui et al., 2007).

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

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

Implications for whitefly pest management

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

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

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

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Figures

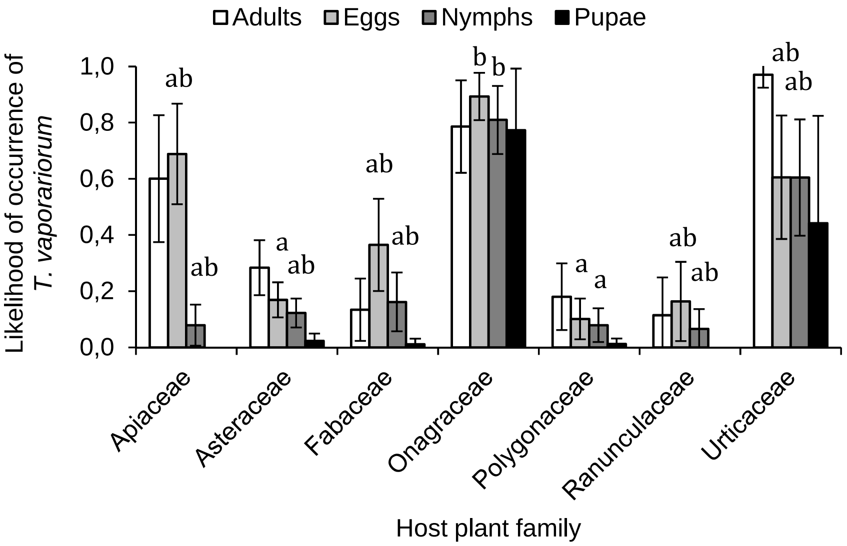

Figure 1 Mean (± SE) estimates of the likelihood of occurrence of *Trialeurodes vaporariorum* on host plant families (family names refer only to the species outlined in Table 1). Means within a development stage capped with different letters are significantly different among plant families (Tukey-Kramer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

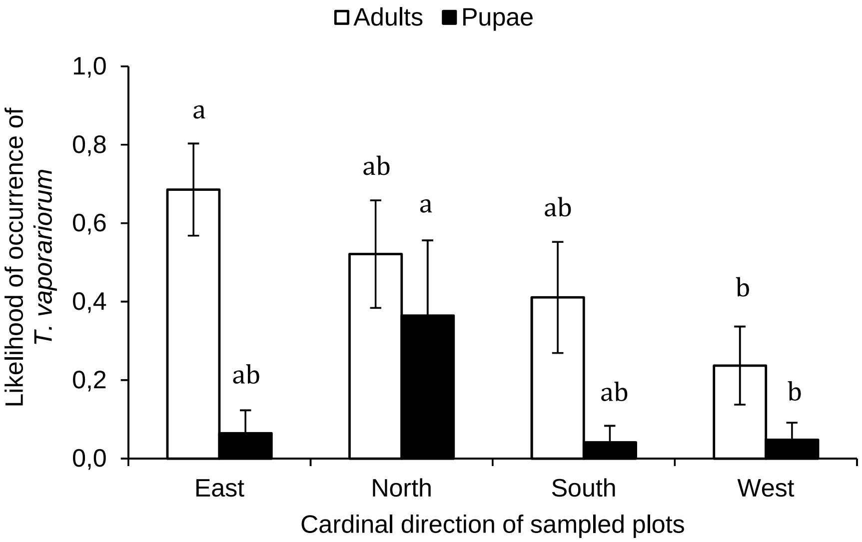

Figure 2 Mean (± SE) estimates of the likelihood of occurrence of *Trialeurodes vaporariorum* in cardinal directions of the surveyed plots. Only variables with significant cardinal direction effect (Table 2) are displayed. Means within a development stage

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

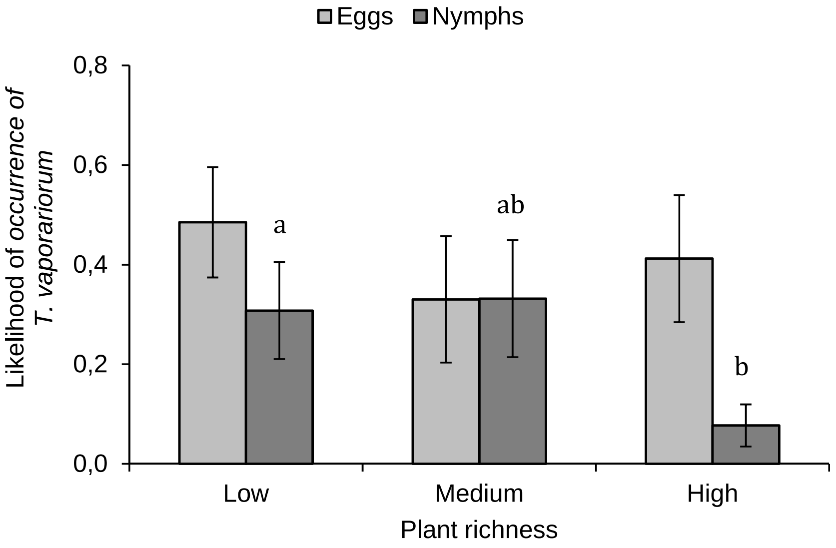

Figure 3 Mean (± SE) estimates of the likelihood of occurrence of *Trialeurodes vaporariorum* in surveyed plots consisting of low, medium, and highly rich flora. Only variables with significant (Table 2) plant diversity effect are displayed. Means capped with different letters are significantly different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

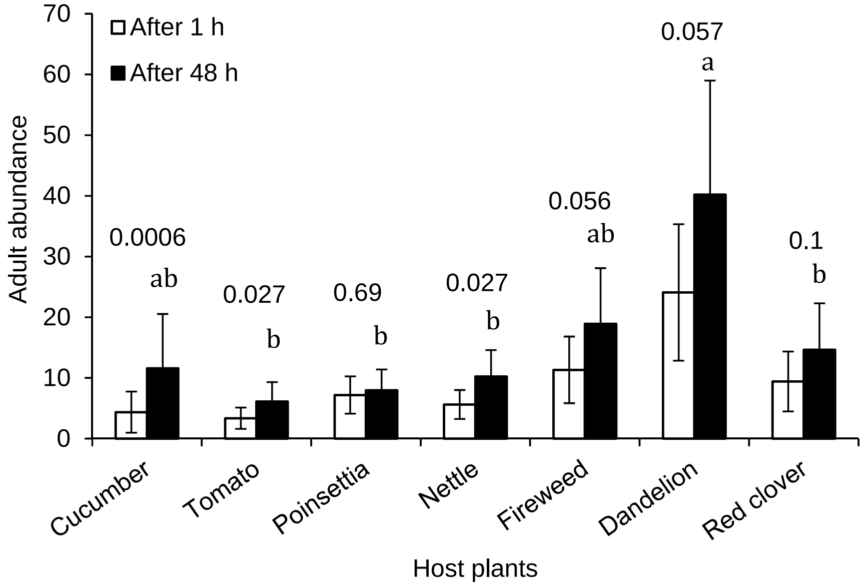

Figure 4 Mean (± SE) estimates of abundance of *Trialeurodes vaporariorum* adults after 1 h vs. 48 h on seven offered hosts. The numbers above the various host plants indicate P-values based on pairwise comparisons of abundance after 1 vs. 48 h (estimated by differences of least-squares means). Mean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

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

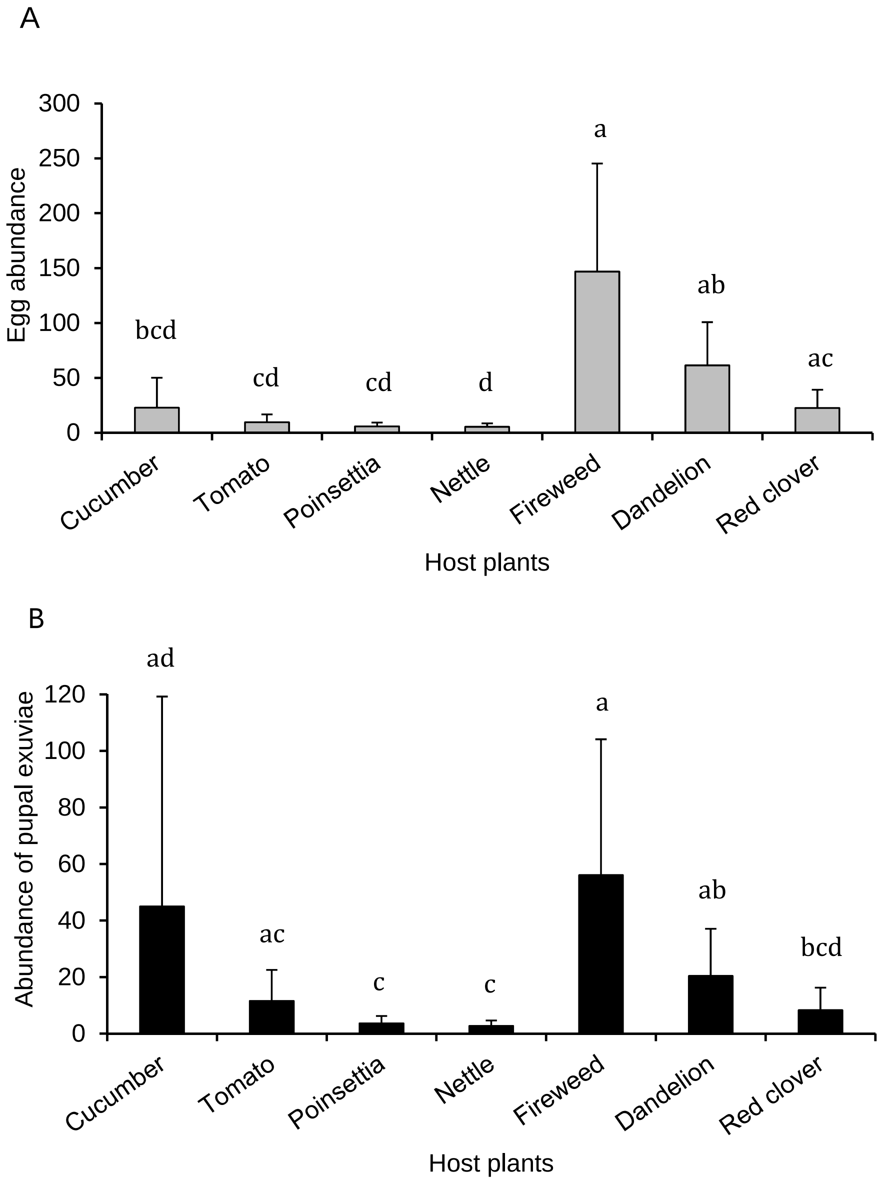

Figure 5 Mean (+ SE) estimates of abundance of *Trialeurodes vaporariorum* (A) eggs and (B) pupal exuviae on the seven offered hosts. Means within a panel capped with different letters are significantly different (Tukey-Kramer adjusted P<0.05).

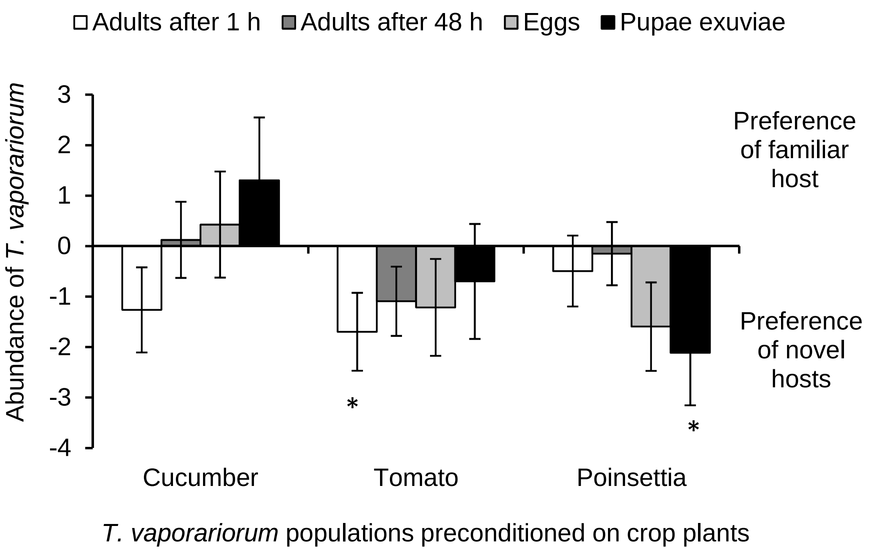

Figure 6 Mean (± SE) estimates of preference of *Trialeurodes vaporariorum* of original host used for preconditioning vs. six other host plants, based on abundance of adults after 1 h and 48 h, eggs, and pupal exuviae. When an estimate is positive, the original host used for preconditioning has higher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

Table 1 Outdoor plants infested by *Trialeurodes vaporariorum*. Suitable hosts are indicated by presence of pupae. Absence of reference denotes host novelty and is indicated in bold. Flowering time in Finland and life span were taken from NatureGate (2013). Flowering time and life span 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 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	*Chenopodium album* L.	Annual	June–September	Adults	B,R	R
Apiaceae	*Aegopodium podagraria* L.	Perennial	June–August	Adults, eggs, nymphs		
	Angelica sylvestris L.	Perennial	July–August	Adults, eggs		
	Anthriscus sylvestris (L.) Hoffm.	Perennial	June–July	Adults, eggs		
	Heracleum sphondylium L.	Perennial	July–August	Adults, eggs		
Asteraceae	*Achillea millefolium* L.	Perennial	July–September	Adults, eggs	B	B
	Artemisia vulgaris L.	Perennial	August–October	Adults, eggs, nymphs, pupae	B,M	B,M
	Carduus crispus L.	Biennial	July–September	Adults, eggs, nymphs, pupae		
	Cirsium heterophyllum L.	Perennial	July–September	Adults	B	
	Leontodon autumnalis L.	Perennial	July–September	Adults		
	Senecio viscosus L.	Annual	July–September	Adults, eggs, nymphs, pupae	B	
	Sonchus arvensis L.	Perennial	July–August	Adults, eggs, nymphs, pupae	B,M,R	B,M
	Tanacetum vulgare L.	Perennial	July–September	Adults, eggs, nymphs	B	B
	Taraxacum officinale F.H. Wigg .	Perennial	May–July	Adults, eggs, nymphs, pupae	B,M,R	B
Fabaceae	*Trifolium pratense* L.	Perennial	June–August	Adults, eggs, nymphs, pupae	B,L,M,R	B,L,M,R
	Trifolium repens L.	Perennial	June–August	Eggs, nymphs	B,R	R
	Vicia cracca L.	Perennial	June–August	Adults, eggs, nymphs	B,M,R	B
Geraniaceae	*Geranium* spec.	Annual/perennial	June–September	Adults, eggs, nymphs, pupae	M,R	

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

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

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

Variable	Effects		F, χ^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

Table 3 Estimates of *Trialeurodes vaporariorum* adult abundance at 1 and 48 h, egg and pupae exuviae abundance, as well as *T. vaporariorum* 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			