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***Title: Community-wide impact of an exotic aphid on introduced tall goldenrod***

*Running head: Community-wide impact of exotic aphids*

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1 **Abstract.**

- 2 1. The aphid *Uroleucon nigrotuberculatum* (Homoptera: Aphididae), which is  
3 specialized to the tall goldenrod, *Solidago altissima*, in its native range, has  
4 become a dominant species on the introduced tall goldenrod in Japan. We  
5 examined how this exotic aphid influenced arthropod communities on the  
6 introduced tall goldenrod in aphid-present (spring) and aphid-absent (autumn)  
7 seasons, using an aphid removal experiment.
- 8 2. In spring, aphid presence increased ant abundance because aphid honeydew  
9 attracted foraging ant workers. We found a significant negative correlation  
10 between numbers of ants and herbivorous insects other than aphids on the  
11 aphid-exposed plants, but no significant correlation was detected on the  
12 aphid-free plants. Thus, the aphid presence was likely to decrease the  
13 abundance of co-occurring herbivorous insects through removal behavior of  
14 the aphid-tending ants. There were no significant differences in plant traits  
15 between the aphid-exposed and aphid-free plants.
- 16 3. In autumn, the numbers of lateral shoots and leaves, and the leaf nitrogen  
17 content were increased in response to the aphid infestation in spring. Because  
18 of the improvement of plant traits by aphid feeding, the abundance of leaf  
19 chewers increased on aphid-exposed plants. In contrast, the abundance of sap  
20 feeders decreased on the aphid-exposed plants. In particular, the dominant  
21 scale insect among sap feeders, *Parasaissetia nigra* (Homoptera: Coccidae),  
22 decreased, followed by a decrease in the abundance of ants attending *P. nigra*.  
23 Thus, aphid feeding may have attenuated the negative impacts of the tending  
24 ants on leaf chewers.
- 25 4. Aphid presence did not change herbivore species richness but changed the  
26 relative density of dominant herbivores, resulting in community-wide effects

1 on co-occurring herbivores through ant-mediated indirect effects, and on  
2 temporally separated herbivores through plant- and ant-mediated indirect  
3 effects. The aphid also altered predator community composition by increasing  
4 and decreasing the relative abundance of aphid-tending ants in spring and  
5 autumn, respectively.

6

7 **Key words.**

8 aphid-ant interaction · community-wide impact · exotic insect · introduced plant ·

9 invasion · plant-mediated indirect effect · *Solidago altissima* · tall goldenrod ·

10 *Uroleucon nigrotuberculatum*

11

## 1 **Introduction**

2           It is well accepted that introduced plants lack interactions with herbivores,  
3 mutualists, and competitors associated with their original ranges, but can gain novel  
4 interactions with native species in new habitats (Schiffman 1994; Mitchell *et al.* 2006).  
5 Moreover, the establishment of an introduced plant is often followed by invasion of  
6 exotic herbivorous insects that are specialized to the plant in its original region  
7 (Robinson, 1980; Memmott *et al.*, 2000; Hierro *et al.*, 2005; Ando & Ohgushi, 2008).  
8 These exotic insects may affect arthropod communities on introduced plants by adding  
9 new interactions or modifying existing interactions, such as interspecific competition  
10 for shared resources (Moulton & Pimm, 1983; Louda *et al.*, 1997; Simberloff & Von  
11 Holle, 1999), ant-mediated indirect interactions (Thum *et al.*, 1997), or plant-mediated  
12 indirect interactions (Louda *et al.*, 1997; Louda & Arnett, 2000). Studying these  
13 relationships among introduced plants, exotic and native insects is necessary to answer  
14 the questions of how direct and indirect insect-plant interactions are newly formed on  
15 novel plants (Sax *et al.*, 2007). Specifically, investigation of indirect effects induced by  
16 exotic herbivorous insects at the community level is required to understand the impacts  
17 of introduced species on the assemblage of native organisms (Howarth, 1991; Callaway  
18 *et al.*, 1999; Louda & Arnett, 2000). To our knowledge, no studies have examined how  
19 exotic herbivorous insects affect the organization of the arthropod community in terms  
20 of overall density, species richness, and community composition on introduced plants.  
21 This is because most of the studies examining relationships between introduced plants  
22 and exotic herbivorous insects have focused on the colonization success of such insects  
23 as biological control agents for introduced plants (Crawley, 1989; McClay, 1995;  
24 Wajnberg *et al.*, 2001).

25           Indirect interactions caused by herbivore-induced changes in plants occur  
26 frequently among temporally- and spatially-separated, and taxonomically-distinct

1 species, resulting in community-wide impacts (Van Zandt & Agrawal, 2004; Ohgushi,  
2 2005; Utsumi & Ohgushi, 2009; Utsumi *et al.*, 2009; Poelman *et al.*, 2010). In this  
3 context, aphid colonization can alter host plant traits, such as plant growth, soluble  
4 nitrogen content, amino acid and secondary compound concentrations, and resource  
5 allocation to roots, shoots, and seeds (Moran & Whitham, 1990; Waltz & Whitham,  
6 1997; Petersen & Sandström, 2001; Wimp & Whitham, 2007). These changes in host  
7 plant traits caused by aphid attack can in turn alter arthropod communities. For example,  
8 Waltz & Whitham (1997) demonstrated that leaf-galling aphids increased the abundance  
9 and species richness of arthropods by improving the quality of juvenile cottonwood  
10 ramets. This implies that aphids can affect arthropod communities indirectly through  
11 changes in plant quality.

12           Interactions between ants and honeydew-producing aphids are common and  
13 widespread in arthropod food webs (Kaplan & Eubanks, 2005). Ant-aphid interactions  
14 potentially have community-wide impacts, because the presence of aphids can indirectly  
15 alter the density of other herbivorous insects and predators through the removal  
16 activities of tending ants (Wimp & Whitham, 2001, 2007). As honeydew is a renewable  
17 food resource, ants tending aphids not only protect aphids from predators and/or  
18 parasitoids (Way, 1963; Buckley, 1987), but also exclude potential competitors (Ando &  
19 Ohgushi, 2008). There is increasing evidence that an ant-aphid mutualism has strong  
20 indirect impacts on other herbivorous insects and/or their natural enemies through the  
21 removal behavior of ants, leading to decreases in the species richness and relative  
22 abundance of herbivorous insects (Floate & Whitham, 1994; Wimp & Whitham, 2001,  
23 2007). Herbivore species with a pervasive influence on the overall community  
24 composition are termed “keystone herbivores” (Hunter, 1992), and their removal can  
25 produce a dramatic change in the associated community structure through altering an  
26 interaction web involving the host plant and other community members. Therefore,

1 aphids have the potential to be a keystone herbivore that determines arthropod  
2 community structure through both plant- and ant-mediated indirect effects.

3         The tall goldenrod, *Solidago altissima*, is an herbaceous plant which was  
4 introduced to Japan from North America approximately 100 years ago, and has since  
5 then spread widely over Japan. The aphid *Uroleucon nigrotuberculatum* is one of the  
6 most dominant species on the tall goldenrod in Japan, and it also came from North  
7 America in the early 1990s. This exotic aphid-tall goldenrod system could provide  
8 profound insights into how an exotic aphid can affect the arthropod community on  
9 introduced plants through both ant-mediated and plant-mediated indirect effects.

10         In this study, we examined how the exotic aphid affected community  
11 structures of co-occurring and temporally separated herbivorous insects and predators,  
12 using an aphid-removal experiment. Specifically, we focused on plant traits, species  
13 richness and densities of insect herbivores belonging to different feeding guilds and  
14 predators of different taxa.

15

## 16 **Materials and methods**

### 17 Tall goldenrod and aphid

18         Tall goldenrod, *Solidago altissima* Linn (Compositae), is a rhizomatous  
19 perennial herb that was introduced to Japan from North America approximately 100  
20 years ago (Shimizu, 2003). It has spread widely all over Japan, and become one of the  
21 most abundant weeds. It grows in open and disturbed areas, and frequently invades  
22 abandoned agricultural fields. In their original habitats, tall goldenrods are attacked by  
23 more than 100 herbivorous insect species, including a wide range of feeding guilds,  
24 such as leaf-chewers, suckers, miners, and gall-formers (Messina, 1978; Messina &  
25 Root, 1980).

26         *Uroleucon nigrotuberculatum* is a stem-feeding aphid (Homoptera) that feeds

1 exclusively on terminal shoots of *S. altissima*. It was also introduced from North  
2 America in the early 1990s (Ôtake, 1999), and more recently it has become very  
3 common in Japan. This aphid emerges from overwintered eggs in early March, and  
4 disappears by early August. It commonly occurs on *S. altissima* in North America, and  
5 at least seven predators and two parasitoids have been recorded to attack this species  
6 (Moran 1986). In contrast, this aphid is almost free from natural enemies in Japan  
7 (Ôtake, 1999). Although we observed two ladybirds, *Coccinella septempunctata* and  
8 *Harmonia axyridis*, and a crab spider, *Misumenops tricuspidatus*, preying on the aphid,  
9 the intensity of predation was negligible in our study area (Y. Ando, personal  
10 observation).

11

## 12 Experimental design of aphid exclusion

13         This study was conducted in a common garden of the Center for Ecological  
14 Research, Kyoto University, in Otsu, Shiga Prefecture, central Japan. To investigate the  
15 effects of the aphid colonization on other herbivorous insects and predators, we  
16 performed an aphid exclusion experiment in 2001. Eighty seedlings of different clones  
17 of tall goldenrods were randomly taken from a 0.75-ha field of the Experimental Forest  
18 of Field Science Education and Research Center of Kyoto University in Kyoto  
19 (35°04'N, 135°46'E; altitude 109 m, annual mean temperature 14.6 °C, and mean  
20 precipitation 1 582 mm), and were planted in pots individually in early May, 2001. Two  
21 weeks later, all of the potted plants were transplanted into an experimental plot in a 6  
22 m×16 m grid in the common garden by burying the bottom half of a pot in the ground,  
23 with individual plants being spaced 1.5 m apart without boundary fences.  
24 Aphid-exposed and aphid-free treatments were alternately arranged, and plants of the  
25 aphid-exposed treatment were allowed to undergo natural colonization by aphids. We  
26 checked all plants every day from mid-May to August, and removed aphids from the



1 aphid-free plants with forceps when they were found. To confirm whether aphid  
2 colonization occurred in the aphid-exposed treatment, we counted aphids weekly  
3 throughout the season. We used 40 potted plants for an arthropod community census  
4 and the other 40 plants for an experiment to examine the effects of aphids on host plant  
5 traits. In both experiments, 20 plants each were assigned to the aphid-free treatment, and  
6 the remaining 20 plants to the aphid-exposed treatment.

7

## 8 Effects of aphid colonization on herbivore and predator communities

9         To examine how the aphid affected herbivore and predator communities in the  
10 common garden, we conducted censuses three times a week from mid-May to late  
11 October 2001. The number of species and abundance of each arthropod species were  
12 recorded in the aphid-free and aphid-exposed plants. As the aphid colonization occurs  
13 from mid-May to early August and none of the herbivorous insect species except one  
14 found in the aphid-present season appeared in the aphid-absent season (see Appendix 1),  
15 we analyzed the aphid effects separately in “early season” (aphid-present season, i.e.,  
16 mid-May to August) and “late season” (aphid-absent season, i.e., September to late  
17 October). The census data for each arthropod species were averaged for the early and  
18 late season, respectively, and then we calculated the overall abundance and species  
19 richness of the herbivore and predator communities on each plant. The Wilcoxon signed  
20 rank test was used to compare these community properties between the aphid-free and  
21 aphid-exposed plants. Also, we compared the abundance of each feeding guild of  
22 herbivorous insects and predator taxa between the aphid-free and aphid-exposed plants.  
23 Herbivorous insects found on each plant were classified into two feeding guilds, namely,  
24 leaf chewers (caterpillars, grasshoppers, chrysomelid beetles, and scarab beetles) and  
25 sap feeders (aphids, leafhoppers, stinkbugs, scales, and spittlebugs). We excluded leaf  
26 miners from this analysis, because it was difficult to determine whether individual leaf

1 miners were alive. Predators were categorized in terms of taxa: spiders, ants, and others  
2 (Cantharidae, Coccinellidae, and Reduviidae, Appendix 2). The Wilcoxon signed rank  
3 test was used to compare overall abundances of herbivore feeding guilds and predator  
4 taxa on the aphid-free and aphid-exposed plants. To examine the numerical relationships  
5 among aphids, ants, and co-occurring herbivores, we calculated Pearson's correlation  
6 coefficients between numbers of aphids and ants, between numbers of ants and leaf  
7 chewers, and between numbers of ants and sap feeders.

8         To examine whether arthropod communities differed between the treatments,  
9 we used nonmetric multidimensional scaling analysis (NMDS) with the Bray-Curtis  
10 dissimilarity coefficient. This is a robust technique which represents samples as points  
11 in low-dimensional space (usually two dimensions) such that the relative distances apart  
12 of all points are in the same rank order as the relative dissimilarities of the samples  
13 (Minchin, 1987). Points that are close together represent samples that are very similar in  
14 community composition, based on number of species and relative abundance of each  
15 species. For this analysis, the number of each herbivore and predator species used in the  
16 analysis was averaged for the early and late seasons. *Uroleucon nigrotuberculatum* on  
17 the aphid-exposed plants was excluded from the analysis. Individual numbers of each  
18 species were  $\log(n+1)$ -transformed and standardized by variance prior to calculating the  
19 coefficient.

20         An optimal NMDS solution was obtained by minimizing the stress value as  
21 described in Clarke & Gorley (2001). The stress value (goodness-of-fit of the NMDS  
22 plot) is an index to indicate how faithfully the high-dimensional relationships among  
23 samples are represented in a two-dimensional ordination plot. The stress value, which  
24 decreases as the rank-order agreement between distances and dissimilarities improves,  
25 was calculated as described by Kruskal (1964). When stress values are  $\leq 0.1$ , the NMDS  
26 plot is considered to be an acceptable representation (Clarke, 1993). The relationships

1 among samples were represented in a plot of the first two dimensions of the NMDS  
2 solution. Then, differences in community compositions of predators and herbivores  
3 between the aphid-exposed and aphid-free plants were determined by the R value in an  
4 analysis of similarity (ANOSIM; Clarke, 1993). This analysis uses non-parametric  
5 permutation/randomization methods with a dissimilarity matrix (Clarke, 1993). In  
6 addition, we used similarity percentages (SIMPER) to identify which arthropod species  
7 primarily accounted for the differences in herbivore and predator communities between  
8 the two plants. SIMPER is used to examine the contribution of each species or group to  
9 the average Bray-Curtis dissimilarity between samples (Clarke, 1993). We conducted  
10 NMDS, ANOSIM, and SIMPER analysis using the software program PRIMER-5  
11 version 5.2.9 (Plymouth Marine Laboratory, Plymouth, UK).

12

### 13 Effects of aphid colonization on plant traits

14 Because aphid infection induces subsequent branching, thereby enhancing  
15 new leaf production late in the season (Ando & Ohgushi, 2008), it has the potential to  
16 affect late-emerging arthropods on the tall goldenrod through the enhancement of plant  
17 regrowth.

18 To examine how plant traits differed between treatments in the common  
19 garden in the early and late seasons, we prepared aphid-exposed plants ( $n = 20$ ) and  
20 aphid-free plants ( $n=20$ ) in the common garden, as described in the experimental design  
21 above. After the number of newly emerged lateral shoots and leaves were counted, ten  
22 leaves were randomly taken from ten each of aphid-exposed plants and aphid-free plants  
23 for measurement of foliar nitrogen and water contents in mid-July and in early  
24 September 2001 just before the emergence of late season herbivores, the number of  
25 shoots and leaves of the remaining ten each of aphid-exposed plants and aphid-free  
26 plants were counted, and then ten leaves were randomly collected from each plant to

1 measure foliar nitrogen and water contents. Individual leaves were weighed in the  
2 laboratory and oven-dried at 60°C for 48 h to calculate water content. After the dried  
3 leaves were powdered, nitrogen content was measured using an elemental analyzer  
4 (Macro Corder JM1000CN, J-Science, Kyoto, Japan). The Wilcoxon signed rank test  
5 was used to compare these traits between the aphid-exposed and aphid-free plants.

6

## 7 **Results**

### 8 Effects of aphids on overall density and species richness

9 We recorded a total of 1701 individuals in 29 species as herbivores (Appendix 1) and a  
10 total of 1379 individuals in 62 species as predators (Appendix 2). All of the  
11 aphid-exposed plants were colonized by aphids throughout the early season (Mean of  
12 aphid abundance  $\pm$  SE;  $9.01 \pm 0.39$ ). We found no aphids on the aphid-free plants  
13 throughout the season. The aphid-exposed plants had significantly lower overall  
14 herbivore density, i.e., number per plant, than the aphid-free plants in both the early and  
15 late seasons (Wilcoxon signed rank test:  $Z = 82.32$ ,  $P < 0.001$  for early season;  $Z =$   
16  $20.02$ ,  $P < 0.001$  for late season, Fig. 1). Although herbivore species richness in the  
17 early season showed a tendency to be lower on the aphid-exposed plants than on the  
18 aphid-free plants, the difference was not statistically significant ( $Z = 3.12$ ,  $P = 0.07$  for  
19 early season;  $Z = 1.65$ ,  $P = 0.13$  for late season). Of 29 herbivorous insect species, 86%  
20 were found on both the aphid-exposed and aphid-free plants (Appendix 1). Overall  
21 predator density on the aphid-exposed plants was significantly higher in the early  
22 season ( $Z = 52.36$ ,  $P < 0.001$ ) but was lower in the late season ( $Z = 47.78$ ,  $P < 0.001$ )  
23 than that on the aphid-free plants. Also, there were marginally significant differences in  
24 species richness in both seasons ( $Z = 3.11$ ,  $P = 0.06$  for early season;  $Z = 3.28$ ,  $P = 0.06$   
25 for late season, Fig. 1). Predator species richness on the aphid-exposed plants in both

1 seasons tended to be lower than that on the aphid-free plants. Of 62 predator species,  
2 90% were found on both the aphid-exposed and aphid-free plants (Appendix 2).

#### 3 4 Effects of aphids on community composition

5         NMDS analysis of the dissimilarity of arthropod community composition  
6 revealed that both herbivore and predator communities on the aphid-exposed plants  
7 were clearly distinct from those on the aphid-free plants in both seasons (ANOSIM:  
8 herbivore:  $R = 0.60$ ,  $P < 0.001$  for early season;  $R = 0.82$ ,  $P < 0.001$  for late season;  
9 predator:  $R = 0.66$ ,  $P < 0.001$  for early season;  $n = 20$ ,  $R = 0.22$ ,  $P < 0.001$  for late  
10 season, Fig. 2). SIMPER analysis indicated that the leafhopper *Nephotettix cincticeps*  
11 Uhler and the moth caterpillar *Ascotis selenaria* Butler accounted for 46% and 35%  
12 of the dissimilarity of herbivore communities between the aphid treatments in the  
13 early season. The leafhopper constituted 66% and 89% of the overall sap feeder  
14 abundance on the aphid-exposed plants and aphid-free plants, respectively. Also, the  
15 moth caterpillar constituted 78% and 86% of the overall leaf chewer abundance,  
16 respectively. In the late season, the scale insect *Parasaissetia nigra* Nietner and the  
17 grasshopper *Atractomorpha lata* Motschulsky accounted for 62% and 29% of the  
18 dissimilarity of herbivore communities between treatments. The scale insect  
19 constituted 79% and 91% of the overall sap feeder abundance on the aphid-exposed  
20 plants and aphid-free plants, respectively. Also, the grasshopper constituted 85% and  
21 41% of the overall leaf chewer abundance on the aphid-exposed plants and aphid-free  
22 plants, respectively. The ant *Formica japonica* accounted for 95% and 92% of the  
23 dissimilarities of predator communities in the early season and the late season,  
24 respectively. Regarding the overall ant abundance on the aphid-exposed and  
25 aphid-free plants, the ant constituted 98% and 74% in the early season, and 91% and  
26 93% in the late season, respectively. These results suggest that the differences

1 between arthropod communities with and without aphids were due to the differences  
2 in relative abundances of the dominant herbivore species and ants.

#### 3 4 Effects of aphids on densities of herbivore guilds and predator taxon

5 In the early season, the densities of leaf chewers and sap feeders were  
6 significantly lower on the aphid-exposed plants than on the aphid-free plants (Wilcoxon  
7 signed rank test:  $Z = 24.37$ ,  $P < 0.001$  for leaf chewers;  $Z = 38.66$ ,  $P < 0.001$  for sap  
8 feeders, Fig. 3). In the late season, there was significantly higher density of leaf chewers  
9 but lower density of sap feeders on the aphid-exposed plants than on the aphid-free  
10 plants ( $Z = 32.12$ ,  $P < 0.001$  for leaf chewers;  $Z = 39.65$ ,  $P < 0.001$  for sap feeders).

11 Regarding arthropod predators, ant density was significantly higher in the  
12 early season but was lower in the late season on the aphid-exposed plants than on the  
13 aphid-free plants ( $Z = 36.94$ ,  $P < 0.001$  for early season;  $Z = 62.34$ ,  $P < 0.001$  for late  
14 season, Fig. 3). Neither spiders nor other predators differed significantly between the  
15 two treatments in either season (early season:  $Z = 1.12$ ,  $P = 0.07$  for spiders;  $Z = 0.84$ ,  $P$   
16  $= 0.13$  for others; late season:  $Z = 0.58$ ,  $P = 0.64$  for spiders;  $Z = 0.21$ ,  $P = 0.84$  for  
17 others).

18 The number of ants was positively correlated with the number of aphids on  
19 the aphid-exposed plants (Pearson correlation coefficient:  $r = 0.82$ ,  $P < 0.001$ ,  $n = 20$ ;  
20 two-tailed test). The numbers of leaf chewers and sap feeders were negatively correlated  
21 with the number of ants on the aphid-exposed plants (ants vs. leaf chewers:  $n=20$ ,  $r =$   
22  $-0.75$ ,  $P < 0.001$ ; ants vs. sap feeders:  $n=20$ ,  $r = -0.77$ ,  $P < 0.001$ ). In contrast, no  
23 significant correlations were found between the numbers of herbivorous insects and ants  
24 on the aphid-free plants (ants vs. leaf chewers:  $n=20$ ,  $r = -0.41$ ,  $P = 0.07$ ; ants vs. sap  
25 feeders:  $n=20$ ,  $r = -0.53$ ,  $P = 0.07$ ).

26

## 1 Effects of aphids on plant traits

2           Aphid infestation enhanced the production of newly emerged lateral shoots  
3 and leaves. The new leaf flush increased the foliar nitrogen content by 150% in the late  
4 season, but not in the early season (Table 1). There was no significant difference in the  
5 foliar water content between the aphid treatments. The aphid-exposed plants had about  
6 three times more leaves in the late season, compared to the aphid-free plants. Most of  
7 the increase of leaves in aphid-exposed plants was due to secondary growth in response  
8 to the early aphid colonization. These results suggest that the aphid colonization not  
9 only enhanced the production of lateral shoots and leaves, but also improved the quality  
10 of leaves that emerged in the late season.

11

12 **Discussion**

## 13 Effects of aphids on the co-occurring arthropod community

14           This study clearly demonstrated the community consequences of aphid-ant  
15 interaction as a driver structuring arthropod communities. In the early season, the ant  
16 density was twelve times higher on the aphid-exposed plants than on the aphid-free  
17 plants, as a result of the provision of aphid honeydew to ant workers. Aphid-tending  
18 ants protect aphids from their natural enemies or competitors (Sloggett & Majerus,  
19 2000; Stadler & Dixon, 2005). Although there are many studies on aphid-ant mutualistic  
20 interactions (Stadler & Dixon, 2005), to date the community consequences of their  
21 interactions have received little attention (but see Wimp & Whitham, 2001; Styrsky &  
22 Eubanks, 2007; Mooney & Agrawal, 2008; Sanders & van Veen 2010). Our study  
23 showed that ants had a negative impact on other herbivores on the aphid-exposed plants,  
24 because the ants frequently removed herbivorous insects. In particular, the aphid  
25 presence decreased the dominant sap feeder, *N. cincticeps*, and the dominant leaf  
26 chewer *A. selenaria*, resulting in significant alterations in the herbivore community

1 structure.

2           The aphid may have affected early-season insect herbivores through  
3 exploitative competition or induced plant responses that changed plant quality.  
4 Co-occurring phloem feeders often compete for assimilates in the phloem vessels of  
5 host plants (Denno & Kaplan, 2007). Inbar *et al.* (1995) reported that aphids increased  
6 the mortality of co-occurring sap feeders via diversion of assimilates. In addition,  
7 aphids can change leaf nitrogen, plant growth, and resource allocation to roots, shoots,  
8 and seeds (Moran & Whitham, 1990; Petersen & Sandström, 2001), resulting in  
9 decreased food availability to leaf chewers or sap feeders. However, it is not likely that  
10 such effects on leaf chewers occurred in this study, because aphid colonization changed  
11 neither leaf nitrogen nor water content, nor production of lateral shoots or leaves of *S.*  
12 *altissima*.

13           The aphid presence also significantly increased predator abundance due to an  
14 increase in aphid-tending ants, although spiders and other predators were unaffected. On  
15 the other hand, predator species richness was marginally lower on the aphid-exposed  
16 plants, because three spider species found on aphid-free plants were lacking (see  
17 Appendix 2). This negative impact of ants on other predators is in accord with the  
18 finding of an aphid removal experiment on cottonwood trees (Wimp & Whitham 2001),  
19 showing that species richness of generalist predators was two times greater when aphids  
20 and associated ants were absent than when they were present. Hence, the community  
21 composition of predators differed significantly depending on whether the aphids were  
22 present or absent.

23

24 Effects of aphids on the temporally separated arthropod community

25           The aphid colonization in the early season impacted the herbivore community  
26 in the late season when the aphid was no longer present. Aphids influenced the



1 late-season herbivore community composition by decreasing the sap feeder *P. nigra* and  
2 increasing the leaf chewer *A. lata*, both of which contributed robustly to the difference  
3 in the community composition of herbivorous insects.

4         The aphid colonization in the early season influenced temporally separated  
5 herbivorous insects in the late season by alteration of food quality and quantity,  
6 depending on the feeding guild. Ando & Ohgushi (2008) showed that the aphid  
7 infestation in the early season did not affect plant traits in terms of secondary growth or  
8 foliar nitrogen, but rather increased the number of newly emerged lateral shoots and  
9 leaves and the foliar nitrogen in the late season. This trend was also supported by the  
10 present study. In late August, leaf flush continuously occurred in the aphid-exposed  
11 plants, although it rarely occurred in the aphid-free plants. This increase in newly  
12 flushed leaves in aphid-exposed plants resulted in an increase in leaf nitrogen level,  
13 which improved food availability to the grasshopper *A. lata* (Ando & Ohgushi, 2008).  
14 Such a trait change in host plants due to regrowth following early-season herbivory  
15 often has positive effects on late-emerging herbivorous insects because of increased  
16 resource quality and/or quantity (Mopper *et al.*, 1991; Masters *et al.*, 2001; Ohgushi,  
17 2005).

18         In contrast, aphid infestation often decreases the abundance of subsequent sap  
19 feeders by reducing the nutritional quality of the sap of host plants, inducing amino acid  
20 alterations or increasing secondary compounds (Petersen & Sandström, 2001; Denno &  
21 Kaplan, 2007). Sap feeders would be strongly affected by qualitative changes in phloem  
22 sap but not by increased leaf production of the aphid-infested plants. Ando & Ohgushi  
23 (2008) showed that population growth and survival of *P. nigra* in autumn were  
24 decreased by spring aphid infestation. Moreover, aphids may have increased leaf  
25 chewers through a decrease in *P. nigra*. Since honeydew of the scale insect attracts ants  
26 (Williams & Watson, 1990), a decrease of scale insects on the aphid-exposed plants may

1 decrease the removal of other herbivores by tending ants. In the present study, ant  
2 density was decreased by 23% on aphid-exposed plants. Hence, the presence of aphids  
3 in the early season may attenuate the negative impact of the ants attending scale insects  
4 on leaf chewers in the late season.

5         The predator abundance significantly decreased on the plants with  
6 early-season aphid infestation because of the decreased number of ants tending scale  
7 insects. However, the early-season aphid infestation did not affect the abundance of  
8 spiders or other predators. Also, predator species richness was lower on the  
9 aphid-exposed plants with low density of ants attending scale insects relative to the  
10 aphid-free plants. As a result, the community composition of predators on the  
11 aphid-exposed plants with early-season aphid infestation differed significantly from that  
12 on the aphid-free plants.

13

14 Aphid as a keystone herbivore forming indirect interaction webs

15         The ant-aphid interactions would act as ‘keystone interactions’ in arthropod  
16 communities, and thus lead to community-wide impacts (Wimp & Whitham, 2001;  
17 Styrsky & Eubanks, 2005). On the other hand, aphid colonization can also significantly  
18 affect the performance and/or preference of other herbivorous insects by altering the  
19 quality and quantity of host plants (Way & Cammell, 1970; Waltz & Whitham, 1997;  
20 Petersen & Sandström, 2001), which may alter the structure of herbivore communities.  
21 Our study highlighted that plant-mediated indirect effects of the aphid colonization  
22 significantly influenced the community structure of temporally separated herbivorous  
23 insects via alteration of not only food quality and quantity, but also the strength of  
24 ant-mediated indirect effects. Note that indirect effects of aphids on temporally  
25 separated herbivorous insects depend on the feeding modes, resulting in a decrease in  
26 sap feeders but an increase in leaf chewers. This suggests that aphid infestation can have

1 strong and different impacts on herbivorous insects through ant-aphid mutualism in the  
2 early season and can cause changes in host plants in the late season, extending to  
3 community-level consequences. Thus, aphids can act as a keystone herbivore in  
4 determining arthropod community structure through both ant-mediated and plant  
5 trait-mediated indirect effects. Future studies will be needed to obtain more information  
6 on the relative importance of plant-mediated indirect effects, ant-mediated indirect  
7 effects, and their interactions in community organization on plants, to achieve a better  
8 understanding of herbivore-induced indirect effects on ecological communities in  
9 nature.

10           Several studies on biological weed control argued that exotic herbivorous  
11 insects employed as control agents for introduced plants affected not only the target  
12 plants but also native organisms in a novel habitat through direct and/or indirect  
13 interactions (Howarth, 1991; Callaway et al., 1999; Louda & Arnett, 2000). In this  
14 context, this study revealed that the exotic aphid *U. nigrotuberculatum* played a key role  
15 in structuring the arthropod community on introduced tall goldenrods in both the early  
16 and late season. Investigating the relative importance of exotic herbivorous insects in  
17 interaction webs on introduced plants is a fruitful challenge for clarifying how exotic  
18 herbivorous insects that invade following the establishment of introduced plants have  
19 community-level consequences in invasion processes.

20

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2

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- 17

1 Table 1. Effects of aphid colonization on traits of aphid-exposed plants and aphid-free  
 2 plants.

3

Trait	Season	Mean $\pm$ SE		Wilcoxon signed rank test	
		Aphid-exposed	Aphid-free	<i>Z</i>	<i>P</i>
Number of lateral shoots	mid-July	0	0		
	early Sep.	2.02 $\pm$ 0.63	0	-6.16	< 0.001
Number of leaves	mid-July	13.4 $\pm$ 3.13	12.8 $\pm$ 3.09	-1.18	0.24
	early Sep.	47.8 $\pm$ 7.72	17.5 $\pm$ 1.43	-6.24	< 0.001
Nitrogen content (%DW)	mid-July	1.36 $\pm$ 0.14	1.32 $\pm$ 0.18	-0.84	0.40
	early Sep.	2.64 $\pm$ 0.27	1.80 $\pm$ 0.23	-6.15	< 0.001
Water content (%FW)	mid-July	60.0 $\pm$ 2.30	61.4 $\pm$ 3.23	-0.51	0.61
	early Sep.	64.7 $\pm$ 1.82	63.8 $\pm$ 2.89	-0.12	0.23

1 **Figure Legends**

2

3 **Fig. 1.** Overall density (number per plant) and species richness of herbivores and  
4 predators on the aphid-exposed and aphid-free plants in the early season (mid-May  
5 to August) and late season (September to late October). Data from the  
6 aphid-exposed plants do not include *U. nigrotuberculatum*. Vertical bars indicate  
7 means with SE. \* $P < 0.001$  (Wilcoxon signed rank test).

8

9 **Fig. 2.** Community compositions of herbivores and predators on the aphid-exposed  
10 plants (●) and aphid-free plants (○) in the early season (mid-May to August) and  
11 late season (September to late October) (herbivore; NMDS stress = 0.12,  
12 ANOSIM:  $R = 0.60$ ,  $P < 0.001$  for early season, NMDS stress = 0.11,  $R = 0.82$ ,  $P$   
13  $< 0.001$  for late season; predator, NMDS stress = 0.20, ANOSIM:  $R = 0.66$ ,  $P <$   
14  $0.001$  for early season, NMDS stress = 0.23,  $R = 0.22$ ,  $P < 0.001$  for late season).  
15 Data from the aphid-exposed plants do not include *U. nigrotuberculatum*.

16

17 **Fig. 3.** Densities of herbivore guilds (left) and predator taxa (right) on the  
18 aphid-exposed and aphid-free plants in the early season (mid-May to August) and  
19 late season (September to late October). Data from the aphid-exposed plants do not  
20 include *U. nigrotuberculatum*. Vertical bars indicate means with SE. \* $P < 0.001$   
21 (Wilcoxon signed rank test).

22

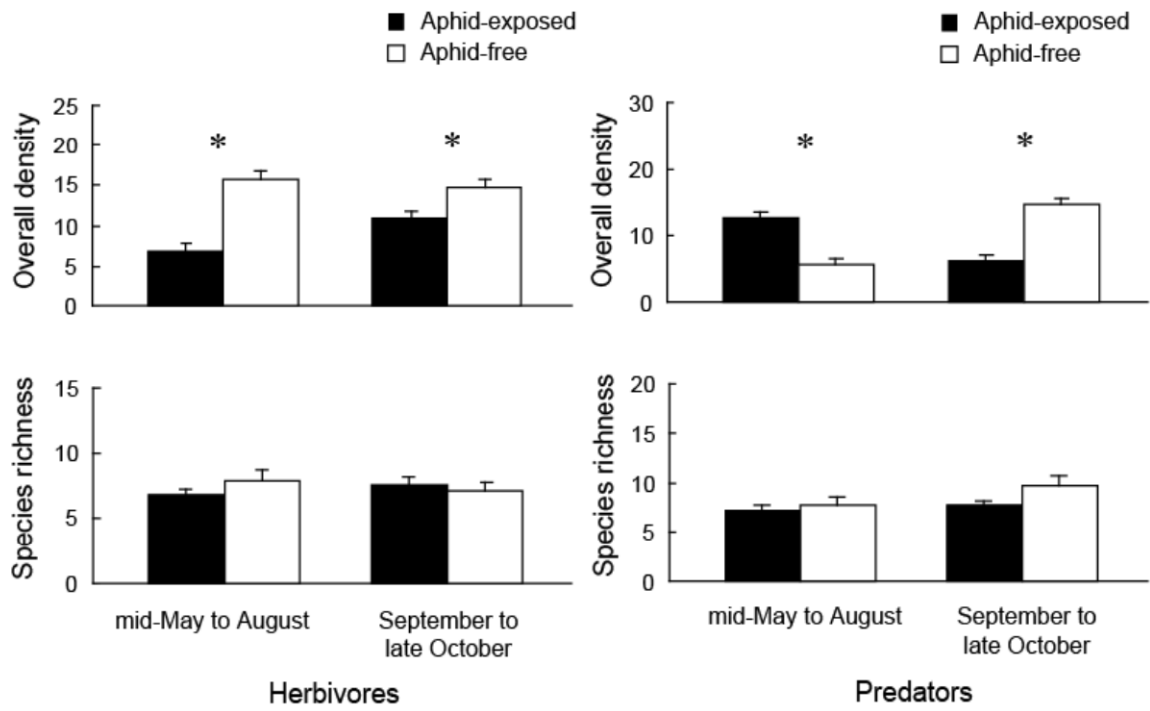
23

24

25

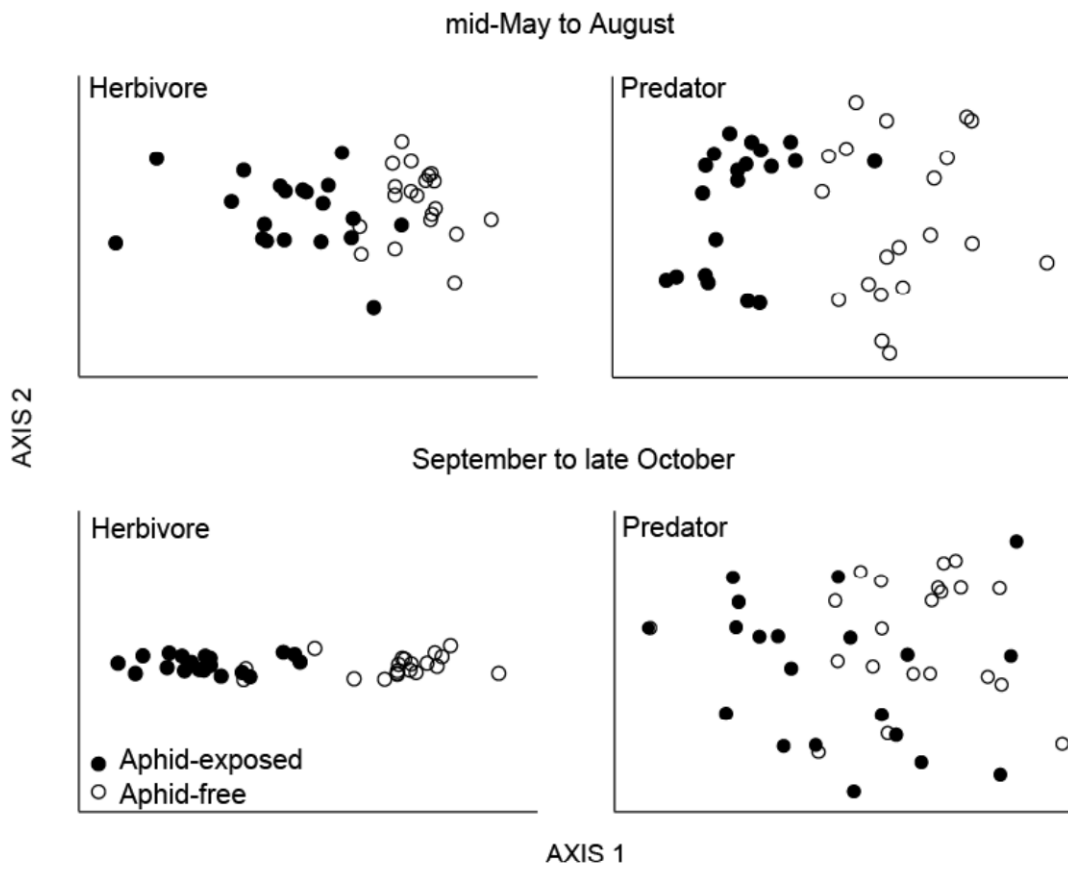
1 **Fig. 1**

2



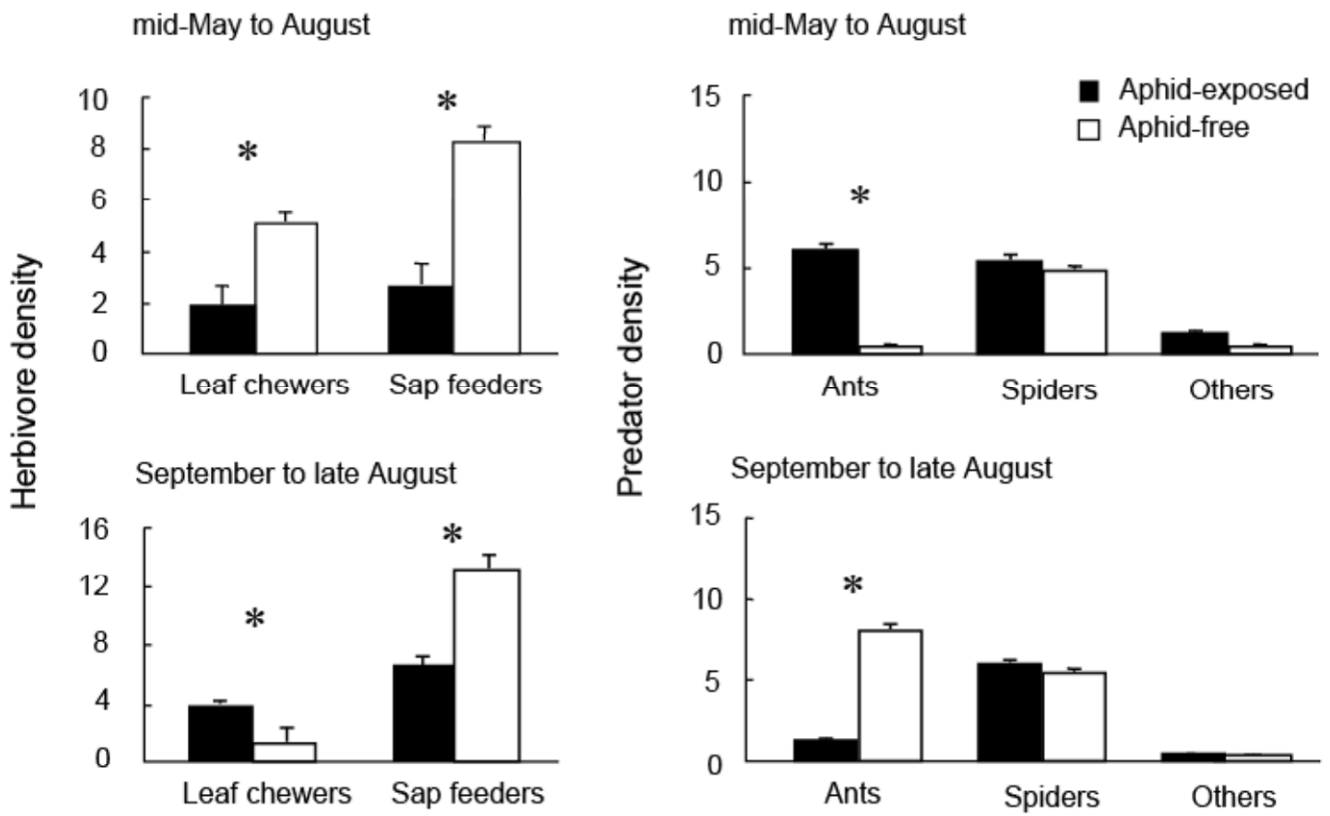
1 Fig. 2

2



1 **Fig. 3**

2



1 **Appendix 1.** Herbivorous insects found on *S. altissima*.

Species	Feeding guild <sup>a</sup>	Host-plant specificity <sup>b</sup>	Stage	Season	Aphid-exposed	Aphid-free
Coleoptera						
Cerambycidae						
Cerambycidae spec. 1	LC	poly	adult	early	Y	Y
Chrysomelidae						
<i>Aulacophora femoralis</i>	LC	poly	adult	early	Y	Y
<i>Chrysolina aurichalcea</i>	LC	oligo	adult	early	Y	Y
Chrysomelidae spec. 1	LC	poly	adult	early	Y	Y
Scarabaeidae						
Scarabaeidae spec. 1	LC	poly	adult	both	Y	Y
Diptera						
Agromyzidae						
Agromyzidae spec. 1	LM	?	larva	early	Y	Y
Hemiptera						
Acanthosomatidae						
Acanthosomatidae spec. 1	S	poly	adult	late	Y	Y
Aphididae						
<i>Uroleucon nigrotuberculatum</i>	S	mono	nymph, adult	early	Y	N
<i>Macrosiphoniella yomogicola</i>	S	oligo	nymph, adult	late	Y	Y
Aphididae spec. 1	S	poly	nymph, adult	late	Y	Y
Aphididae spec. 2	S	poly	nymph, adult	late	Y	Y
Aphididae spec. 3	S	poly	nymph, adult	late	Y	N
Aphididae spec. 4	S	poly	nymph, adult	late	Y	Y
Aphididae spec. 5	S	poly	nymph, adult	late	N	Y
Aphididae spec. 6	S	poly	nymph, adult	late	Y	Y
Coccidae						
<i>Parasaissetia nigra</i>	S	poly	nymph, adult	late	Y	Y
Coccidae spec. 1	S	poly	nymph, adult	late	Y	Y
Cercopidae						
<i>Aphrophora maritima</i>	S	poly	adult	late	Y	Y
Deltocephalidae						
<i>Nephotetix cincticeps</i>	S	poly	subadult	early	Y	Y
Lygaeidae						
Lygaeidae spec. 1	S	poly	adult	early	Y	Y
Plataspidae						
<i>Megacopta punctatissimum</i>	S	poly	adult	early	Y	Y
Tettigellidae						
<i>Bothrogonia ferruginea</i>	S	poly	subadult	early	Y	Y
<i>Cicadella viridis</i>	S	poly	subadult	early	Y	Y
Lepidoptera						
Geometridae						
<i>Ascotis selenaria</i>	LC	oligo	larva	early	Y	Y
Geometridae spec. 1	LC	poly	larva	early	Y	Y
Geometridae spec. 2	LC	?	larva	early	Y	N
Geometridae spec. 3	LC	?	larva	early	Y	Y
Orthoptera						
Pyrgomorphidae						
<i>Atractomorpha lata</i>	LC	poly	nymph, adult	late	Y	Y
Tettigoniidae						
<i>Phaneroptera falcata</i>	LC	poly	nymph, adult	late	Y	Y

2 Y = present, N = absent.



- 1 <sup>a</sup> LC = leaf chewer, LM = leaf miner, S = sap feeder. <sup>b</sup> mono = monophagous (feeds on
- 2 the genus *Solidago*), oligo = oligophagous (feeds on Composites), poly = polyphagous
- 3 (feeds on several families). <sup>c</sup> both = early and late seasons.
- 4

1 **Appendix 2.** Predators found on *S. altissima*.

Species	Taxa	Stage	Season	Aphid-exposed	Aphid-free
Araneae					
Argiopidae					
<i>Oxyopes sertatus</i>	spider	nymph, adult	early / late	Y	Y
Salticidae					
Salticidae spec. 1-spec. 25	spider	nymph, adult	early / late	Y: spec. 1-22 N: spec. 23-25	Y: spec. 1-20, 22-25 N: spec. 21
Thomisidae					
<i>Misumenops tricuspidatus</i>	spider	nymph, adult	early / late	Y	Y
unidentified spider spec. 1- 25	spider	adult	early / late	Y	Y
Coleoptera					
Cantharidae					
<i>Athemellus adusticollis</i>	other	adult	early	Y	Y
Coccinellidae					
<i>Coccinella septempunctata</i>	other	larva, adult	early	Y	Y
<i>Harmonia axyridis</i>	other	larva, adult	early	Y	Y
<i>Propylea japonica</i>	other	adult	early	N	Y
Unidentified spec. 1	other	adult	early	N	Y
Hemiptera					
Reduviidae					
<i>Ectrychotes andreae</i>	other	adult	early / late	Y	Y
<i>Sphedanolestes impressicollis</i>	other	adult	early / late	Y	Y
Hymenoptera					
Formicidae					
<i>Camponotus japonicus</i>	ant	adult	early / late	Y	Y
<i>Formica japonica</i>	ant	adult	early / late	Y	Y
<i>Pristomyrmex pungens</i>	ant	adult	early / late	Y	Y

2

3 Y = present, N = absent.

4