

Potential Impact of an Exotic Plant Invasion on Both Plant and Arthropod Communities in a Semi-natural Grassland on Sugadaira Montane in Japan

journal or publication title	Journal of Developments in Sustainable Agriculture
volume	12
number	1
page range	52-64
year	2017-05-26
URL	http://hdl.handle.net/2241/00150273

doi: 10.11178/jdsa.12.52

Potential Impact of an Exotic Plant Invasion on Both Plant and Arthropod Communities in a Semi-natural Grassland on Sugadaira Montane in Japan

Yukie Sato^{1*}, Yuta Mashimo^{1,2}, Ryo O. Suzuki¹, Akira S. Hirao¹, Etsuro Takagi^{1,3},
Ryuji Kanai¹, Daisuke Masaki¹, Miyuki Sato¹ and Ryuichiro Machida¹

¹ Sugadaira Montane Research Center, University of Tsukuba,
Sugadaira Kogen 1278–294, Ueda, Nagano 386–2204, Japan

² Graduate School of Symbiotic Systems Science and Technology, Fukushima University,
Kanayagawa 1, Fukushima, Fukushima 960–1296, Japan

³ Department of Tourism Science, Tokyo Metropolitan University,
1–1 Minami-Osawa, Hachioji, Tokyo 192–0397, Japan

Plant and arthropod communities interact closely with one another, therefore, invasive plants can alter not only plant communities, but may also have direct and indirect effects on arthropod communities. Here, we focus on the exotic giant ragweed, which is a serious invasive weed in Japan. Recently, the exotic plant invaded and has dominated part of a semi-natural grassland in Sugadaira Montane Research Center (Nagano Prefecture, Japan). We attempted to evaluate the potential impact of the invasive plant on both plant and arthropod communities by comparing the community composition, abundance, species richness and diversity indices of plants and arthropods between areas where the exotic giant ragweed had and had not invaded, referred to as the invaded and reference areas respectively. We found significant differences in plant and arthropod community compositions between the areas. Plant species richness was lower in the invaded area as predicted. However, the abundance of arthropods including herbivores was higher in the invaded area compared to the reference area in contrast to the expectation that plant invasions reduce arthropod abundance and diversity. We discuss potential causes of the unexpected results.

Key words: *Ambrosia trifida*, biodiversity, biological invasion, trophic level, *Miscanthus sinensis*

Introduction

The impacts of exotic plant invasions on communities and ecosystems are a matter of conservation concern (Levine *et al.*, 2003). Invasive plants often form monospecific stands by outcompeting native plants, resulting in the loss of plant diversity (Gaertner *et al.*, 2009; Hejda *et al.*, 2009; Powell *et al.*, 2011; Vilà *et al.*, 2006). Such changes in plant communities also affect higher trophic levels, such as arthropod communities, not only via the loss of plant diversity

(Chittka and Schürkens, 2001; Simao *et al.*, 2010), but also due to changes in food availability (Gerber *et al.*, 2008; Toft *et al.*, 2001) and plant architecture (Pearson, 2009). Conversely, the plant and arthropod communities present in an ecosystem can affect the outcome of exotic plant invasions (Knops *et al.*, 1999). For example, higher species diversity in resident plant communities increases resistance against exotic plant invasions (Elton, 1958; Naeem *et al.*, 2000; Tracy *et al.*, 2004). The success of invasive plants is partly due to the absence of herbivores, which can regulate the

Received: December 28, 2016, Accepted: January 10, 2017

* Corresponding author: Sugadaira Montane Research Center, University of Tsukuba, Sugadaira Kogen 1278–294, Ueda, Nagano 386–2204, Japan

Tel: +81-(0)268-74-2002, Fax: +81-(0)268-74-2016, E-mail: uchietan@gmail.com

growth and spread of plants (the enemy release hypothesis) (Elton, 1958; Keane and Crawley, 2002; Maron and Vilà, 2001; Siemann and Rogers, 2003; Wolfe, 2002). Thus, plant and arthropod communities interact closely (Borer *et al.*, 2012) and it is important to investigate changes in both communities when evaluating the impacts of invasive plants on native ecosystems. Despite this, few studies have simultaneously investigated both communities (Almeida-Neto *et al.*, 2011; Gerber *et al.*, 2008; Harris *et al.*, 2004; Spyreas *et al.*, 2009).

Here, we attempt to evaluate the impact of exotic giant ragweed (*Ambrosia trifida* L.) invasion on plant and arthropod communities in a semi-natural grassland, which has been maintained by annual mowing for more than 80 years and was originally dominated by the Japanese pampas grass (*Miscanthus sinensis* Andersson). The exotic giant ragweed originates from North America, and has spread to Europe and Asia. In Japan, the plant was first detected in Shizuoka and Chiba Prefectures, and has since spread all over Japan (Washitani, 2001; Yasuda *et al.*, 2009). This invasive plant is able to outcompete other plant species for light due to its woody stem, rapid growth and height (2–6 m) (Abul-Fatih *et al.*, 1979; Abul-Fatih and Bazzaz, 1979; Harrison *et al.*, 2001; Jurik, 1991). As a result, the exotic giant ragweed often forms monospecific stands (Sickels and Simpson, 1985) and reduces plant species richness (Washitani, 2001). Invasion of the ragweed leaf beetle (*Ophraella communa* LeSage), a specialist herbivore of other *Ambrosia* species such as *A. artemisiifolia*, has been reported in Japan (Miyatake and Ohno, 2010; Moriya and Shiyake, 2001). In addition, the beetle's intensive feeding on giant ragweed was also recently reported in Japan (Fukano *et al.*, 2016). However, the giant ragweed still thrives and has been expanding its distribution (Yasuda *et al.*, 2009). Furthermore, pollen of *Ambrosia* plants, including the giant ragweed, is an aggressive human allergen (e.g. Ghosh *et al.*, 1991). Hence, giant ragweed is listed in the invasive alien species list compiled by the Ministry of Environment, Japan and also in the Ecological Society of Japan's "Japan's worst invasive alien species 100".

Recently, the exotic giant ragweed invaded a semi-natural grassland in Sugadaira Montane Research Center (SMRC, University of Tsukuba), and has dominated a part of the grassland. In this study, we investigated both the plant and arthropod community com-

positions in two areas of this grassland: where the giant ragweed has invaded (hereafter, the invaded area) and where the exotic giant ragweed has not invaded (hereafter, the reference area). We then compared the compositions, abundance, species richness, and diversity indices of plants and arthropods between invaded and reference areas. We predicted that all measurements would be lower in the invaded area, since exotic plant invasions often decrease plant diversity (Gaertner *et al.*, 2009; Hejda *et al.*, 2009; Powell *et al.*, 2011; Vilà *et al.*, 2006) and plant productivity (Cardinale *et al.*, 2007; Tilman *et al.*, 1996), and such negative effects on plant communities may also reduce the abundance and diversity of higher trophic levels (Borer *et al.*, 2012; Chittka and Schürkens, 2001; Simao *et al.*, 2010).

Material and Methods

Study site and design

The study location was SMRC (University of Tsukuba) in Nagano Prefecture, central mainland Japan. SMRC is at 1300 m above sea level and as such is classified as a subarctic zone despite its temperate latitude (36° 31' N, 138° 21' E). A semi-natural grassland has been maintained at SMRC for more than 80 years by annual mowing of a 6 ha area (usually conducted in Oct.). The grassland is adjacent to forest consisting of Japanese red pine (*Pinus densiflora* Sieb. & Succ.) and Japanese oak (*Quercus crispula* Blume), and the climax community of the area is thought to be Japanese oak - beech forest. Although the grassland is dominated by the Japanese pampas grass (*M. sinensis*), as is common in Japanese grasslands, the total plant diversity of the grassland is high; more than 100 species of herbaceous plants have been found (Suzuki, 2014). Several exotic plant species have been found in the grassland, such as *Erigeron annuus* (L.) Pers., *Phleum pratense* L., and *Oenothera biennis* L., but their abundance has typically been low (Suzuki, 2014) (Table 1). However, a decade ago, the giant ragweed suddenly appeared in the grassland, possibly with sediment inflow, and has become established and dominant in part of the grassland (a single invaded area of less than 20% of the total grassland; Fig. 1).

Since the invaded area was a single area in the grassland, it was difficult to set research quadrats in a randomized block design. Hence, we selected the invaded area from the middle of the dominated area and the reference area to be in relatively close prox-

Table 1. Plants harvested from reference and invaded areas in the grassland

Species (or genus)	Family	Reference area		Invaded area	
		Dry weight (g)	Proportion (%)	Dry weight (g)	Proportion (%)
<i>Miscanthus sinensis</i>	Poaceae	440.709	46.773	38.2	2.513
<i>Pteridium aquilinum subsp. japonicum</i>	Dennstaedtiaceae	353.899	37.560	242.046	15.920
<i>The genus Thalictrum</i>	Ranunculaceae	74.648	7.922	47.919	3.152
<i>Sanguisorba officinalis</i>	Rosaceae	20.182	2.142	—	—
<i>Artemisia indica var. maximowiczii</i>	Asteraceae	10.104	1.072	—	—
<i>Amphicarpaea bracteata subsp. edgeworthii var. japonica</i>	Fabaceae	7.429	0.788	0.552	0.036
<i>Cirsium oligophyllum</i>	Asteraceae	6.952	0.738	—	—
<i>Erigeron annuus</i> *	Asteraceae	5.089	0.540	—	—
<i>Potentilla freyniana</i>	Rosaceae	5.005	0.531	—	—
<i>Rubus parvifolius</i>	Rosaceae	3.546	0.376	—	—
<i>Spodiopogon sibiricus</i>	Poaceae	2.541	0.270	—	—
<i>Poa pratensis subsp. pratensis</i> *	Poaceae	2.341	0.248	—	—
<i>Fallopia japonica var. japonica</i>	Polygonaceae	2.116	0.225	433.913	28.540
<i>Lysimachia clethroides</i>	Primulaceae	1.960	0.208	—	—
<i>Rosa multiflora</i>	Rosaceae	1.737	0.184	—	—
<i>Phleum pratense</i> *	Poaceae	0.974	0.103	—	—
<i>Convallaria majalis var. manshurica</i>	Asparagaceae	0.456	0.048	—	—
<i>Arundinella hirta</i>	Poaceae	0.453	0.048	—	—
<i>Carex nervata</i>	Cyperaceae	0.404	0.043	—	—
<i>Thelypteris palustris</i>	Thelypteridaceae	0.384	0.041	—	—
<i>Ixeridium dentatum subsp. dentatum</i>	Asteraceae	0.348	0.037	—	—
<i>Ambrosia trifida</i> *	Asteraceae	0.298	0.032	695.361	45.737
<i>Aster microcephalus var. ovatus</i>	Asteraceae	0.231	0.025	—	—
<i>Artemisia japonica</i>	Asteraceae	0.180	0.019	—	—
<i>Geranium thunbergii</i>	Geraniaceae	0.086	0.009	—	—
<i>Solidago virgaurea subsp. asiatica</i>	Asteraceae	0.051	0.005	—	—
<i>Ranunculus japonicus</i>	Ranunculaceae	0.043	0.005	—	—
<i>Picris hieracioides subsp. japonica</i>	Asteraceae	0.035	0.004	—	—
<i>Halenia corniculata</i>	Gentianaceae	0.018	0.002	—	—
<i>Cerastium glomeratum</i> *	Caryophyllaceae	0.015	0.002	—	—
<i>Humulus lupulus var. cordifolius</i>	Cannabaceae	—	—	38.371	2.524
<i>Angelica pubescens</i>	Apiaceae	—	—	13.305	0.875
<i>Senecio cannabifolius</i>	Asteraceae	—	—	10.112	0.665
<i>Chaenomeles japonica</i>	Rosaceae	—	—	0.519	0.034
<i>Oenothera biennis</i> *	Onagraceae	—	—	0.06	0.004
Total		942.234	100.000	1520.358	100.000

Bold: Dominant species of each area

*: Exotic species

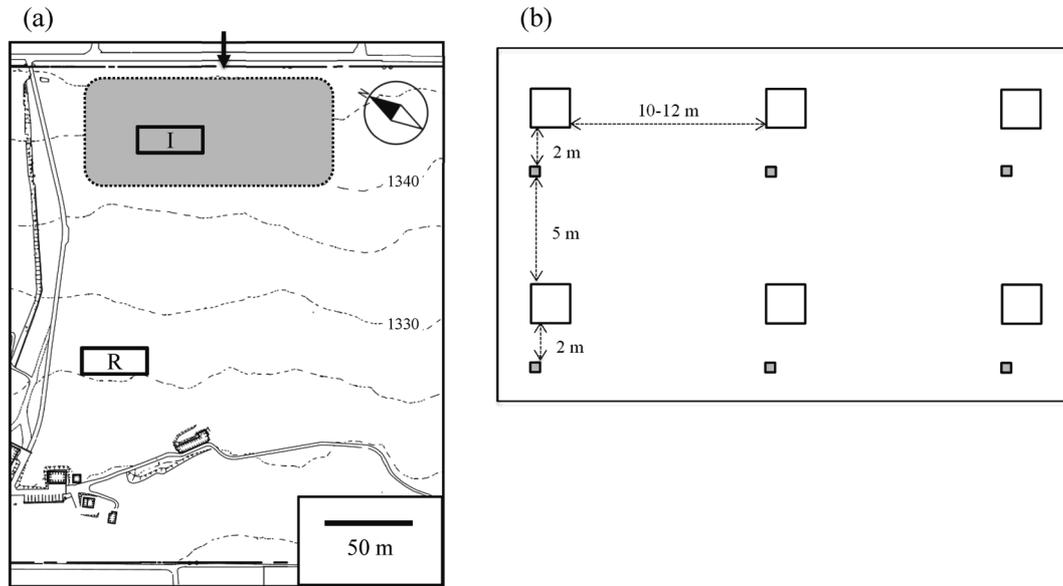


Fig. 1. (a) Location of invaded and reference areas in the grassland at SMRC, and (b) position of quadrats for plant and arthropod surveys in each area. (a): Gray zone surrounded by dotted line shows the area where the exotic giant ragweed has apparently dominated, although it has also invaded other areas in the grassland. The invaded area shown by 'I' was selected from the middle of the dominated area. The reference area shown by 'R' was selected to be in relatively close proximity to the invaded area, but seemed to not yet be invaded. Sediment inflow appeared to be in the direction shown by the arrow. (b): Filled small squares indicate the quadrats for plant surveys, and open large squares indicate the quadrats for arthropod surveys.

imity to the invaded area, but seemed to not yet be invaded. Then, we set up six quadrats in each of the invaded and reference areas for plant and arthropod surveys (Fig. 1), and simply compared plant and arthropod compositions, biomasses, species richness and diversity indices between the two areas. Although this may not be an ideal sampling design since it does not allow us to segregate the effects of location or giant ragweed presence, because of the history of grassland (as mentioned above) we believe these comparisons can provide useful information to estimate the changes in plant and arthropod composition and also the impact of the giant ragweed invasion.

Plant surveys

For the surveys of plant composition, six quadrats ($0.5\text{ m} \times 0.5\text{ m}$) were set up in each of the invaded and reference areas (Fig. 1). Whole plants in each quadrat were covered using a net ($0.5 \times 0.5 \times 2.0\text{ m}$), and the aboveground parts of all plants were harvested using pruning shears. The harvested plants were classified to species, with the exception of *Thalictrum aquile-*

giifolium var. *intermedium* and *T. minus* var. *hypoleucum*, which were identified to genus-level only. The plant harvest and identification were carried out on September 16, 2014. The aboveground biomass of each plant species was determined after drying in an oven at 70°C for 48 h. Species composition and Simpson's diversity index (Simpson 1949) (based on dry weights), abundance (based on total biomass), and species richness (based on the number of plants) were calculated for each quadrat.

Arthropod surveys

For the surveys of arthropod composition, six quadrats ($2.0\text{ m} \times 2.0\text{ m}$) were set up in each of the invaded and reference areas (Fig. 1). These quadrats were larger than those for the plant survey in order to ensure sufficient numbers of arthropod individuals were collected. Plant and arthropod quadrats were located close to one another (ca. 5 m). Twenty swings of a 42 cm diameter sweep net were used to collect arthropods in each quadrat. One person carried out sweeping of one quadrat in each area (in total, six persons worked

on sweeping). Arthropods were identified to family level and their feeding habitats estimated using stereomicroscopes. Arthropods were categorized into three trophic levels by their feeding habitats: detritivores, herbivores and predators (including parasitoids of animals and omnivores). Samples were subsequently classified to species level where possible. Taxa identifications (except for the Araneae order) were confirmed by the environmental assessment company, Environmental Research Center Co., Ltd in Tsukuba, Japan. The arthropod collections were carried out on September 16, 2014, the same day as the plant harvest and identification, and the arthropod identifications were carried out for a year after collection. The community composition of arthropods was evaluated using the number of arthropod individuals identified at the species level in each quadrat. Abundance (the number of individuals), species richness (the number of arthropod species), and Simpson's diversity index (Simpson, 1949) were calculated separately for detritivores, herbivores and predators, based on the number of arthropod individuals identified at the species level in each quadrat.

Data analyses

All statistical analyses were performed in R (ver. 3.2.0; R Core Team 2015). Plant and arthropod community compositions were compared between invaded and reference areas by a permutational multivariate analysis of variance (perMANOVA) with Bray-Curtis dissimilarity index. Similarities among quadrats were visualized using non-metric multi-dimensional scaling (NMDS) with Bray-Curtis dissimilarity index. For the analyses, we used the package *vegan* (Oksanen *et al.*, 2015).

Plant abundance in invaded and reference areas was compared using the Student's *t*-test. Species richness and Simpson's diversity index of plants were compared between the two areas using the Wilcoxon rank sum test. As mentioned above, besides the giant ragweed several exotic plants are present in the grassland, although their abundance is low. To determine the differences in community composition of indigenous plants only, analyses were repeated excluding exotic plant species and the dominant species in each area (the Japanese pampas grass in the reference area and the exotic giant ragweed in the invaded area). Arthropod abundance, species richness and Simpson's diversity index of arthropods were analyzed using

generalized linear models (GLMs) with area (invaded or reference), trophic level (detritivores, herbivores or predators) and their interaction as explanatory variables. In the models of arthropod abundance (the number of arthropod individuals) and species richness (the number of species), we applied a quasi-Poisson distribution to correct for overdispersion. We analyzed Simpson's diversity index of arthropods with a Gamma distribution. The effect of each explanatory variable was tested using F-tests. When the interaction did not have a significant effect, the interaction term was removed from the model. When the interaction had a significant effect, the models were constructed in each trophic level to compare between invaded and reference areas. Since we did not detect exotic species of arthropods, we did not need to carry out additional analyses for indigenous species only.

Results

Plant community composition and diversity

In total 35 plant species, including the exotic giant ragweed and the Japanese pampas grass, were collected from the grassland (Table 1). Twenty-four species were only found in the reference area, 5 species were only found in the invaded area, whilst 6 species were found in both areas (Table 1). There was a clear significant difference in plant composition between the invaded and the reference areas (per MANOVA: $F'_{1,10}=8.253$, $p=0.002$; Fig. 2a). Plant abundance (total biomass per quadrat) tended to be higher in invaded than reference areas (Fig. 3a), but this difference was not significant (Student's *t*-test: $t=1.602$, $df=10$, $p=0.140$). Plant species richness (based on the number of plant species) was significantly lower in the invaded area compared to the reference (Wilcoxon rank sum test: $U=0$, $p=0.005$; Fig. 3b). However, there was no significant difference in Simpson's diversity index (based on biomass) between the two areas (Wilcoxon rank sum test: $U=26$, $p=0.230$; Fig. 3d). Several exotic plant species (besides the giant ragweed) were detected, especially in the reference area (Table 1). The results of analyses excluding exotic and dominant species did not differ from those in which all species were included; plant abundance was not significantly different between the two areas (Student's *t*-test: $t=1.472$, $df=10$, $p=0.172$), plant species richness was significantly lower in the invaded area (Wilcoxon rank sum test: $U=0$, $p=0.004$; Fig. 3c), and Simpson's diversity index was

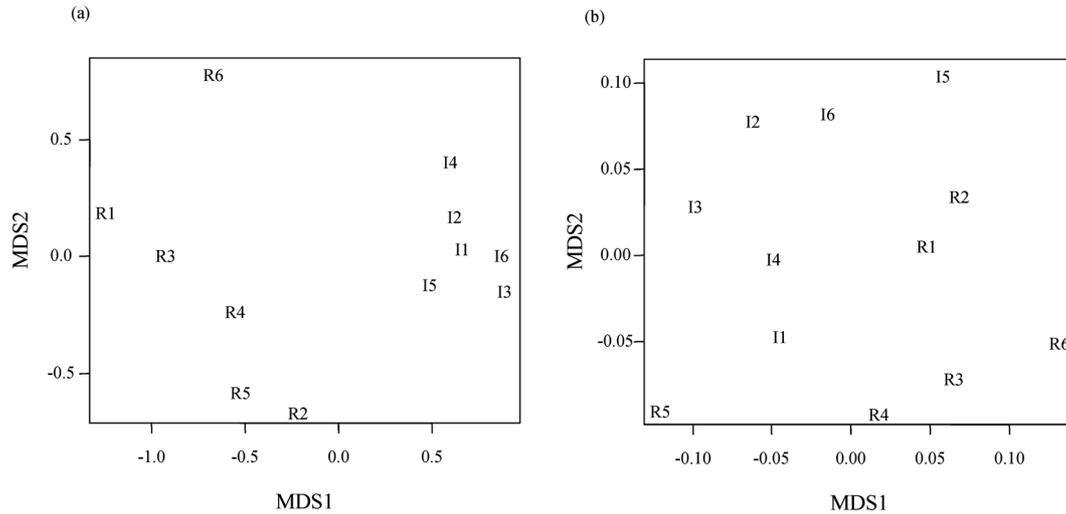


Fig. 2. NMDS plots with Bray-Curtis dissimilarity indices for (a) plant community composition, and (b) arthropod community composition, in invaded and reference areas. I1–I6 indicate quadrats in the invaded area, which is dominated by the exotic giant ragweed, *Ambrosia trifida*, and R1–R6 indicate quadrats in the reference area, which is dominated by the Japanese pampas grass, *Miscanthus sinensis*. Stress values in NMDS plots of plant and arthropod community compositions were 0.07 and 0.20. For the location of each area and quadrat, see Fig. 1.

not significantly different between the two areas (Wilcoxon rank sum test: $U=18$, $p=1.000$; Fig. 3e).

Arthropod community composition and diversity

In total, 427 arthropod individuals and 96 species belonging to 54 families (two classes) were collected from the grassland (Table 2). Among them, families of 17 arthropod individuals (2 Lepidoptera, 13 Araneae and 2 Hymenoptera) were unknown and were omitted from the analyses. Nine species were only found in the reference area, 22 species were only found in the invaded area, whilst 65 species were found in both areas (Table 2). The difference in arthropod community composition between invaded and reference areas was significant (perMANOVA: $F'_{1,10}=2.776$, $p=0.006$), although less clear than the difference observed in plant community composition (Fig. 2b).

Eighty-three detritivore individuals belonging to 21 species and 10 families, 167 herbivore individuals belonging to 34 species and 17 families, and 166 predator (including omnivores and parasitoids) individuals belonging to 39 species and 25 families were sampled (Table 2). The feeding habitats of 8 Cecidomyiidae (Diptera) individuals were unknown; therefore, in addition to the 17 unidentified individuals (see above), they were omitted from the analyses. We

did not find the invasive leaf beetle, *O. communa*, which is a specialist of the exotic giant ragweed, even though its invasion was reported in Nagano Prefecture, Japan (Moriya and Shiyake, 2001). Arthropod abundance (the number of individuals) was significantly different depending on the trophic level (F-test: $F=4.118$, $df=2$, $p=0.026$; Fig. 4a), and overall was significantly higher in invaded areas compared to reference areas (F-test: $F=4.817$, $df=1$, $p=0.036$; Fig. 3a). Species richness (the number of species) was also significantly different depending on the trophic level (F-test: $F=3.735$, $df=2$, $p=0.035$; Fig. 4b) and overall, tended to be higher in invaded than reference areas (F-test: $F=2.929$, $df=1$, $p=0.097$; Fig. 4b). The effect of the interaction between area and trophic level on Simpson's diversity index was marginally significant (F-test: $F=3.274$, $df=2$, $p=0.053$; Fig. 4c), indicating that the effect of area on Simpson's index depends on the trophic level. Hence, Simpson's index was compared at each trophic level separately. There were no significant differences between the two areas for detritivores (F-test: $F=0.773$, $df=1$, $p=0.405$) or herbivores (F-test: $F=0.615$, $df=1$, $p=0.451$). Predators seemed to have a significantly higher index in invaded areas compared to reference areas (F-test: $F=3.754$, $df=1$, $p=0.081$; Fig. 4c).

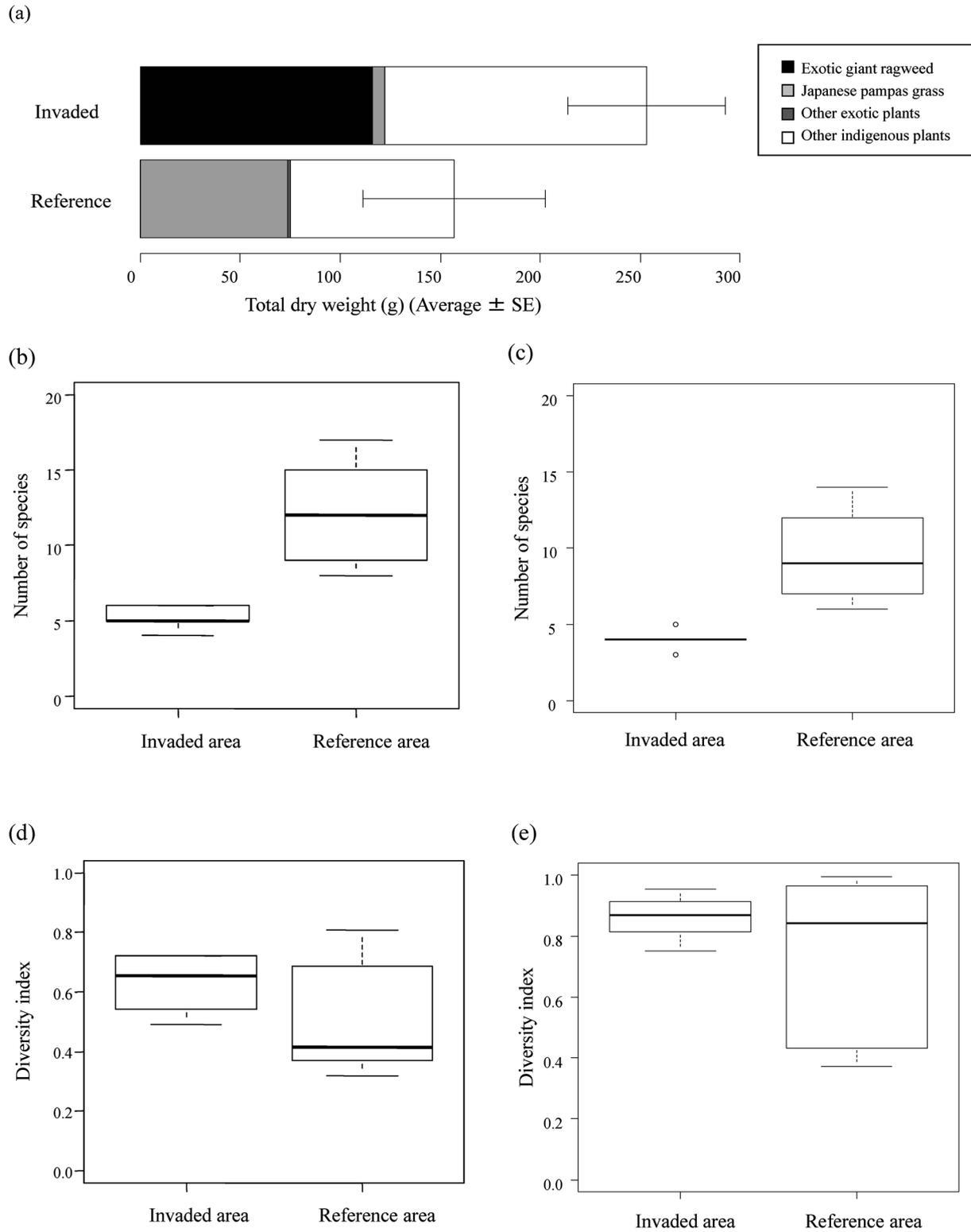


Fig. 3. (a) Bar plots of plant abundance, (b) box plots of plant species richness, (c) box plots of plant species richness excluding exotic species and dominant species in each area, (d) box plots of Simpson's diversity index of plants, and (e) box plots of Simpson's diversity index of plants excluding exotic species and dominant species in invaded and reference areas. For the list of harvested plants, see Table 1.

Table 2. Arthropods collected from reference and invaded areas in the grassland

Feeding niche	Class	Order	Family (suborder, superfamily)	No. of arthropod individuals		No. of species
				Reference area	Invaded area	
Herbivores	Insecta	Thysanoptera	Thripidae	1	0	1
			Aphidoidea	31	26	4
			Miridae	0	2	1
		Hemiptera	Pentatomidae	2	1	2
			Psylloidea	1	1	1
			Coreidae	1	0	1
			Pyrrhocoridae	1	0	1
			Cicadellidae, Cicadellinae	6	7	6
		Coleoptera	Chrysomelidae	3	39	3
		Lepidoptera	Gracillariidae	0	1	1
			<i>Unknown</i>	0	2	<i>Unknown</i>
		Hymenoptera	Tenthredinidae	6	4	2
			Pamphiliidae	0	1	1
		Diptera	Tipulidae	1	1	2
			Chloropidae	6	9	3
			Drosophilidae	2	11	4
		Orthoptera	Acrididae	1	0	1
Total				62	105	34
Detritivores	Insecta	Acari	Cryptostigmata	0	5	2
		Collembola	Sminthuridae	1	0	1
		Diptera	Muscidae	3	6	5
			Sciaridae	6	9	2
			Lauxaniidae	10	1	4
			Psychodidae	0	1	1
			Phoridae	2	4	2
			Sepsidae	0	3	1
			Stratiomyidae	0	26	1
			Chironomidae	2	4	2
Total				24	59	21

Discussion

Plant community composition was significantly different between invaded and reference areas. Plant species richness was much lower in invaded areas compared to reference areas, in accordance with previous studies which showed a decrease in plant species richness with increasing exotic giant ragweed density in moist tall grasslands along rivers (Washitani, 2001). However, Simpson's diversity index of plants was not significantly different between the two areas. The diversity index of plants in the invaded area might not

decrease significantly because of two subdominant plant species in the invaded area, the Japanese knotweed (*Fallopia japonica* var. *japonica*) and the western bracken fern (*Pteridium aquilinum* subsp. *japonicum*). These two species moderately dominated the invaded area (15–30% of abundance; Table 1). Both species have rapid growth and can reach about 2 m in height, hence they might be able to overcome the exotic giant ragweed in the competition for light.

Arthropod composition was also significantly different between invaded and reference areas. Many studies have found lower abundances and/or diversity

Table 2. Arthropods collected from reference and invaded areas in the grassland (continued)

Feeding niche	Class	Order	Family (suborder, superfamily)	No. of arthropod individuals		No. of species			
				Reference area	Invaded area				
Predators	Omnivore	Insecta	Opiliones	Phalangidae	0	2	1		
			Dermaptera	Forficulidae	1	6	1		
			Hymenoptera	Formicidae	4	0	3		
				Eumenidae	1	0	1		
	Predator	Arachnid	Araneae	Acari	Anystidae	1	3	1	
				Tetragnathidae	2	10	2		
				Philodromidae	0	1	1		
				Araneidae	4	1	1		
				Agelenidae	1	1	1		
				Salticidae	6	11	3		
				Dictynidae	0	1	1		
				Clubionidae	8	17	4		
				Corinnidae	0	1	1		
				<i>Unknown</i>	0	13	<i>Unknown</i>		
				Insecta	Hemiptera	Reduviidae	0	1	1
						Nabidae	2	2	1
						Neuroptera	Chrysopidae	0	1
	Coleoptera	Staphylinidae	0				5	2	
	Parasitoid	Insecta	Hymenoptera	Chalcidoidea	0	1	1		
				Braconidae	0	2	1		
				Aphelinidae	0	0	1		
				Eucoilidae	0	1	1		
				Eulophidae	44	4	2		
Ichneumonidae				0	6	6			
Mymaridae				1	1	1			
Total			75	91	39				
Unknown	Insecta		Hymenoptera	<i>Unknown</i>	2	0	<i>Unknown</i>		
			Diptera	Cecidomyiidae	5	3	1		
				Diastatidae	1	0	1		
			Total			8	3	2	
Total				169	258	96			

of arthropods (mainly herbivore arthropods) in invaded ecosystems (or on exotic plants) compared to native ecosystems (or on native plants) (Ernst and Cappuccino, 2005; Gerber *et al.*, 2008; Hagen *et al.*, 2010; Hartley *et al.*, 2010; Holmquist *et al.*, 2011; Procheş *et al.*, 2008; Samways *et al.*, 1996; Southwood *et al.*, 1982; Wu *et al.*, 2008; Zuefle *et al.*, 2007). Some of these findings support the enemy release theory; exotic plant species are free from their natural enemies in new areas and they support lower abundances and diver-

sities of herbivores, therefore they are less down-regulated by herbivores (Ernst and Cappuccino, 2005; Gerber *et al.*, 2008; Hartley *et al.*, 2010; Holmquist *et al.*, 2011; Procheş *et al.*, 2008; Southwood *et al.*, 1982; Zuefle *et al.*, 2007). Another potential explanation is the indirect effect of plant diversity loss (Simao *et al.*, 2010), as plant diversity is often related to arthropod abundance and diversity (Knops *et al.*, 1999; Koricheva *et al.*, 2014). In this study, we did not find the exotic ragweed leaf beetle, *O. communa*,

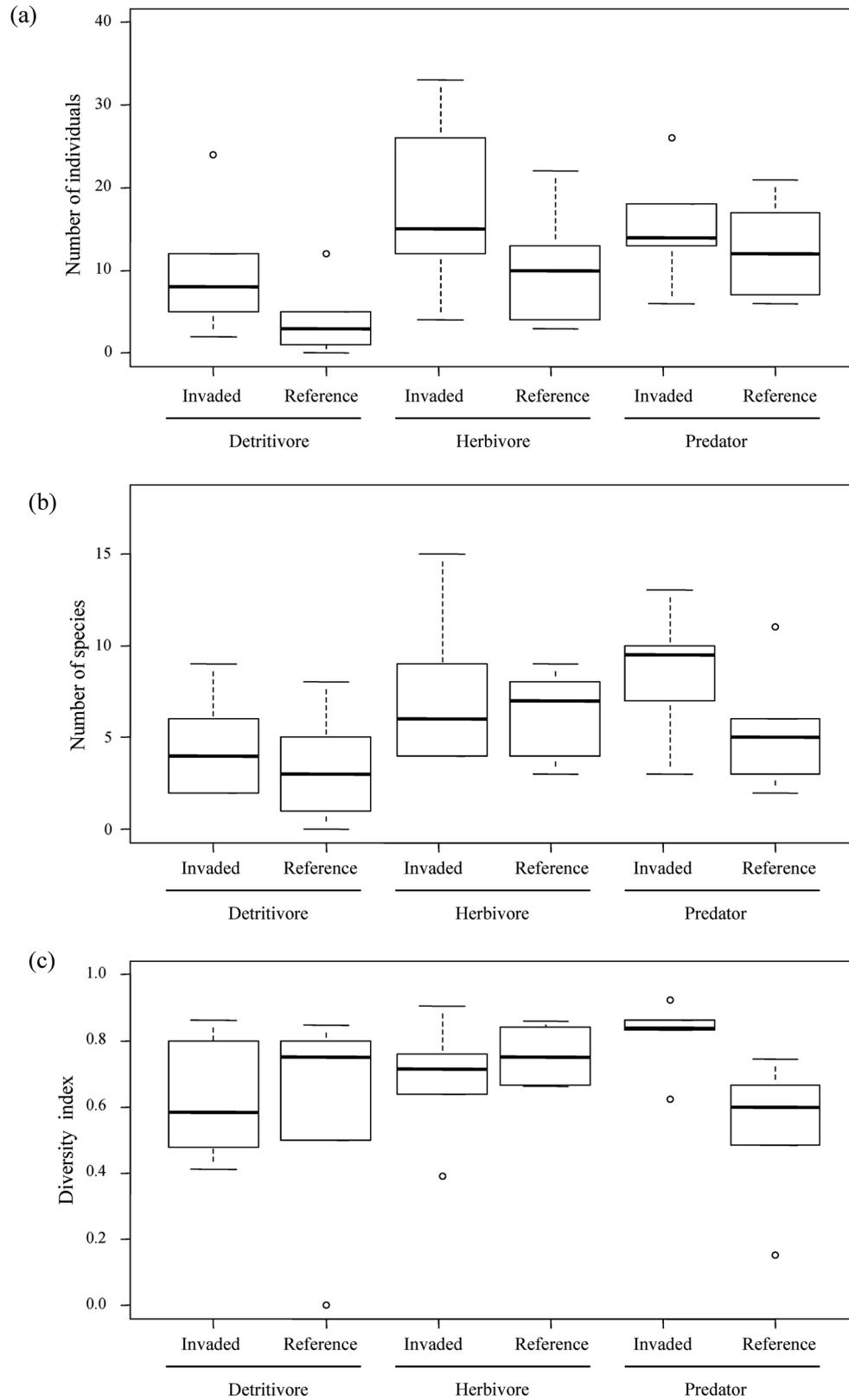


Fig. 4. (a) Box plots of arthropod abundance, (b) species richness, and (c) Simpson's diversity index, for detritivores, herbivores and predators in invaded and reference areas. For the list of collected arthropods, see Table 2.

suggesting the absence of the specialist herbivore of the giant ragweed, and we detected lower plant species richness in invaded areas. Hence, as in previous studies, we predicted there would be lower abundance and diversity of herbivore arthropods in invaded areas. However, contrary to our prediction, arthropod abundance was higher in invaded than reference areas regardless of the trophic level (detritivores, herbivores or predators), and arthropod species richness showed a similar tendency.

In general, exotic plant invasions are seen to have negative effects on arthropod communities. However, recent meta-analysis studies have revealed that the direction and magnitude of effects depend strongly on the characteristics of exotic plants (e.g. woody or herbaceous, N-fixing plant or non N-fixing plant), ecosystem type (e.g. woodlands, grasslands or wetlands), trophic levels of arthropods and composition of food webs (whether primary consumers are herbivores or detritivores) (McCary *et al.*, 2016; van Hengstum *et al.*, 2014; Vilà *et al.*, 2011). In particular, McCray *et al.* (2016) showed that exotic plant invasions are less effective in grasslands compared to woodlands and wetlands, regardless of trophic levels and composition of food webs. This could be due to the inconsistent impacts of exotic plant invasions in grasslands; the negative effects of exotic plant invasion are often counteracted by other factors in grasslands. In our system, we suspect that there is a counteractive effect of a change in vegetation physical structure, following the shift from a grass-dominated plant community (the Japanese pampas grass) to a forb-dominated plant community (the giant ragweed). This effect has also been implied to cause an increase in the number of arthropods (mainly sap-feeding herbivores, pollinators and other Hemiptera and Hymenoptera) associated with exotic baby's breath (a common invasive forb) invasion in sand dunes (Emery and Doran, 2013). A forb-dominated community may support a higher diversity of arthropods by supplying more complex habitat structures compared to grass-dominated communities (Emery and Doran, 2013). Although all three dominant species in the SMRC grassland grow up to 2m high and create spatial structure, the giant ragweed and the Japanese knotweed have a lot of branches and spread broader leaves compared to the Japanese pampas grass. Such structures may provide a greater variety of niches, for example supply places and shadows, which allow arthropods to rest and hunt if they are

predators (Langellotto and Denno, 2004; Pearson, 2009; Rudgers and Whitney, 2006). Hence, such a shift in the plant community might have a stronger influence than plant diversity loss per se on the arthropod community in the grassland.

Conclusion

In this study, we found differences in plant and arthropod compositions between invaded and reference areas, and also found lower plant species richness and higher arthropod abundance in the invaded area. However, we were unable to isolate the effect of exotic giant ragweed invasion from other biotic and abiotic factors. For example, soil moisture content could vary between the two areas and affect plant and arthropod compositions, or the plant and arthropod compositions of the two areas could have been slightly different prior to the exotic giant ragweed invasion. Hence, further research and manipulative experiments controlling for such effects are required. At present, the dominance level of the exotic ragweed is not extremely high (ca. 46% of plant biomass) and the area invaded by the exotic plant is about 20% of the entire grassland. However, the exotic giant ragweed invasion is progressing year by year (personal observation), and even though the reference area defined in this study seemed to be a healthy, Japanese pampas grass area, we did detect the presence of exotic giant ragweed. Hence, in addition to further research, it is necessary to keep monitoring the dynamics of the exotic plant population and changes in plant and arthropod compositions in the grassland for conservation purposes.

Acknowledgements

We thank Dr Leanne Faulks at Sugadaira Montane Research Center (SMRC), University of Tsukuba, for her comments on the manuscript and also for English corrections. We thank Ms Mariko Katsuyama, and Mr Koji Nagaoka at SMRC, University of Tsukuba, for their support and provision of information during the study. We also thank Dr Mari Fujita, Dr Takahiro Ogai, Dr Kensuke Seto, Mr Shodo Mtow, Mr Kazuya Oguro and Mr Masashi Yamada at University of Tsukuba, Mr Ryo Ikeda and Mr Naotaro Okuda at Saitama University, Mr Yukito Aiba at Kyushu University and Mr Ryo Nagasawa at Yokohama City Hall for their assistance in the field surveys. Vegetation and arthropod collections were carried out during educational programs for undergraduate students. We

thank Mr Daichi Kato at Kyushu University for his help in arthropod identification.

References

- Abul-Fatih, H.A., Bazzaz, F.A., 1979. The biology of *Ambrosia trifida* L. II. Germination, emergence, growth and survival. *New Phytol.* 83, 817–827. doi:10.1111/j.1469-8137.1979.tb02313.x
- Abul-Fatih, H.A., Bazzaz, F.A., Hunt, R., 1979. The biology of *Ambrosia trifida* L. III. Growth and biomass allocation. *New Phytol.* 83, 829–838. doi:10.1111/j.1469-8137.1979.tb02314.x
- Almeida-Neto, M., Prado, P.I., Lewinsohn, T.M., 2011. Phytophagous insect fauna tracks host plant responses to exotic grass invasion. *Oecologia* 165, 1051–1062. doi:10.1007/s00442-010-1783-1
- Borer, E.T., Seabloom, E.W., Tilman, D., 2012. Plant diversity controls arthropod biomass and temporal stability. *Ecol. Lett.* 15, 1457–1464. doi:10.1111/ele.12006
- Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proc. Natl. Acad. Sci.* 104, 18123–18128. doi:10.1073/pnas.0709069104
- Chittka, L., Schürkens, S., 2001. Successful invasion of a floral market. *Nature* 411, 653–653. doi:10.1038/35079676
- Elton, C.S., 1958. *The Ecology of Invasions by Animals and Plants*. Springer US, New York.
- Emery, S.M., Doran, P.J., 2013. Presence and management of the invasive plant *Gypsophila paniculata* (baby's breath) on sand dunes alters arthropod abundance and community structure. *Biol. Conserv.* 161, 174–181. doi:10.1016/j.biocon.2013.03.015
- Ernst, C.M., Cappuccino, N., 2005. The effect of an invasive alien vine, *Vincetoxicum rossicum* (Asclepiadaceae), on arthropod populations in Ontario old fields. *Biol. Invasions* 7, 417–425. doi:10.1007/s10530-004-4062-4
- Fukano, Y., Doi, H., Thomas, C.E., Takata, M., Koyama, S., Satoh, T., 2016. Contemporary evolution of host plant range expansion in an introduced herbivorous beetle *Ophraella communa*. *J. Evol. Biol.* 29, 757–765. doi:10.1111/jeb.12824
- Gaertner, M., Breeyen, A.D., Hui, C., Richardson, D.M., 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Prog. Phys. Geogr.* 33, 319–338. doi:10.1177/0309133309341607
- Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., Schaffner, U., 2008. Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biol. Conserv.* 141, 646–654. doi:10.1016/j.biocon.2007.12.009
- Ghosh, B., Perry, M.P., Marsh, D.G., 1991. Cloning the cDNA encoding the AmbtV allergen from giant ragweed (*Ambrosia trifida*) pollen. *Gene* 101, 231–238. doi:10.1016/0378-1119(91)90416-9
- Hagen, E.N., Bakker, J.D., Gara, R.I., 2010. Aerial arthropod communities of native and invaded forests, Robinson Crusoe Island, Chile. *Environ. Entomol.* 39, 1159–1164. doi:10.1603/EN10002
- Harris, R.J., Toft, R.J., Dugdale, J.S., Williams, P.A., Rees, J.S., 2004. Insect assemblages in a native (kanuka – *Kunzea ericoides*) and an invasive (gorse – *Ulex europaeus*) shrubland. *N. Z. J. Ecol.* 28, 35–47.
- Harrison, S.K., Regnier, E.E., Schmoll, J.T., Webb, J.E., 2001. Competition and fecundity of giant ragweed in corn. *Weed Sci.* 49, 224–229.
- Hartley, M.K., Rogers, W.E., Siemann, E., 2010. Comparisons of arthropod assemblages on an invasive and native trees: abundance, diversity and damage. *Arthropod-Plant Interact.* 4, 237–245. doi:10.1007/s11829-010-9105-4
- Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* 97, 393–403. doi:10.1111/j.1365-2745.2009.01480.x
- Holmquist, J.G., Schmidt-Gengenbach, J., Slaton, M.R., 2011. Influence of invasive palms on terrestrial arthropod assemblages in desert spring habitat. *Biol. Conserv.* 144, 518–525. doi:10.1016/j.biocon.2010.10.007
- Jurik, T.W., 1991. Population distributions of plant size and light environment of giant ragweed (*Ambrosia trifida* L.) at three densities. *Oecologia* 87, 539–550. doi:10.1007/BF00320418
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170. doi:10.1016/S0169-5347(02)02499-0
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2, 286–293. doi:10.1046/j.1461-0248.1999.00083.x
- Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J., Huss-Danell, K., 2014. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125, 271–282. doi:10.1007/s004420000450
- Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia* 139, 1–10.
- Levine, J.M., Vilà, M., Antonio, C.M.D., Dukes, J.S., Grigulis, K., Lavorel, S., 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 775–781. doi:10.1098/rspb.2003.2327
- Maron, J.L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95, 361–373. doi:10.1034/j.1600-0706.2001.950301.x
- McCary, M.A., Mores, R., Farfan, M.A., Wise, D.H., 2016. Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a meta-analysis. *Ecol. Lett.* 19, 328–335. doi:10.1111/ele.12562
- Miyatake, T., Ohno, T., 2010. Seasonal abundance of exotic leaf beetle *Orphraella communa* LeSage (Coleoptera: Chrysomelidae) on two different host plants. *Appl. Entomol. Zool.* 45, 283–288. doi:10.1303/aez.2010.283

- Moriya, S., Shiyake, S., 2001. Spreading the distribution of an exotic ragweed beetle, *Ophraella communa* LeSage (Coleoptera: Chrysomelidae), in Japan. *Jpn. J. Entomol. New Ser.* 4, 99–102. (in Japanese with English abstract)
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T., Gale, S., 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91, 97–108. doi:10.1034/j.1600-0706.2000.910108.x
- Oksanen, J., Blanchet F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. *vegan: Community Ecology Package*. URL <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Pearson, D.E., 2009. Invasive plant architecture alters trophic interactions by changing predator abundance and behavior. *Oecologia* 159, 549–558. doi:10.1007/s00442-008-1241-5
- Powell, K.L., Chase, J.M., Knight, T.M., 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *Am. J. Bot.* 98, 539–548. doi:10.3732/ajb.1000402
- Procheş, Ş., Wilson, J.R.U., Richardson, D.M., Chown, S.L., 2008. Herbivores, but not other insects, are scarce on alien plants. *Austral Ecol.* 33, 691–700. doi:10.1111/j.1442-9993.2008.01836.x
- R Core Team, 2015. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rudgers, J.A., Whitney, K.D., 2006. Interactions between insect herbivores and a plant architectural dimorphism. *J. Ecol.* 94, 1249–1260. doi:10.1111/j.1365-2745.2006.01161.x
- Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agric. Ecosyst. Environ.* 59, 19–32. doi:10.1016/0167-8809(96)01047-X
- Sickels, F.A., Simpson, R.L., 1985. Growth and survival of giant ragweed (*Ambrosia trifida* L.) in a Delaware river freshwater tidal wetland. *Bull. Torrey Bot. Club* 112, 368–375. doi:10.2307/2996037
- Siemann, E., Rogers, W.E., 2003. Herbivory, disease, recruitment limitation, and success of alien and native tree species. *Ecology* 84, 1489–1505. doi:10.1890/0012-9658(2003)084[1489:HDRLAS]2.0.CO;2
- Simao, M.C.M., Flory, S.L., Rudgers, J.A., 2010. Experimental plant invasion reduces arthropod abundance and richness across multiple trophic levels. *Oikos* 119, 1553–1562. doi:10.1111/j.1600-0706.2010.18382.x
- Simpson, E.H., 1949. Measurement of diversity. *Nature*, *Nature* 688–688.
- Southwood, T.R.E., Moran, V.C., Kennedy, C.E.J., 1982. The richness, abundance and biomass of the arthropod communities on trees. *J. Anim. Ecol.* 51, 635–649. doi:10.2307/3988
- Spyreas, G., Wilm, B.W., Plocher, A.E., Ketzner, D.M., Matthews, J.W., Ellis, J.L., Heske, E.J., 2009. Biological consequences of invasion by reed canary grass (*Phalaris arundinacea*). *Biol. Invasions* 12, 1253–1267. doi:10.1007/s10530-009-9544-y
- Suzuki, R.O., 2014. Combined effects of warming, snowmelt timing, and soil disturbance on vegetative development in a grassland community. *Plant Ecol.* 215, 1399–1408. doi:10.1007/s11258-014-0396-x
- Tilman, D., Wedin, D., Knops, J., 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379, 718–720. doi:10.1038/379718a0
- Toft, R.J., Harris, R.J., Williams, P.A., 2001. Impacts of the weed *Tradescantia fluminensis* on insect communities in fragmented forests in New Zealand. *Biol. Conserv.* 102, 31–46. doi:10.1016/S0006-3207(01)00091-X
- Tracy, B.F., Renne, I.J., Gerrish, J., Sanderson, M.A., 2004. Effects of plant diversity on invasion of weed species in experimental pasture communities. *Basic Appl. Ecol.* 5, 543–550. doi:10.1016/j.baee.2004.08.007
- van Hengstum, T., Hooftman, D.A.P., Oostermeijer, J.G.B., van Tienderen, P.H., 2014. Impact of plant invasions on local arthropod communities: a meta-analysis. *J. Ecol.* 102, 4–11. doi:10.1111/1365-2745.12176
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708. doi:10.1111/j.1461-0248.2011.01628.x
- Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., Lambdon, P., Manca, M., Médail, F., Moragues, E., Traveset, A., Troumbis, A.Y., Hulme, P.E., 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *J. Biogeogr.* 33, 853–861. doi:10.1111/j.1365-2699.2005.01430.x
- Washitani, I., 2001. Plant conservation ecology for management and restoration of riparian habitats of lowland Japan. *Popul. Ecol.* 43, 189–195. doi:10.1007/s10144-001-8182-8
- Wolfe, L.M., 2002. Why alien invaders succeed: support for the escape-from-enemy hypothesis. *Am. Nat.* 160, 705–711. doi:10.1086/343872
- Wu, Y.-T., Wang, C.-H., Zhang, X.-D., Zhao, B., Jiang, L.-F., Chen, J.-K., Li, B., 2008. Effects of saltmarsh invasion by *Spartina alterniflora* on arthropod community structure and diets. *Biol. Invasions* 11, 635–649. doi:10.1007/s10530-008-9279-1
- Yasuda, T., Ikeguchi, H., Nakano, T., 2009. Spatial distribution of *Ambrosia trifida* at Lake Yamanaka. *Mt Fuji Res.* 3, 29–31. (in Japanese)
- Zuefle, M.E., Brown, W.P., Tallamy, D.W., 2007. Effects of non-native plants on the native insect community of Delaware. *Biol. Invasions* 10, 1159–1169. doi:10.1007/s10530-007-9193-y