

# Amensalism via webs causes unidirectional shifts of dominance in spider mite communities

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**Abstract** Competitive displacement is considered the most severe consequence of interspecific competition; if a superior competitor invades the habitat of an inferior species, the inferior species will be displaced. Most displacements previously reported among arthropods were caused by exotic species. The lack of investigation of displacement among native species may be due to their apparently harmonious coexistence, even if it is equivalent to an outcome of interspecific association. A seasonal change in the species composition of spider mites, from *Panonychus ulmi* to *Tetranychus urticae*, is observed in apple trees worldwide. Previous laboratory experiments have revealed amensal effects of *T. urticae* on *P. ulmi* via their webs. Using manipulation experiments in an orchard, we tested whether this seasonal change in species composition occurred as the result of interspecific competition between these spider mites. Invasion by *T. urticae* prevented an increase in *P. ulmi* densities throughout the experimental periods. Degree of overlap relative to the independent distribution on a leaf-surface basis ( $\omega_s$ ) changed from positive to negative with increasing density of *T. urticae*. *T. urticae* invasion drove *P. ulmi* toward upper leaf surfaces

(competitor-free space). The niche adjustment by *P. ulmi* occurred between leaf surfaces but not among leaves. Our findings show that asymmetrical competition between *T. urticae* and *P. ulmi* plays an important role in this unidirectional displacement and that the existence of refuges within a leaf produces the apparently harmonious coexistence of the mites and obscures their negative association.

**Keywords** Competitive displacement · Refuge · *Tetranychus urticae* · *Panonychus ulmi* · Apple trees

## Introduction

Whether interspecific competition is an important force structuring herbivorous arthropod communities has long been debated (Shorrocks et al. 1984; Denno et al. 1995; Stewart 1996; Reitz and Trumble 2002). In the course of the debate, the potential importance of indirect interactions, e.g., apparent competition (Holt and Kotler 1987; Holt and Lawton 1993, 1994; Bonsall and Hassell 1997), has been widely examined, and substantial evidence of their importance in herbivorous arthropods has recently begun to accumulate (e.g., Morris et al. 2004). Nonetheless terrestrial herbivorous arthropod communities are complex, and asymmetric effects among phytophagous arthropod species caused by severe damage to host plants are probably common (Harrison et al. 1995). Community structure is likely to be affected by the combined effects of various biological factors, including both competition for resources and the actions of natural enemies, and the context of the population structures (Harrison et al. 1995; Dyer and Letourneau 1999; Chase et al. 2002; González-Megías

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and Gómez 2003; Kneitel and Chase 2004; van Veen et al. 2005, 2006).

Species displacement is often observed among phytophagous arthropods in agricultural ecosystems (Reitz and Trumble 2002). Most displacements previously reported among arthropods were caused by exotic species, including both herbivores and their natural enemies, which were introduced to or invaded particular localities. Displacements among native species comprised only 14% of the cases surveyed by Reitz and Trumble (2002). Changes in species composition across a broad geographical area represent a dramatic form of displacement. However, it is difficult to conclusively identify the mechanism underlying such displacements because, in many cases, these changes had already occurred by the time they were recognized (Brown et al. 1995). Therefore, many accounts have been anecdotal and incomplete, and the process has rarely been documented adequately (Reitz and Trumble 2002). Further, the lack of investigation of displacement among native species may be due to their apparently harmonious coexistence, and few workers have decided to investigate this even if it is equivalent to an outcome of interspecific association (Stewart 1996).

The seasonal change in the species composition of spider mites, from *Panonychus ulmi* (Koch) to *Tetranychus urticae* Koch (Acari: Tetranychidae), has been observed in apple orchards around the world (Lienk and Chapman 1951; Rodriguez 1958; Foott 1962, 1963). *P. ulmi* is an oligophagous spider mite that uses primarily pomaceous fruit trees as its host plants. In contrast, *T. urticae* is a polyphagous spider mite that can use various families of herbaceous and woody plants. After the larvae hatch from overwintering eggs on branches of apple trees, *P. ulmi* continuously maintains its population on the trees. In contrast, *T. urticae* hibernates as diapausing adult females under rough bark on trees or in ground litter. In spring, overwintered adult females move to ground vegetation and reproduce there. *T. urticae* that have reproduced in ground vegetation occupy trees later in the season (Kim and Lee 2003). Rodriguez (1958) reported that apple leaves were nutritionally unsuitable for *T. urticae* in early spring.

Spider mites are characterized by their web-spinning behavior, but the thread structures vary among species. *T. urticae* produces complicated webs that provide protection from predators (Putman 1962; McMurtry and Scriven 1964; McMurtry and Johnson 1966; Osakabe 1988; Janssen et al. 1998). In contrast, *P. ulmi* uses threads as lifelines and egg covers but never constructs webs; its sibling species *Panonychus citri* (McGregor) avoids its own threads when they accumulate beyond a

certain level (Saito 1979). When a large portion of a leaf is covered by webs produced by *T. urticae*, active forms of *P. ulmi* are trapped by the webs (Foott 1962). This implies that *T. urticae* is a superior competitor, whereas *P. ulmi* is an inferior competitor. Several authors have therefore speculated that *T. urticae* suppresses the population growth of *P. ulmi* as a consequence of interspecific competition (Foott 1962, 1963; Slone and Croft 2001; but see Belczewski and Harmsen 1997). However, field observations have not been able to elucidate the effects of interspecific competition between them (Foott 1962, 1963; Slone and Croft 2001).

Nevertheless, in laboratory experiments, the complicated webs produced by *T. urticae* and *Amphitetranychus viennensis* (Zacher), another species that constructs complicated webs on apple trees, severely inhibit juvenile development of both *P. ulmi* and *P. citri*, whereas there is no effect of *P. ulmi* and *P. citri* threads on *T. urticae* and *A. viennensis* (Morimoto et al. 2006). The question arises whether interspecific competition actually has no effect on species associations in these spider mites. We conducted manipulation experiments in an apple orchard to test whether the displacement of *P. ulmi* is caused by *T. urticae*'s invasion of habitats in which *P. ulmi* populations have been established.

## Materials and methods

Six apple trees (Fuji, 7–8 years old, 3–3.5 m high) in an experimental field (0.2 ha) of the Akita Fruit-Tree Experiment Station (Hiraka, Akita, Japan; 39°23'N, 140°3'E) were used for the manipulation experiments. These trees were located within a row of 11 apple trees spaced at 3-m intervals, with 4 m between adjacent rows. We selected this location because annual observations had revealed the absence of spider mites, and we could control the agrochemicals sprayed on the trees. Prior to experiments, we confirmed that the trees carried no overwintering *P. ulmi* eggs and that no apparent patches of *T. urticae* were established on the ground cover around the trees.

### Manipulation experiment in 2004

On 22 April 2004, four pieces of apple branch (about 5 cm long and 1–2 cm in diameter) taken from apple trees in other experimental fields of the Akita Fruit-Tree Experiment Station were individually attached with wire near the bases of four 1-year-old branches on each of the six test apple trees. Each piece of branch

carried ~100 overwintering *P. ulmi* eggs. For three of the four experimental branches on each tree, to prevent naturally occurring predators from invading by crawling, we applied a sticky agent (Fuji-Tangle; Fujiyakuhi, Saitama, Japan) around the base of the branches. In contrast, we left the remaining one branch unmanipulated to allow predators to invade. On this date, buds on the branches had just begun to sprout, and so shoots used for examination in this study had not yet extended.

On 12 June, we selected one extended shoot as a test shoot on each of the four 1-year-old branches described above. After we equalized the number of leaves on each test shoot to ten, we counted adult female *P. ulmi* on the upper and lower leaf surfaces separately for every leaf on the selected shoot. Test shoots from branches treated with the sticky material were allocated to two plots in which adult female *T. urticae* (competitor) were released at densities 5 times and equal to the number of adult female *P. ulmi* (hereafter, 1:5 release shoots and 1:1 release shoots, respectively), and to one plot in which no competitors had been released (non-release shoots). The sticky material was also applied to the base of these shoots. A test shoot from the remaining branch, to which no sticky substance had been applied, was relocated to the *T. urticae* non-release plot (unprotected non-release shoots).

To introduce the competitor, we transferred the appropriate number of adult female *T. urticae* from stock cultures on potted kidney bean plants to kidney bean leaf squares ( $2 \times 4 \text{ cm}^2$ ) placed on water-soaked cotton in Petri dishes, in which both ends of the longer side were covered with wet tissues (1 cm width) to retain margins for handling. We then attached the kidney bean leaves bearing adult female *T. urticae* to the test shoots using parafilm (Parafilm M; American National Can, Chicago, Ill.). The leaves were attached between the base and the lowest leaf of a shoot. These operations were performed to simulate the naturally occurring invasion of *P. ulmi* by *T. urticae*.

Adult female *P. ulmi* and *T. urticae* on upper and lower leaf surfaces were separately counted on all leaves of test shoots using a loupe every 14 days for 56 days (until 6 August) after the release of *T. urticae*. Simultaneously, we counted the natural enemies that had invaded the test shoots. When natural enemies were found, they were removed from the protected test shoots but were left on the unprotected test shoots. Before and during these experiments, the test trees were sprayed once with petroleum oil (1 April) and 5 times with fungicides (cyprodinil on 12 May and 3 June, dithianon on 17 June, and chlorothalonil on 2

and 23 July). After the experiment was completed, the test trees were sprayed with an acaricide (bifenazate) to remove spider mites for the experiment in the following year.

### Manipulation experiment in 2005

On 19 April 2005, we attached two pieces of apple branch carrying about 100 overwintering *P. ulmi* eggs to two 1-year-old branches in each of the six test apple trees as described above. Most of the test trees were the same as those used in 2004, and we confirmed that no overwintering *P. ulmi* eggs remained on these trees. All branches to which overwintering *P. ulmi* eggs were attached were protected using sticky material as above.

On 17 June we selected one shoot with more than ten leaves on each branch as a test shoot and treated it as in 2004. One test shoot per tree was allocated to the 1:5 release shoot, where adult female *T. urticae* (competitor) at a density 5 times higher than that of adult female *P. ulmi* were released, and the other was allocated to the non-release shoot. The sticky agent was applied to the base of each test shoot. Adult female *T. urticae* were released in the same manner as in 2004, except that the kidney bean leaf squares were attached to the shoots using staples.

Adult female *P. ulmi* and *T. urticae* were counted approximately every 14 days after the release of *T. urticae* until 12 August. We simultaneously counted and removed the natural enemies that invaded the test shoots. The test trees were sprayed once with petroleum oil (17 April), 5 times with fungicides (a mixture of triflumizole, cyprodinil, and ziram on 6 May; dithianon on 25 May and 12 June; and chlorothalonil on 4 and 19 July), and once with a microbial insecticide (*Bacillus thuringiensis* on 19 June).

### Data analysis and statistics

Differences in *P. ulmi* densities among treatments and among trees on the days when *T. urticae* were introduced (20 June 2004, 17 June 2005) were analyzed using two-way ANOVA without replication (Sokal and Rohlf 2000). Differences in the fluctuation of mite populations were analyzed using repeated measures ANOVA, followed by pair-wise comparisons of means using the Tukey–Kramer method in StatView Version 5.0 (SAS Institute, Cary, N.C.). The effects of the presence of *T. urticae* on the spatial distribution of *P. ulmi* were analyzed with an  $R \times C$  test of independence using a  $G$ -test (the  $G$ -value was corrected using Williams's correction:  $G_{\text{adj}}$ ), following unplanned tests of the homogeneity ( $G_H$ ) of treatments for all possible

sets of the 2004 data (Sokal and Rohlf 2000). Interspecific associations in spatial distribution were analyzed using the degree of overlap relative to the independent distribution,  $\omega$ , which ranged from 1 for complete overlap to 0 for independent occurrence to  $-1$  for complete exclusion (Iwao 1977).  $\omega$  was computed based on the density of adult females per leaf surface and per leaf for each shoot on each sampling day. The correlation between competitor density and  $\omega$  was analyzed using Kendall's coefficient of rank correlation in StatView Version 5.0 (SAS Institute).

## Results

### Population development

No spider mites except *P. ulmi* and *T. urticae* were found on test shoots during both experiments. Densities of adult female *P. ulmi* on protected test shoots were not significantly different among treatments when competitors were first introduced [two-way ANOVA:  $F = 1.166$ , not significant (NS) in 2004;  $1.613$ , NS in 2005; Fig. 1a, b]. The densities were also not significantly different among trees in 2005 ( $F = 1.342$ , NS), although they were different among trees in 2004 ( $F = 7.140$ ,  $P < 0.005$ ).

Population development differed among treatments in 2004 (repeated measures ANOVA:  $F = 4.609$ ,  $P < 0.05$ ; Fig. 1a). The *P. ulmi* population continuously increased from days 14 to 56 on shoots on which *T. urticae* were not released (non-release shoots). In contrast, density of *P. ulmi* on shoots on which *T. urticae* were released at a ratio of 1:5 (1:5 release shoots) were lower than those on non-release shoots (Tukey–Kramer method,  $P < 0.05$ ). On 1:1 release shoots, the *P. ulmi* density peaked on day 28, and then decreased

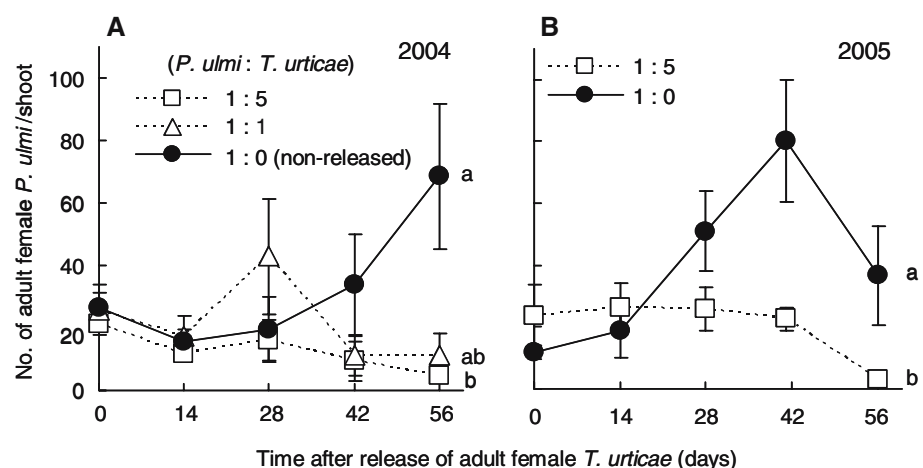
to a density lower than that on non-release shoots on day 56, although there was no significant difference between 1:1 release shoots and non-release shoots.

In 2005, the density of *P. ulmi* on 1:5 release shoots was also significantly lower than that on non-release shoots (repeated measures ANOVA:  $F = 11.602$ ,  $P < 0.005$ ; Fig. 1b). The density of *P. ulmi* on 1:5 release shoots never increased, whereas on non-release shoots, the mean density peaked on day 42.

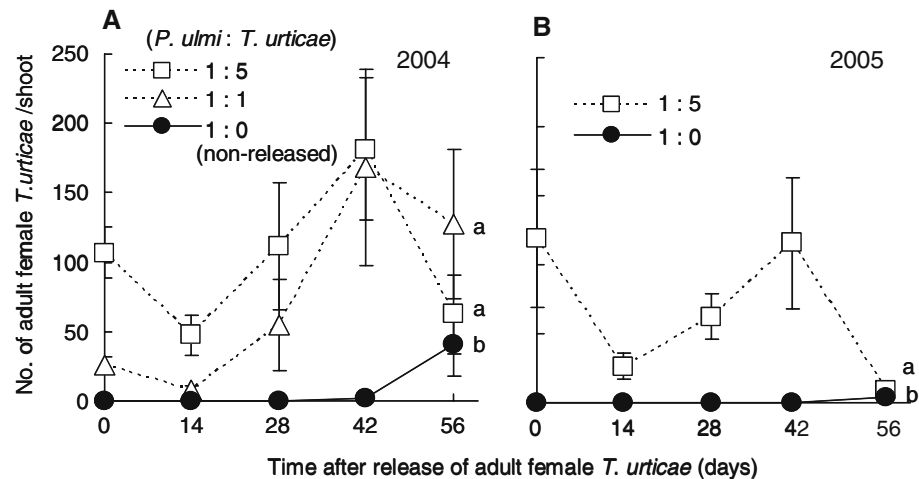
The density of *T. urticae* increased from days 14 to 42 on 1:5 and 1:1 release shoots in 2004 (Fig. 2a) and on 1:5 release shoots in 2005 (Fig. 2b). Non-release shoots were maintained under *T. urticae*-free conditions during the experiments in both 2004 and 2005, although a small *T. urticae* population was observed on day 56 in 2004 (Fig. 2a).

Natural enemies found on the test trees included phytoseiid mites and several predatory insects (one adult *Oligota* sp., one nymph of *Orius* sp., and one larval *Feltiella* sp.) in 2004, and phytoseiid mites in 2005. All these natural enemies were on the lower leaf surfaces. Although we did not identify the phytoseiid mites, all slide specimens (about 20 adult females) collected in the same orchard in a preliminary observation were identified as *Typhlodromus vulgaris* Ehara, which prefer *P. ulmi* to *T. urticae* (McMurtry and Croft 1997; Toyoshima 2003). In 2004, phytoseiid mites increased on protected shoots until day 56, despite the fact that we removed all predators at every observation. However, we found no statistical difference in phytoseiid mite densities among treatments (repeated-measures ANOVA:  $F = 1.272$ , NS). We found few predatory insects, as described above. Therefore, we assumed that natural enemies did not cause the differences among treatments in 2004. We speculated that the phytoseiid mites invaded the protected shoots by aerial dispersion (Sabelis and Dicke 1985). In 2005, the test

**Fig. 1** Fluctuation in the density of adult female *Panonychus ulmi* on protected apple shoots on which *Tetranychus urticae* were released or were not released in 2004 (a) and 2005 (b). Vertical bars indicate SEs. Different lowercase letters indicate significant differences among treatments (Tukey–Kramer method,  $P < 0.05$  in 2004; repeated-measure ANOVA,  $P < 0.01$  in 2005)



**Fig. 2** Fluctuation in the density of adult female *T. urticae* on protected apple shoots on which *T. urticae* were released or were not released in 2004 (a) and 2005 (b). Vertical bars indicate SEs. Different lower-case letters indicate significant differences among treatments (Tukey–Kramer method,  $P < 0.01$  in 2004; repeated-measure ANOVA,  $P < 0.001$  in 2005)



shoots were maintained under enemy-free conditions, although several phytoseiid mites were found during the second half of the experiment.

Densities of *P. ulmi* on unprotected non-release shoots were very low during the first half of the experiment in 2004 (Fig. 3a), implying the effects of predation by phytoseiid mites. A small peak in phytoseiid mite density was observed on day 14 (Fig. 3b). During the second half of the experiment, *P. ulmi* rapidly increased and reached the mean density equivalent to that of non-release shoots protected by the sticky agent (Fig. 3a), despite an increase in phytoseiid mites (Fig. 3b). These unprotected non-release shoots were kept free of *T. urticae* during experiments except a small *T. urticae* population on day 56 (Fig. 3a).

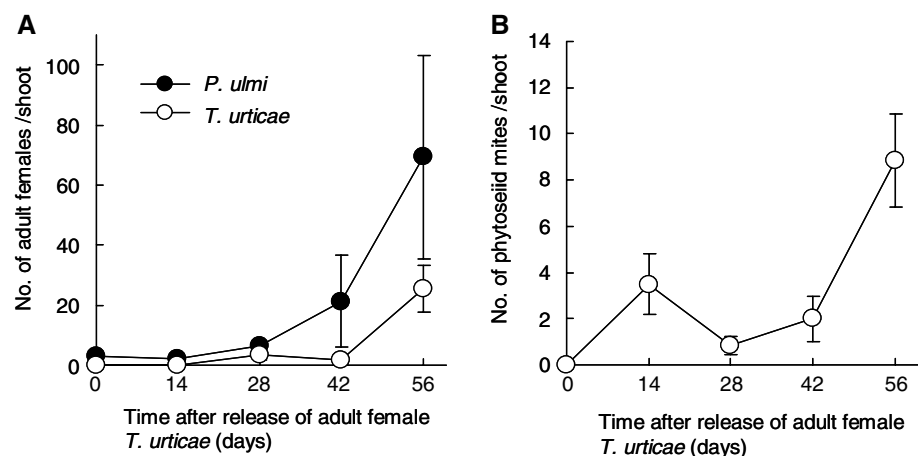
### Spatial distribution

Most *T. urticae* were found on lower leaf surfaces throughout the experimental periods; only 0.2% ( $n = 4,563$ ) and 1.4% ( $n = 1,283$ ) of adult females were

found on upper leaf surfaces in 2004 and 2005, respectively. A larger proportion of adult female *P. ulmi* occupied lower leaf surfaces on non-release shoots, except on day 42 in 2004 (Fig. 4). The increase in *P. ulmi* on the upper leaf surfaces with population increases on protected and unprotected non-release shoots may have been the result of avoiding leaf areas on which their own threads had accumulated, as has been reported for *P. citri* (Saito 1979).

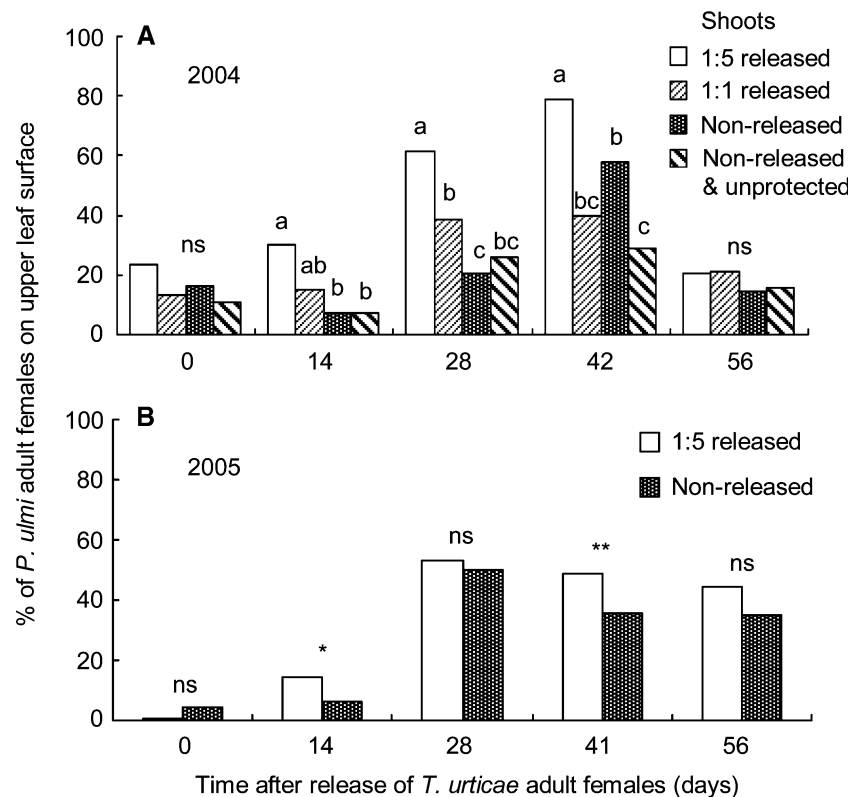
The spatial distribution between upper and lower leaf surfaces of *P. ulmi* was not different between *T. urticae* release and non-release shoots at the beginning of experiments (day 0) in both 2004 ( $G_{\text{adj}} = 5.335$ , NS) and 2005 ( $G_{\text{adj}} = 2.606$ , NS) (Fig. 4a, b). From days 14 to 42 in 2004, the presence of *T. urticae* on the lower leaf surfaces drove *P. ulmi* toward the upper leaf surfaces ( $G_{\text{adj}} = 14.994$ ,  $P < 0.005$  on day 14; 41.546,  $P < 0.001$  on day 28; 51.772,  $P < 0.001$  on day 42), although on day 42 the percentage of females on 1:1 release shoots was marginally smaller than that on protected non-release shoots (unplanned test of

**Fig. 3** Fluctuation in the densities of adult female *P. ulmi* and *T. urticae* (a) and phytoseiid mites (b) on unprotected apple shoots on which *T. urticae* were not released in 2004. Vertical bars indicate SEs





**Fig. 4** Effects of invasion by *T. urticae* on the spatial distribution of *P. ulmi* in 2004 (**a**) and 2005 (**b**). Different lower-case letters indicate significant differences among treatments (unplanned tests of homogeneity, *G*-test:  $P < 0.05$ ). Asterisks indicate significant differences between treatments (*G*-test: \* $P < 0.05$ , \*\* $P < 0.01$ , *ns* not significant)



homogeneity:  $G_H = 6.958$ , NS) and equivalent to that on unprotected non-release shoots ( $G_H = 2.324$ , NS) (Fig. 4a). Similarly, in 2005, the presence of *T. urticae* drove *P. ulmi* toward upper leaf surfaces on day 14 and on day 41 ( $G_{adj} = 4.871$ ,  $P < 0.05$  on day 14; 7.145,  $P < 0.01$  on day 41), although the effect was unclear on day 28 ( $G_{adj} = 0.346$ , NS) (Fig. 4b). In 2005, *T. urticae* abundance on 1:5 release shoots was smaller than in 2004, while *P. ulmi* on the non-release shoots increased more rapidly than in 2004. This possibly makes the effect of *T. urticae* on *P. ulmi* behavior obscure on day 28 in 2005.

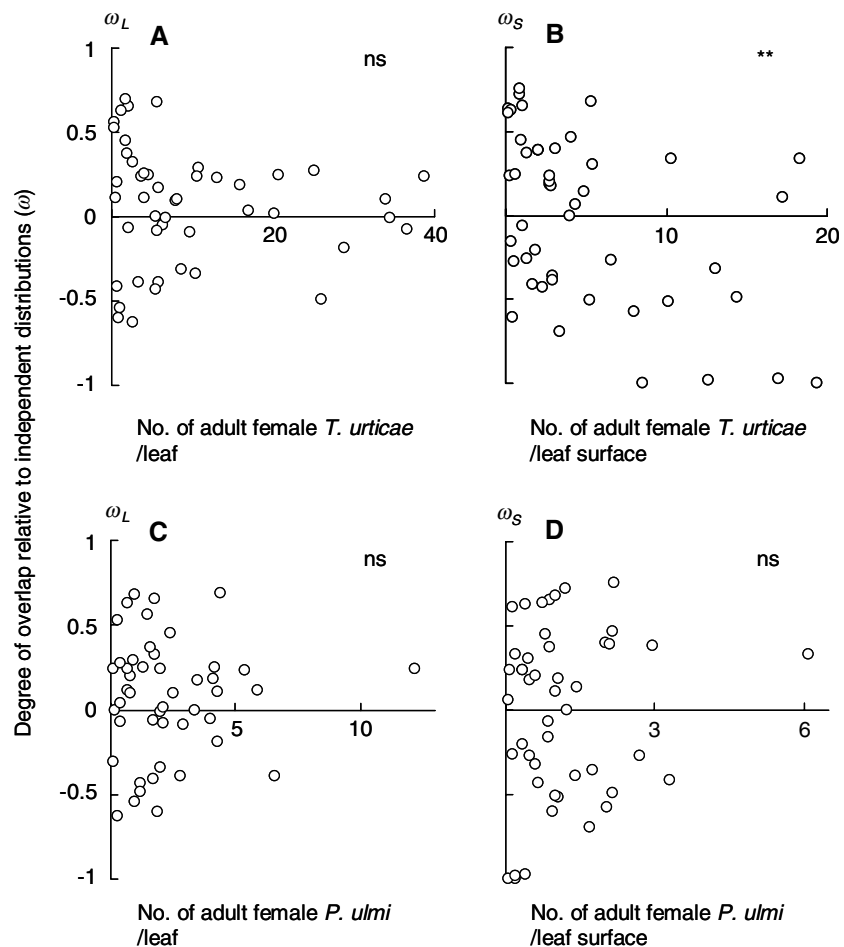
The effect of the presence of *T. urticae* on the distribution of *P. ulmi* was unclear on day 56 in both 2004 ( $G_{adj} = 2.119$ , NS) and 2005 ( $G_{adj} = 0.610$ , NS) (Fig. 4a, b). Leaf damage became severe by day 56; many leaves turned brownish and several leaves had already fallen. Moreover, the *T. urticae* population was notably reduced on day 56 in both 2004 and 2005 (Fig. 2a, b), which may have occurred in response to leaf degradation. A theoretical study has suggested that such inferior habitat quality affects the outcome of competition. When community size is shrinking, superior invaders are less likely to experience positive growth when rare, making them susceptible to loss due to stochastic forces, whereas inferior invaders are relatively more likely to secure victory because they rely on stochastic

forces to achieve victory (Orrock and Fletcher 2005). Therefore, we excluded data from day 56 from the following analysis of interspecific associations in spatial distribution.

Values of  $\omega$  based on mite density per leaf surface ( $\omega_S$ ) ranged from 0.750 (positive association) to  $-1$  (complete negative association) and indicated negative associations in 21 of 47 cases. Values of  $\omega$  based on mite density per leaf ( $\omega_L$ ) ranged from 0.691 to  $-0.630$  and showed negative associations in 18 of 47 cases. Because of the wide range of  $\omega$ -values, we assumed that the association changed temporarily with environmental change, and analyzed the relationships between  $\omega$  and competitor density.

We found a negative correlation in the relationship between  $\omega_S$  and *T. urticae* density per leaf surface (Kendall's coefficient of rank correlation:  $\tau = -0.333$ ,  $P = 0.001$ ; Fig. 5b). There was no significant correlation in the relationships between  $\omega_L$  and *T. urticae* density per leaf ( $\tau = -0.126$ ,  $P = 0.211$ ; Fig. 5a),  $\omega_L$  and *P. ulmi* density per leaf ( $\tau = 0.010$ ,  $P = 0.920$ ; Fig. 5c), or  $\omega_S$  and *P. ulmi* density per leaf surface ( $\tau = 0.080$ ,  $P = 0.430$ ; Fig. 5d). This indicates that increasing the *T. urticae* density changed the association between the two spider mite species from positive to negative, through a niche adjustment within a leaf by *P. ulmi*.

**Fig. 5** Relationships between the degree of overlap relative to the independent distributions ( $\omega$ ) and mean densities of *T. urticae* per leaf (a) and per leaf surface (b), and *P. ulmi* per leaf (c) and per leaf surface (d).  $\omega_L$   $\omega$  computed based on density of mites per leaf,  $\omega_S$   $\omega$  computed based on density of mites per leaf surface. Asterisks indicate significant correlations (Kendall's coefficient of rank correlation,  $P = 0.01$ )



## Discussion

Competitive displacement is considered the most severe consequence of interspecific competition; if a superior competitor invades the habitat of an inferior species, the inferior species will be displaced (Reitz and Trumble 2002; Orrock and Fletcher 2005). Previous laboratory experiments have demonstrated that *T. urticae* is a superior competitor, whereas *P. ulmi* is an inferior competitor (Foott 1962; Morimoto et al. 2006), and field observations have indicated that *T. urticae* annually invades the habitats of *P. ulmi* (Lienk and Chapman 1951; Rodriguez 1958; Kim and Lee 2003).

We revealed that invasion by *T. urticae* drove *P. ulmi* toward upper leaf surfaces and significantly prevented an increase in the density of *P. ulmi*. The associations in spatial distribution on a leaf-surface basis ( $\omega_S$ ) changed from positive to negative with increasing *T. urticae* density, whereas densities of *P. ulmi* had no effect on the interspecific associations. This means that adult female *P. ulmi* changed their behavior depending upon the densities of *T. urticae* coexisting on leaves. Despite the disadvantage of the presence of *T. urticae*

webs on lower leaf surfaces (Morimoto et al. 2006), juvenile *P. ulmi* tend to occupy lower leaf surfaces (Foott 1963). These results, i.e., the suppression of populations and niche adjustment of adult female *P. ulmi* caused by *T. urticae*, provide evidence that *T. urticae* exerts amensal effects on *P. ulmi* on apple trees in the field.

Belczewski and Harmsen (1997) described phylloplane fungi as an extrinsic factor that changes the association between *T. urticae* and *P. ulmi* on apple trees; the former is more prevalent on trees where *Alternaria alternate* (Fr.) Keissler is present, whereas the latter is more common on trees where this fungus is absent. They concluded that differences in the use of such fungi and their by-products between these spider mites accounted for the results; phylloplane fungi have a positive effect on *T. urticae* population growth (Belczewski and Harmsen 2000). Although we did not monitor phylloplane fungi, our data were not likely affected by the fungi because a series of treatments were imposed on every test tree. Therefore, the presence of *T. urticae* was considered to inhibit the increase of *P. ulmi* regardless of the presence or absence of phylloplane

fungi. The description by Belczewski and Harmsen (1997) was based on the premise that mutual competitive exclusion occurred between *T. urticae* and *P. ulmi*. However, the presence of *Tetranychus* spp. has lethal effects on *Panonychus* spp. (Foott 1963; Morimoto et al. 2006), but not vice versa. Positive effects on *T. urticae* of using the fungus likely enhanced the amensalism by *T. urticae* on *P. ulmi*. However, why *P. ulmi* increased on trees where the fungus was absent and no predatory mites were found (Belczewski and Harmsen 1997) is unclear. Amensalism explains only unidirectional change from an inferior competitor (*P. ulmi*) to a superior competitor (*T. urticae*). A theoretical study has also suggested that a strong invading competitor usually wins in a growing population, although it does not necessarily win in small or shrinking populations (Orrock and Fletcher 2005).

Slone and Croft (2001) comprehensively analyzed the associations among mite species, including herbivores and their predators, on apple trees using an 8-year dataset (Slone and Croft 1998). With regard to associations among four phytophagous mites, only one positive association [between *P. ulmi* and *Aculus schlechtendali* Nalepa (Acari: Eriophyidae)] was found, contrary to their speculation that *T. urticae* would be more negatively associated with other phytophagous mites (Slone and Croft 2001). The lack of a negative association between *T. urticae* and other phytophagous mites was interpreted to be a consequence of the former seldom reaching densities high enough to show significant webbing (Slone and Croft 2001) and to cause food-limiting effects (Slone and Croft 1998). Further, it was considered inevitable that the predators exert an influence on the mite communities (Slone and Croft 1998). Our data demonstrate that the association between *P. ulmi* and *T. urticae* varied from positive to negative, and did not contradict the data of Slone and Croft (2001): a negative association between *P. ulmi* and *T. urticae* was found in 142 cases, whereas a positive association was found in 85 cases. Slone and Croft (2001) analyzed the association based on the distribution among leaves, whereas our results indicated that the niche adjustment by *P. ulmi* occurred within a leaf (i.e., between leaf surfaces), but not among leaves.

The extremely asymmetrical distribution of *T. urticae* between leaf surfaces enables *P. ulmi* adult females to use upper leaf surfaces as competitor-free space (refuge). The existence of such refuges within a leaf possibly helps these mites to coexist apparently on the same leaf, and thus may obscure the negative association between them on a leaf basis. Nevertheless, adult female *P. ulmi* lay a significant portion of their eggs on lower leaf surfaces, and the majority of the juveniles

remain on lower leaf surfaces, even when *T. urticae* are present (Foott 1963). Eventually, juvenile *P. ulmi* should be subjected to a greater degree of amensalism via the webs of *T. urticae* than adult females (Foott 1963). However, the intensity of amensal effects should depend on the density of *T. urticae* (or their accumulated webs) (Morimoto et al. 2006). This may be the reason that the *P. ulmi* population persisted during the first half in our experiments but was almost eliminated after the peak in *T. urticae*. The same phenomena were found in greenhouse experiments by Foott (1962). We speculate that the cost of this amensalism may be outweighed by the possible benefit of avoiding rain (Tanaka and Inoue 1970; Jeppson et al. 1975; Furuhashi and Nishino 1979) and so on. This may be the main mechanism of successive suppression of *P. ulmi* by *T. urticae*.

Species displacements across a broad geographical area caused by exotic species have been dramatic and have mainly drawn, therefore, the attention of ecologists (Denno et al. 1995; Reitz and Trumble 2002). However, species displacement can also occur in a particular microhabitat (or a particular host), rather than across a large geographical area, and if species are distributed as metapopulations, this allows for some degree of persistence by the displaced species (Harrison et al. 1995; Reitz and Trumble 2002). Therefore, displacement among native species may incompletely exclude inferior competitors from a particular locality (Brown et al. 1995; Harrison et al. 1995; Kneitel and Chase 2004) and allow a reversion or dynamic change in dominance with environmental change. Such mechanisms should also be important in determining community structure in nature.

Type-II phytoseiid mites, which are selective predators of *Tetranychus* mites (McMurtry and Croft 1997), are common in deciduous fruit tree orchards in Japan (Kishimoto 2002; Toyoshima 2003), although only *T. vulgaris* (type III; McMurtry and Croft 1997) was found at the experimental site. Predators that prefer to eat competitive dominants equalize competitive abilities, and thus, promote the coexistence of competitors (Chase et al. 2002). Differential dispersal is also an important factor that enhances the coexistence of competitors on a regional scale (Kneitel and Chase 2004). Spider mites, mainly young adult females, exhibit long-distance aerial dispersal (Jeppson et al. 1975; Kennedy and Smitley 1985). The aerodynamic processes involved in aerial dispersal likely differ among *Panonychus* (by ballooning) and *Tetranychus* (windborne) species (Fleschner et al. 1956; Boykin and Campbell 1984; Margolies and Kennedy 1985; Lawson et al. 1996), probably resulting in a diversity of population



structures (Tsagkarakou et al. 1997; Osakabe et al. 2005).

To understand the comprehensive mechanisms that structure mite communities, further investigations to evaluate the effects of each factor and their interactions on interspecific interactions, e.g., unidirectional displacement and asymmetric predation, are essential. The knowledge gained from these investigations will help to elucidate how native herbivorous arthropod communities are structured.

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