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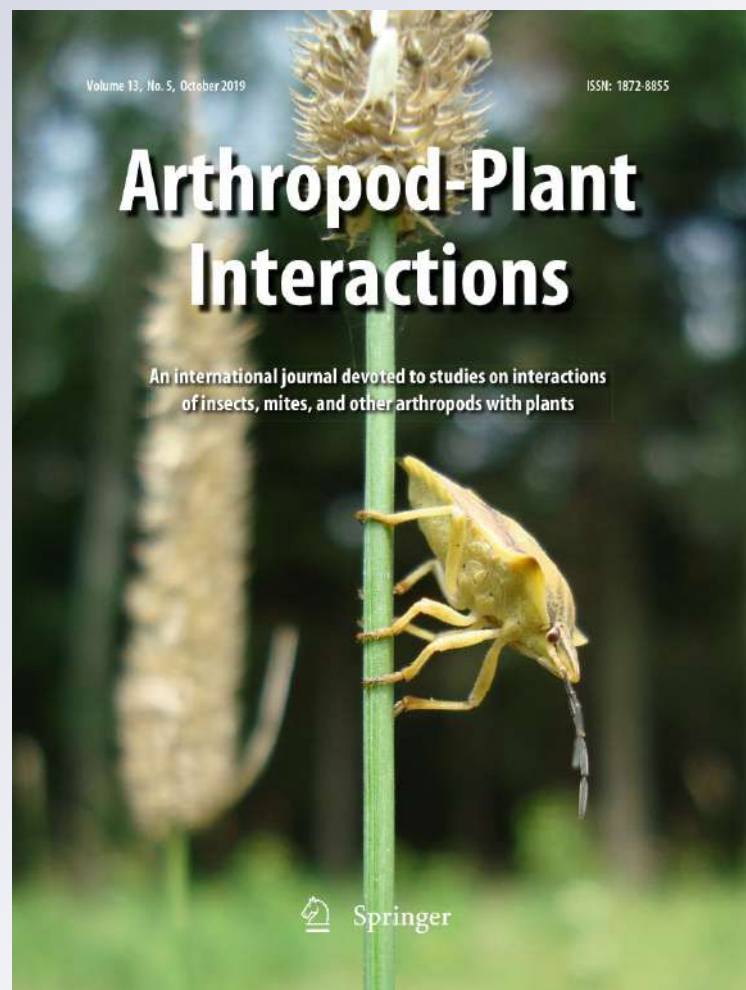
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Impacts of alien invasive *Parthenium hysterophorus* on flower visitation by insects to co-flowering plants

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Abstract

The exotic invasive plant *Parthenium hysterophorus* is invading many tropical habitats. While much work has been done on its interactions with other native plants, little is known about its interaction with insect floral visitors and how it impacts pre-existing pollination networks when it invades a site. We carried out surveys on sites with and without *P. hysterophorus* (invaded and uninvaded, respectively) to investigate its impact on plant–pollinator interactions with two common indicator or target plants (*Ocimum gratissimum* and *Ageratum conyzoides*) in Tanzania. During multiple 15 min observation periods in quadrats, the number of arriving flower visitors, duration of visits and visitation rate were measured and compared between sites. Visitation networks of flower visitors were developed by observing flower visitor taxonomic groups and plants visited across both invasion categories. *Parthenium hysterophorus* was heavily visited by a diversity of flies as taxonomic groups. Indicator plants received fewer flower visitors overall in the invaded site, implying *P. hysterophorus* may be disrupting pollen flow. Foraging behaviour and flower visitation by *Apis mellifera* and flies on target plants were particularly negatively affected in the invaded quadrats. Flower visitation rate to target plants was significantly lower in invaded quadrats than in uninvaded quadrats. This study supports work in other parts of the world demonstrating that invasive species can strongly disrupt pollination networks. By attracting flower visitors that could otherwise serve as pollinators of native plant species, *P. hysterophorus* which is rapidly spreading in eastern African ecosystems could have complex deleterious effects on the wider ecosystem.

Keywords Biodiversity · Exotic species · Insects · Pollinators · Africa · Tanzania

Introduction

Pollination services are important in maintaining plant diversity and consequently biodiversity conservation (Bjerknes et al. 2007; Martins 2014). In flowering plants, pollination is a vital process that contributes to production of fruits and seeds (Lázaro et al. 2013; Martins 2014; Barrios et al. 2016; Weissman and Schaefer 2017). It occurs when flower visitors (pollinators) transfer pollen from the male part of a flower (anthers) to the female part (stigmas) of the same or another flower which results into fertilisation (Albano et al. 2009; Flanagan et al. 2009; Lázaro et al. 2013). Almost 90% of flowering plants rely on insects for pollination (Engel and Irwin 2003). Many plants are obligate insect-pollinated and will not set seed without pollinator visits. Although pollination is an important process for ecological functioning, it has often been ignored when studying the impact of introduced invasive plant species on biodiversity (Bjerknes et al. 2007; Stiers et al. 2014). Previously, studies have shown that

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introduce plants affect pollination and reproductive success of native plants (Brown et al. 2002; Morales and Traveset 2008; Flanagan et al. 2009; Emer et al. 2015). However, the effect varies with plant species (Larson et al. 2006; Bjerknes et al. 2007), season and site where invasion has occurred as well as the magnitude and time of invasion (Emer et al. 2015). Not all introduced plants have negative effects on biodiversity and pollination but rather have neutral or positive effects (Bartomeus et al. 2008; Molina-Montenegro et al. 2008; Albano et al. 2009; Traveset and Richardson 2014; Ye et al. 2014). Introduced invasive plants with positive effects tend to facilitate visitation of flower visitors to native flowering plants, while those with negative effect compete for flower visitors with native plants (Moragues and Traveset 2005; Morales and Traveset 2008). Furthermore, introduced plants with negative effects may outcompete native flowering plants (Larson et al. 2006; Nielsen et al. 2008) and alter ecological processes such as changes in composition of native plants (decreasing species richness and population size) in the invaded habitats (Emer et al. 2015). While sharing of flower visitors is common in a plant community (Aizen et al. 2008; Bjerknes et al. 2007; Emer et al. 2015; Lopezaraiza-Mikel et al. 2007; Morales and Traveset 2008), competition for flower visitation due to sharing of flower visitors between introduced and native plants (McKinney and Goodell 2011; Ye et al. 2014) can affect pollination of native flowering plants by reducing visits to co-flowering plants (Aizen et al. 2008).

Some introduced plants are described as *magnet* species because they attract flower visitors (Molina-Montenegro et al. 2008; Nielsen et al. 2008; Gibson et al. 2013) due to their numerous attractive or colourful flowers (Brown et al. 2002; Nielsen et al. 2008) with greater amounts of pollen and nectar (Morales and Traveset 2008; Emer et al. 2015). They also form large monospecific patches with abundant flowers (Traveset and Richardson 2014), which makes them outcompete native flowering plants as a result of insufficient visits (Larson et al. 2006; Albano et al. 2009). This reduces reproductive success and seed set in native plants (Albano et al. 2009; Gibson et al. 2013; Ballantyne et al. 2015). If pollen from the invasive plant is deposited on the stigma of native flowers, pollination networks may be disrupted (Lopezaraiza-Mikel et al. 2007). Conspecific pollen loss on heterospecific flowers can decrease the volume of pollen conveyed between conspecific flowers (Morales and Traveset 2008; Jakobsson et al. 2008; Molina-Montenegro et al. 2008). Heterospecific pollen deposition on conspecific flowers or stigma can cause stigma clogging (Nielsen et al. 2008), thus reducing fruit and seed production. Jakobsson et al. (2008) found a reduced seed set of native *Helichrysum stoechas* as a result of clogging due to alien pollen from invasive *Carpobrotus* spp. Similarly, Nielsen et al. (2008) showed that

invasive *Heracleum mantegazzianum* reduced the seed set of *Mimulus guttatus* via heterospecific pollination. Moreover, most invasive plants displace native plants via competition for resources and/or allelopathy besides competition for flower visitors (Nielsen et al. 2008; Kaiser-Bunbury and Müller 2009).

Parthenium hysterophorus is native to North and South America but introduced in Africa, Asia, Australia, and Oceania (Shabbir and Bajwa 2006; Kaur et al. 2014; Usharani and Raju 2018). In Africa, it has invaded many countries in sub-Saharan Africa (Wakjira et al. 2009). In Tanzania, *P. hysterophorus* has invaded agricultural fields and rangelands in Arusha, Kilimanjaro, Manyara and Kagera regions. Prompt germination, high fecundity, rapid growth and spread are traits that have facilitated its successful rapid invasion (Shabbir et al. 2013). Similar to other invasive plants, *P. hysterophorus* may have positive, negative or neutral effect on pollination of native plants because of competition for flower visitors (Gibson et al. 2013; Ballantyne et al. 2015; Usharani and Raju 2018). Because *P. hysterophorus* shares flower visitors with native flowering plants, we postulated that it can exert negative effects on native plants by attracting flower visitors away from the latter. *Parthenium hysterophorus* pollen contains allelopathic compounds (Kaur et al. 2014; Shrestha et al. 2015) which may additionally impact the flower visitors since most flower visitors have not had the time to co-evolve with the rapid invasion of *P. hysterophorus*. The allelopathic compounds expressed in pollen can damage the pollinator fitness as shown in other plant studies (Arnold et al. 2014; Tiedeken et al. 2015). While evidence about the negative impact of *P. hysterophorus* on crop productivity, diversity and composition of native plants through allelopathy (de Miranda et al. 2014) and competition for space, light, nutrients and water (Shabbir and Bajwa 2006; Shabbir et al. 2013; Shrestha et al. 2015) is accumulating, there remains a gap in knowledge about the impact of *P. hysterophorus* on pollination services for co-flowering plants. Also, the flower visitors and pollinator guild of *P. hysterophorus* have not been investigated. Therefore, the overall study questions were (i) what insect species visit *P. hysterophorus* and other co-flowering plants? (ii) does *P. hysterophorus* negatively affect neighbouring co-flowering plants by competing for flower visitors? The two target plant species (native *Ocimum gratissimum* and introduced *Ageratum conyzoides*) commonly found in invaded areas were used to investigate the effect of *P. hysterophorus* by hypothesising that (i) *P. hysterophorus* shares flower visitors with neighbouring co-flowering target plants, (ii) it reduces the number of arriving flower visitors and visitation rate to target plants, (iii) it decreases the duration of visits on target plants, and (iv) it integrates in the networks of plant-flower visitors. These hypotheses were tested by surveying the flower visitor insect species on ecologically similar sites with and without

P. hysterophorus invasion and observing their flower-visiting behaviour.

Materials and methods

Study plant species

Parthenium hysterophorus is an annual herbaceous plant (1.0–1.2 m tall) with on average 810 small creamy-white flower heads per plant (Fig. 1) (Kushwaha and Maurya 2012). These flowers produce abundant pollen of about 624 million grains per plant (Kaur et al. 2014). Its inflorescence is 0.5–1.5 cm in diameter, and corymb like (Kushwaha and Maurya 2012). In addition to benefiting from insect pollination, the flowers are pollinated by wind. *Ocimum gratissimum* (Lamiaceae) and *A. conyzoides* (Asteraceae) were used as target species to investigate the mediated impact of *P. hysterophorus* on flower visitations and foraging behaviours of flower visitors on neighbouring co-flowering plant species (Fig. 1). *O. gratissimum* is an erect shrub growing 0.5–3.0 m tall (Nweze and Eze 2009) and native to East Africa. It has zygomorphic, nectar-rich inflorescences attracting flower visitors. *Ageratum conyzoides* is an annual erect branched herb with 0.5–1.0 m height (Kohli et al. 2006). The branched

inflorescence of *A. conyzoides* carries pale purple-coloured flower heads which are arranged in flat-topped clusters. Although *A. conyzoides* is non-native to Tanzania, it was chosen because (i) it has morphologically similar flowers with *P. hysterophorus*, and (ii) like *O. gratissimum* it was abundant co-flowering plant with *P. hysterophorus* in field sites.

Field sites

The field work was conducted at two sites invaded with *P. hysterophorus*, at Tengeru (3°22.002'S, 36°47.008'E, 1387 m a.s.l) and Mikuuni-King'ori (3°20.613'S, 36°59.892'E, 1165.86 m a.s.l) in Meru district, Arusha region of Tanzania. The mean annual temperatures in Tengeru and Mikuuni-King'ori are 19.5 °C and 19.6 °C, and average annual rainfall amounts are 1078 mm and 1361 mm, respectively. Each site (ca. 4 ha) was situated within an agricultural landscape and relatively close (<200 m) to settlements. At each study site, two areas ca. 100 m apart, with and without *P. hysterophorus* invasion (invaded and uninvaded quadrats, respectively) were selected for studying foraging behaviour, visitation of flowers and visitation networks. The two sites had similar soil type, vegetation type and coverage. Prior to observations

Fig. 1 Pictures of **a** *P. hysterophorus* on the invaded site and **b** its flowers (Capitula), **c** *O. gratissimum* and **d** close-up of its inflorescence and **e** *A. conyzoides* Photos: F. Ojija, 2018



uninvaded and invaded quadrats were assessed to ensure that the target co-flowering plant species were present.

Visitation of flower visitors and experimental design

Five permanent quadrats (plots) of 25 m² were randomly established over co-flowering patches within invaded and uninvaded sites at Tengeru between January and April 2018 during *P. hysterothorus* flowering periods. Each quadrat was marked using a marker stick positioned at each corner of the quadrat. Prior to observations, the number of floral units of each target plant species within each 25 m² quadrat was counted. The flower visitors were observed within quadrats over 2 days per week in each month. Each quadrat was observed twice per day, once in the morning (08:00–12:00) and once in the afternoon (14:00–18:00) for 15 min in the same order. The observer noted the number of arriving flower visitors and taxonomic groups in the quadrats. The time spent per flower on the target plant species by each visitor was recorded using a stop watch. Photographs and video clips of flower visitors were taken during field work to aid in identification. Every site was observed on the same day in the absence of rainfall and harsh winds that would affect the activity of flower visitors. Any flower insect visitor that touched the floral parts or reproductive parts of a flower (anthers or stigmas) of *O. gratissimum*, *A. conyzoides*, and *P. hysterothorus* during the 15 min period was considered as a potential pollinator (Stiers et al. 2014; Ballantyne et al. 2015). However, the term flower visitor instead of pollinator is used in this text as it was not feasible to confirm whether every flower visitor was an effective pollinator. Visit in this study refers to landing of an insect visitor on a flower, which may include probing for nectar and/or pollen, which results in contact with the anthers or stigmas. Flower visitors were identified to taxonomic group level, using the categories: Hymenoptera (honey bees, other bees, wasps, and ants), Lepidoptera (brown veined white butterflies, acraea butterflies, monarch butterflies and other butterflies), Coleoptera (blister beetles, ladybird beetles, chafer beetles, and other beetles), Diptera (hoverflies, and other flies), and Hemiptera. Visitation rate was calculated according to Stiers et al. (2014) as the number of flower visitors to the individual target plant divided by the number of open flowers or inflorescences of that plant within the quadrat to avoid the bias of unequal flower numbers between replicates.

Plant–flower visitor network analysis

Considering the absence of studies on flower visitor guilds of *P. hysterothorus* and guilds of flower visitors shared with native flowers, we set out to map the interactions of flower visitors and flowering plants available in the study site. Five 36 m² quadrats were randomly established in

the invaded and uninvaded sites at Mikuuni and Tengeru. Twice a week from April to June 2018, quadrats were observed in the same order, in the morning (08:00–12:00) and afternoon (14:00–17:00) for 15 min while recording plant–flower visitor interactions. Since it was difficult to identify all flower visitors on *P. hysterothorus* and co-flowering plants to species level in the field, visitors were identified by eye where possible, some were photographed, and a representative subset were captured using a sweep net. These preserved specimens were then taken to the University of Dar-es-Salaam, Department of Zoology, for identification. A quantitative plant–flower insect visitor network or interaction for each site was constructed using R bipartite package 2.08 (Dormann et al. 2009) based on the number of visits by flower visitors to each plant species. Interaction networks are tools, which help to understand plant–flower visitor communities, and to investigate possible threats to plant diversity and food production if the ecosystem service (pollination) provided by pollinators decreases (Dormann et al. 2009; Ferrero et al. 2013; Ballantyne et al. 2015). The network-level metrics including connectance, nestedness, linkage density, links per species, and generality were calculated based on the number of visits by flower visitors to each plant species (Blüthgen et al. 2008; Dormann et al. 2009; Padrón et al. 2009; Ferrero et al. 2013; Ballantyne et al. 2015).

Statistical data analysis

The impact of *P. hysterothorus* on visitation (the number of arriving flower visitors and visitation rate) and foraging behaviour (duration of visits) on target native *O. gratissimum* and exotic *A. conyzoides* plants was analysed using one-way ANOVA (general linear model procedure) with the number of quadrats as the unit of replication and invasion status as categorical predictor. Flower visitor taxonomic groups were compared between the invaded and uninvaded quadrats. Homogeneity of variance and normality were tested using Levene's test and Shapiro–Wilk test, respectively. When the parametric assumptions were not confirmed after transformations (Box-cox or log transformation), the non-parametric Kruskal–Wallis test was used. Significant differences were confirmed using the post hoc Tukey–Kramer HSD and Mann–Whitney Pairwise comparison test. A 5% significance level was used for all the tests. Statistical tests were performed with Origin version 9.0 SR1 (2013), while R version 3.5.1 (2018) was used to construct pollinator visitation network and calculate network level metrics. Hemiptera were not compared between sites because their sample size was small, and therefore they were considered as minor flower visitors.

Results

Flower visitor guild in invaded and uninvaded sites

The flower visitors on *P. hysterophorus*, *O. gratissimum*, and *A. conyzoides* comprised a diversity of insect species (Table 1; Fig. 2). We recorded twice as many visits to flowers of *O. gratissimum* and *A. conyzoides* in the uninvaded quadrats compared to invaded quadrats (Table 2). In the invaded quadrats, *P. hysterophorus* received 1209 visits also about twice as many visits compared to the other two indicator plant species (Table 2). Hymenoptera and Diptera were the dominant taxa recorded with > 50% of all recorded visits (Table 2). *Apis mellifera* was the most frequent visitor to target species in both invaded and uninvaded quadrats as well as to flowers of both *O.*

gratissimum (55%) and *A. conyzoides* (50%) in the uninvaded quadrats (Table 2). *Apis mellifera* also made about 55% of visits to flowers of *P. hysterophorus* compared to *O. gratissimum* and *A. conyzoides* in the invaded quadrats (Table 2).

Flower visitor-mediated impact of *P. hysterophorus*

The relative proportion of visits to *O. gratissimum* and *A. conyzoides* by different visitor taxa changed significantly in the presence of *P. hysterophorus*. Both target plants experienced a significant reduction in visits by Hymenoptera (*A. mellifera*, ants, and wasps), most beetles, butterflies, and flies on the invaded quadrats (Table 3). Post hoc tests revealed that the number of visits of *A. mellifera* to target plants was significantly higher on the uninvaded quadrats, about twice the number of visits on the invaded quadrats (*O.*

Table 1 Flower visitor guild of *P. hysterophorus*, *O. gratissimum*, and *A. conyzoides*

Order	Common name	Species name or family	
Hymenoptera	Honey bees	<i>Apis mellifera</i>	
	Wasps	Vespidae	
	Ants	Formicidae	
	Other bees	Xylocopa	
Coleoptera	Lunate blister beetles	<i>Hycleus lugens</i>	
	Black blister beetles	<i>Epicauta</i> spp.	
	Blister beetles	Meloidae	
	Chafer beetles	<i>Rhabdotis</i> spp., <i>Pchnoda</i> spp.	
	Chafer beetles	Scarabaidae	
	Groove-winged flower beetles	<i>Melyris</i> spp.	
	Lunate ladybird beetles	<i>Cheilomenes</i> spp.	
	Potato ladybird beetles	<i>Epilachna</i> spp.	
	Ladybird beetles	Coccinellidae	
	Lepidoptera	Brown-veined white	<i>Balenois aurota</i>
African monarch		<i>Danaus chrysippus</i>	
Tiny acraea		<i>Acraea uvui</i>	
Dancing acraea		<i>Acraea eponina</i>	
Encedon acraea		<i>Acraea encedon</i>	
Butterflies		<i>Vanessa virginiensis</i>	
Flower moths		Scythrididae	
Orange tiger moths		<i>Secusio</i> spp.	
Chief butterflies		<i>Amauris</i> spp.	
Diptera		Hoverflies	Syrphidae
		Soldier flies	Stratiomyiidae
		Bee flies	Bombyliidae
		Flies	<i>Stomorphina lunata</i>
	Flies	Calliphoridae, Muscidae	
	Drone flies	<i>Eristalis</i> spp.	
	Blowflies	<i>Chrysomya</i> spp.	
	Green bottles	Calliphoridae	
	Fruit flies	<i>Didacus</i> spp.	
	Housefly	<i>Musca domestica</i> L.	

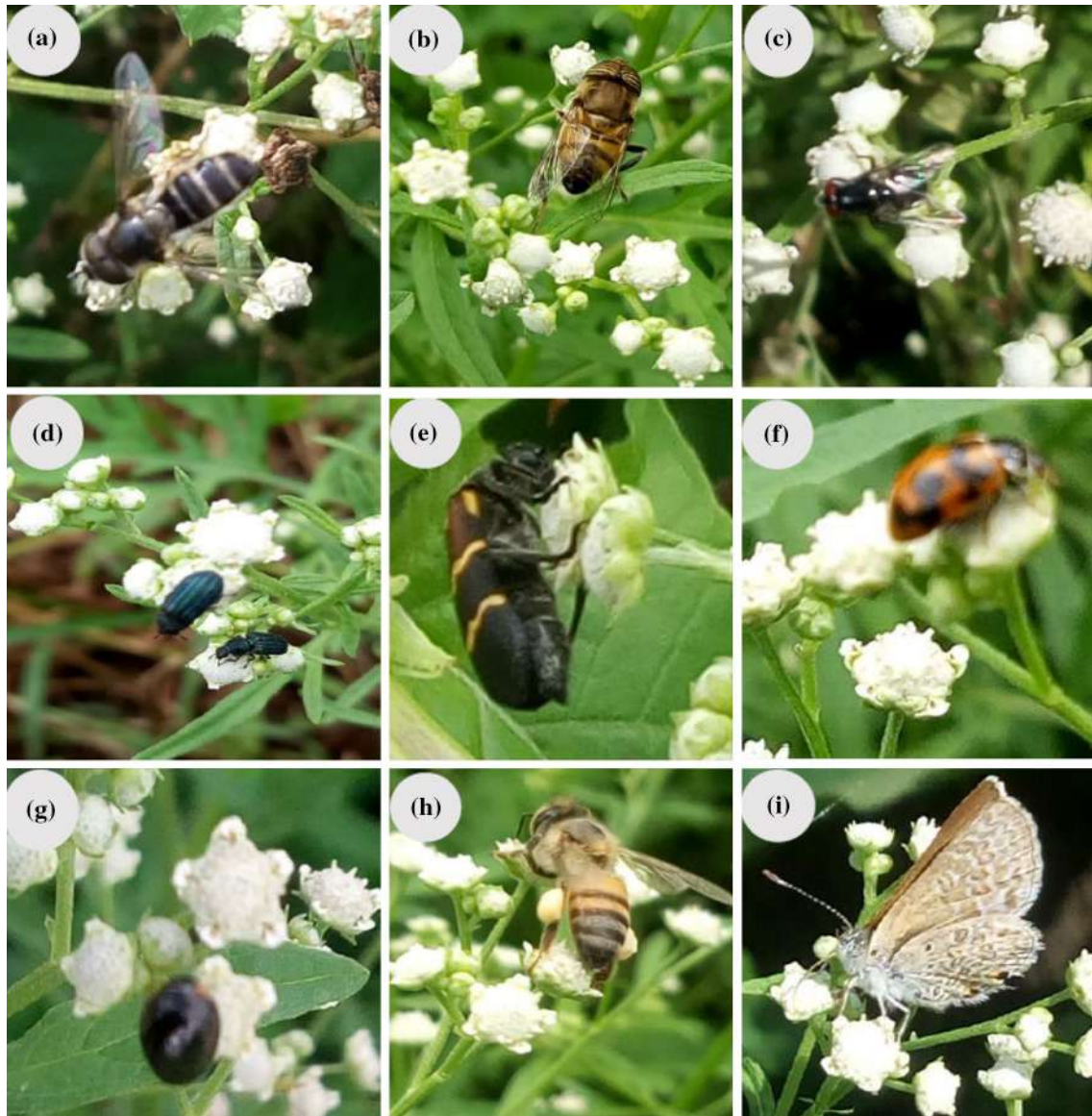


Fig. 2 Flower visitors foraging on flowers of *P. hysterophorus*: Syrphidae (Hoverflies: **a** and **b**), Calliphoridae (**c**), Melyridae (**d**), Meloidae (**e**), Coccinellidae (Ladybird beetles: **f** and **g**), Apidae (*A. mellifera*: **h**), and Lepidoptera (**i**) Photos: F. Ojija, 2018

gratissimum: $p=0.0122$; *A. conyzoides*: $p<0.0001$, Fig. 3a, b). The number of arriving blister beetles ($p=0.0117$), and ladybird beetles ($p=0.0157$) to *O. gratissimum* (Fig. 3c), and ladybird beetles to *A. conyzoides* ($p=0.0013$, Fig. 3d) on the uninvaded quadrats was twice as high compared to that on the invaded quadrats. Similarly, the number of acraea butterflies visiting *O. gratissimum* ($p=0.0026$, Fig. 3e) and other butterflies visiting *A. conyzoides* ($p=0.0283$, Fig. 3f) on the uninvaded quadrats was about twice the number of visits on the invaded quadrats. Moreover, the number of visits of hoverflies ($p=0.0001$), and other flies ($p=0.0001$) to flowers of *O. gratissimum* and other flies ($p=0.0013$) to *A. conyzoides* on the uninvaded quadrats was about three times

the number of visits on the invaded quadrats (Fig. 3g, h). Moreover, the number of arriving chafer beetles, monarch butterflies, ants, other bees, and wasps were not negatively affected by *P. hysterophorus* (Fig. 3a–f).

Duration of visits and flower visitation rate in invaded and uninvaded sites

Duration of visits and visitation rate of insect taxonomic groups, the bees, ants and wasps, beetles, butterflies, and flies to flowers of target plants was significant different between the invaded and uninvaded quadrats but not the visitation rate of butterflies and flies to flowers of *A. conyzoides*

Table 2 Flower visitors, number of insects observed (*N*), and percentage of frequency (%) of total visits that each pollinator made to invasive *P. hysterophorus*, native *O. gratissimum* and exotic *A. conyzoides*

Flower visitors	Order	Invaded site						Uninvaded site			
		<i>P. hysterophorus</i>		<i>O. gratissimum</i>		<i>A. conyzoides</i>		<i>O. gratissimum</i>		<i>A. conyzoides</i>	
		<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
<i>A. mellifera</i>	Hymenoptera	652	54	325	50	226	38	649	55	525	51
Other bees	Hymenoptera	82	7	76	12	108	18	112	10	142	14
Wasps	Hymenoptera	38	3	22	3	34	6	43	4	63	6
Ants	Hymenoptera	0	0	17	3	25	4	8	1	8	1
<i>B. aurora</i>	Lepidoptera	18	1	20	3	9	2	24	2	6	1
Acraea butterflies	Lepidoptera	5	0	7	1	5	1	1	0	5	0
Monarch butterflies	Lepidoptera	13	1	5	1	7	1	9	1	26	3
Other butterflies	Lepidoptera	24	2	18	3	23	4	32	3	23	2
Blister beetles	Coleoptera	52	4	28	4	32	5	43	4	44	4
Ladybird beetles	Coleoptera	57	5	19	3	6	1	42	4	27	3
Other beetles	Coleoptera	23	2	7	1	5	1	24	2	2	0
Hoverflies	Diptera	130	11	47	7	19	3	86	7	74	7
Other flies	Diptera	99	8	48	7	72	12	72	6	43	4
Bugs	Hemiptera	16	1	17	3	17	3	28	2	40	4
Total visits		1209	100	656	100	588	100	1173	100	1028	100

Data are summed over the study period

Table 3 Kruskal–Wallis and one-way ANOVA test statistics of the numbers of arriving flower visitors, duration of visits and visitation rates of flower visitor functional groups to flowers of *O. gratissimum* and *A. conyzoides* on the invaded and uninvaded quadrats

Flower visitor groups	<i>O. gratissimum</i>			<i>A. conyzoides</i>		
	Number of visits	Visitation rate	Duration of visits	Number of visits	Visitation rate	Duration of visits
Bees, wasps, ants	$F_{(7, 32)} = 155.75^*$	$H_{(7, 32)} = 35.53^*$	$H_{(7, 32)} = 34.98^*$	$F_{(7, 32)} = 204.03^*$	$H_{(7, 32)} = 34.23^*$	$H_{(7, 32)} = 33.22^*$
Beetles	$F_{(7, 32)} = 29.79^*$	$H_{(7, 32)} = 18^*$	$H_{(7, 32)} = 37.52^*$	$F_{(7, 32)} = 19.56^*$	$H_{(7, 32)} = 31.70^*$	$H_{(7, 32)} = 34.14^*$
Butterflies	$F_{(7, 32)} = 4.98^*$	$H_{(7, 32)} = 11.89^*$	$H_{(7, 32)} = 30.35^*$	$F_{(7, 32)} = 6.74^*$	$H_{(7, 32)} = 16.13$	$H_{(7, 32)} = 28.40^*$
Flies	$F_{(3, 16)} = 34.28^*$	$H_{(3, 16)} = 14.79^*$	$H_{(3, 16)} = 15.61^*$	$F_{(3, 16)} = 31.00^*$	$H_{(3, 16)} = 6.91$	$H_{(3, 16)} = 16.14^*$

Values differ significantly at $p < 0.05$, *indicates significant difference

(Table 3). In general, insects spent longer time interacting with individual flowers of both target species on the uninvaded quadrats, the duration of visits of *A. mellifera* to flowers of *O. gratissimum* ($p = 0.0216$, Fig. 4a) and *A. conyzoides* ($p = 0.0122$, Fig. 4b) on the uninvaded quadrats was about two and three times the duration of visits on the invaded quadrats, respectively. The duration of visits of ladybird beetles ($p = 0.0122$, Fig. 4c), other beetles ($p = 0.0119$, Fig. 4c), acraea butterflies ($p = 0.0117$, Fig. 4e), other butterflies ($p = 0.0022$, Fig. 4e), and hoverflies ($p = 0.0122$, Fig. 4g) to flowers of *O. gratissimum* on the uninvaded quadrats was about twice the duration of visits on the invaded quadrats. Also, other flies (*O. gratissimum*: $p = 0.0119$, Fig. 4g), ladybird beetles (*A. conyzoides*: $p = 0.0122$, Fig. 4d), and other butterflies (*A. conyzoides*: $p = 0.0122$, Fig. 4f) had longer duration of visits to flowers of target plants on the uninvaded quadrats, about three times the duration of visits on the invaded quadrats. Moreover, the duration of visits of blister

beetles ($p = 0.0122$, Fig. 4d) and other flies ($p = 0.0122$, Fig. 4h) to flowers of *A. conyzoides* on the uninvaded quadrats was twice the duration of visits on the invaded quadrats, and that of hoverflies ($p = 0.0121$, Fig. 4h) on the uninvaded quadrats was four times the duration of visits on the invaded quadrats.

Furthermore, the visitation rate by *A. mellifera* to the flowers of *O. gratissimum* ($p = 0.0012$, Fig. 5a) and *A. conyzoides* ($p = 0.0001$, Fig. 5b) on the uninvaded quadrats was about twice the visitation rate of *A. mellifera* on the invaded quadrats. Also, the visitation rate of blister beetles ($p = 0.0119$, Fig. 5c), ladybird beetles ($p = 0.0032$, Fig. 5c), and acraea butterflies ($p = 0.0432$, Fig. 5e) to flowers of *O. gratissimum*, and lady beetles ($p = 0.0367$, Fig. 5d) to flowers of *A. conyzoides* on the uninvaded quadrats was about twice as high compared to that on the invaded quadrats. Moreover, the visitation of rate of hoverflies ($p = 0.0178$, Fig. 5g) to flowers of *O. gratissimum* on the uninvaded

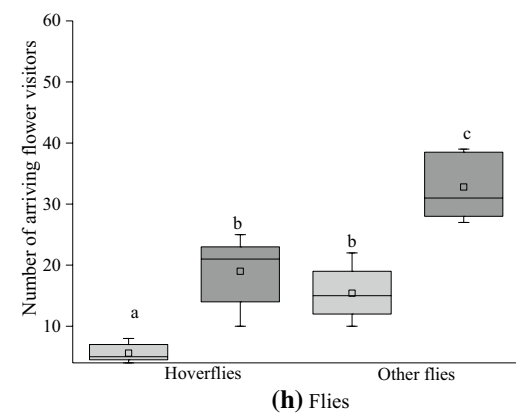
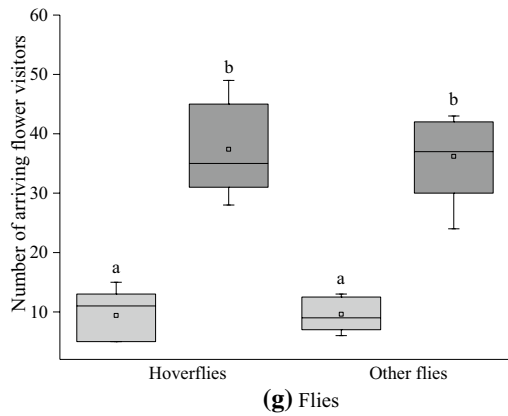
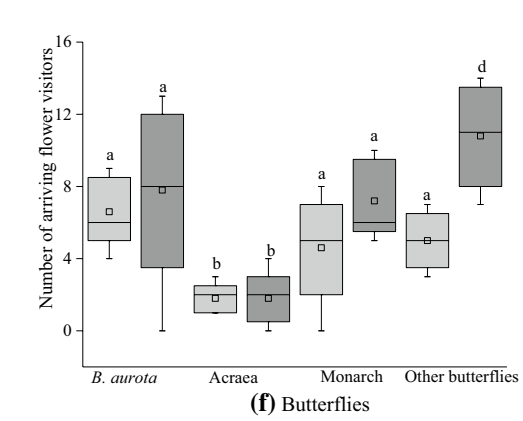
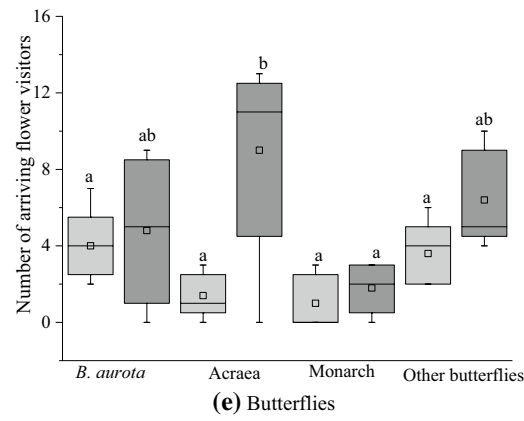
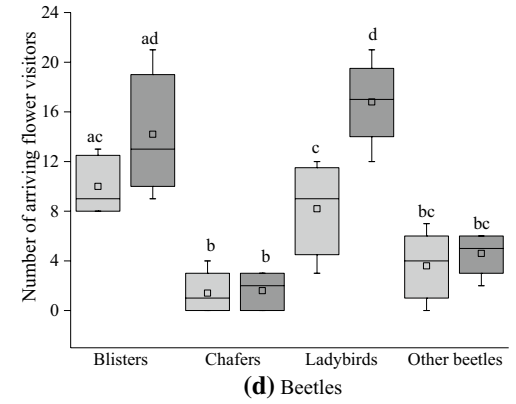
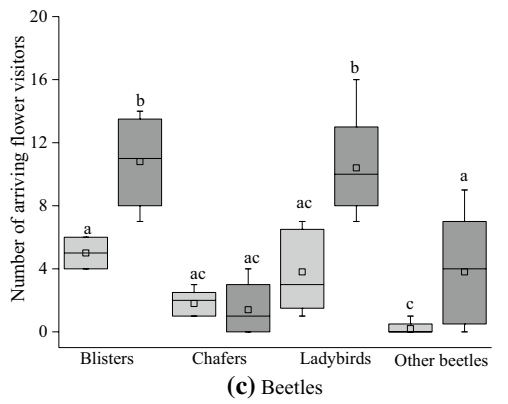
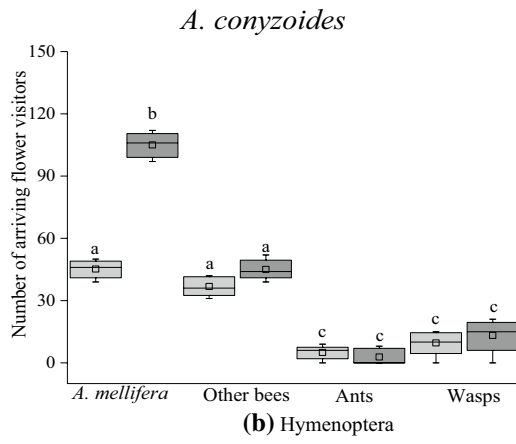
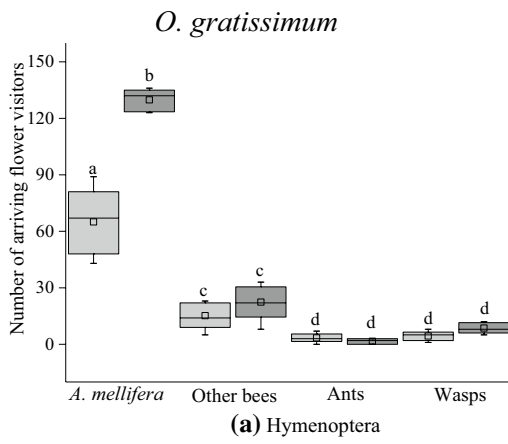


Fig. 3 The number of arriving Hymenoptera (a, b) beetles (c, d), butterflies (e, f), and flies (g, h) to flowers of *O. gratissimum* (left panels) and *A. conyzoides* (right panels) on the invaded (light grey) and uninvaded (grey) sites per 15-min observation period. Boxplots show the mean (a square within boxes) and ranges from 25 to 75% quartile, and the tips of the whiskers indicate the 5th and 95th percentiles. Different letters on bars indicate significant differences by Tukey's HSD test at $p=0.05$

quadrats was three times the visitation rate on invaded quadrats. In contrast, the visitation rate of flies ($H=6.91$, $df=3$, $p>0.05$, Fig. 5h) and butterflies ($H=16.13$, $df=7$, $p<0.05$, Fig. 5f) to flowers of *A. conyzoides* did not differ statistically between the invaded and uninvaded quadrats (Table 3).

Visitation network of plant–flower visitors

A total of 1103 and 987 interactions between co-flowering plant species and flower-visiting insects on the invaded sites, and 429 and 555 interactions on the uninvaded sites were recorded at Tengeru and Mikuuni, respectively. The mean number of interactions per site was similar between invaded and uninvaded sites (766 and 771, respectively). *P. hysterophorus* interacted with 27% and 63% of co-flowering invasive and native plant species, respectively, via the flower visitors. Plant species shared *A. mellifera* as the main flower visitor, which also was the most frequent visitor to *P. hysterophorus* in both sites with a total of 60% of visits. Flower visitors visited more than one plant species, however, no plant species seemed to be pushed out of the network in the invaded sites (Fig. 6). At taxonomic level, insect taxa did not differ significantly between the two sites. Although some taxa appeared to alter their visitation patterns subtly in the presence of *P. hysterophorus*—for instance, hoverflies seem to stop visiting other plants and mostly go to *P. hysterophorus* (Fig. 6). Network metrics were similar, regardless of whether the site was invaded or not (connectance, and specialisation, Table 4). However, nestedness was higher at both uninvaded sites compared to their corresponding invaded ones, indicating a higher level of randomness in the interactions on the uninvaded sites (Table 4). Generality and links per species are lower on the uninvaded sites as all insect groups showed more generalised behaviour on the invaded sites (interacting with a larger number of plants) (Table 4).

Discussion

Parthenium hysterophorus is considered as superlative competitor that crowds out native plants via allelopathy and competition for nutrients, light, water and space (Witt et al. 2018). While this direct impact to native plants is known, our study highlighted its indirect impact to natives through interactions with insect flower visitors. We found

that *P. hysterophorus* received visits from a diversity of different insect flower visitors, mainly *A. mellifera*, Calliphoridae, Coccinellidae, Syrphidae, *B. aurata*, Melyridae, Meloidae, and Hemiptera. The invasive ray florets (female part), rich in nectar and pollen, in the capitulum acted as primary attractant of flower visitors (Usharani and Raju 2018) but the flowers have been previously observed as pollen-rich overall (Martins 2014). This enhanced the visitors' foraging activity on invasive flowers. Thus, the occurrence of *P. hysterophorus* significantly increased the number of potential pollinators, especially *A. mellifera*, in the invaded quadrats in our study. However, the presence of the invasive plant attracted these flower visitors away from other plants (*O. gratissimum* and *A. conyzoides*), which in the case of native plants implies the potential for a strong negative effect on wild plant reproductive success.

Flower visitors and potential pollinators to flowering plants are attracted by floral abundance (Ghazoul 2004; Lopezaraiza–Mikel et al. 2007) and floral morphology (McKinney and Goodell 2011). Generalised flowers with easy access to the nectar tend to attract a larger diversity of non-specialist visitors compared to flowers with specialised morphology such as long corollas or complex mechanisms (Johnson and Steiner 2000). Common to many Asteraceae, the non-tubular flowers of *P. hysterophorus* (Kaur et al. 2014; Usharani and Raju 2018) likely attract predominantly generalist flower visitors such as *A. mellifera* and Syrphidae (hoverflies). These generalists visited other wild plants in the area less frequently in the presence of *P. hysterophorus*, which agrees with many previous studies on invasive plants (Totland et al. 2006; Brown et al. 2002; Jakobsson et al. 2008; Sun et al. 2013). Our results are consistent with that of Stiers et al. (2014) which showed that invasive *Ludwigia grandiflora*, a plant with similarly generalised floral morphology and accessible nectar/pollen, can negatively impact on the number of arriving pollinators and visitation rate of native *Lythrum salicaria*, and Totland et al. (2006), who showed that presence of the invasive *Phacelia tanacetifolia* had strong negative effects on the visitation rate to the native *Melampyrum pratense*. A high visitation rate from effective pollinators enhances gene flow within plant populations, and contributes to community stability of native plants (Lopezaraiza–Mikel et al. 2007; Gibson et al. 2013; Albrecht et al. 2016). However, our findings that *P. hysterophorus* lowered flower visitor frequencies and visitation rates to wild plants indicates *P. hysterophorus* invasion may interrupt pollen flow between native plants in invaded ecosystems (Albano et al. 2009; Gibson et al. 2013; Sun et al. 2013) and significantly harm native plants' reproduction by reducing seed set (Chittka and Schürkens 2001; Albano et al. 2009; Stiers et al. 2014). The potential ecological damage of *P. hysterophorus* can affect more the

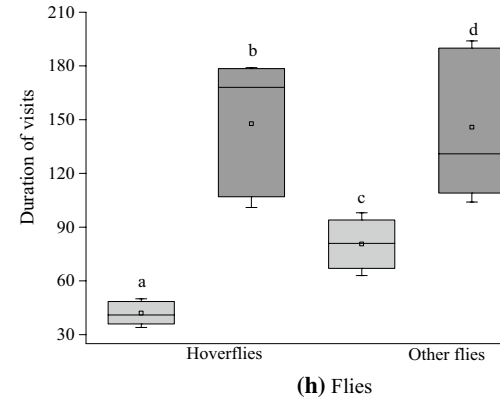
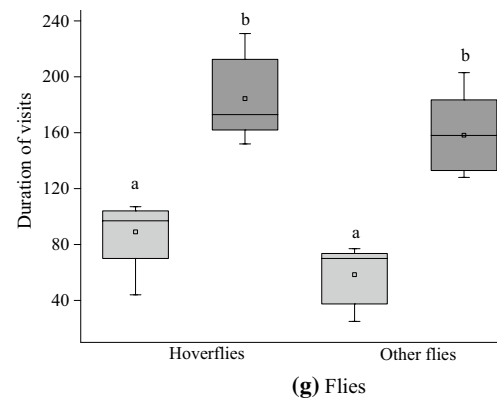
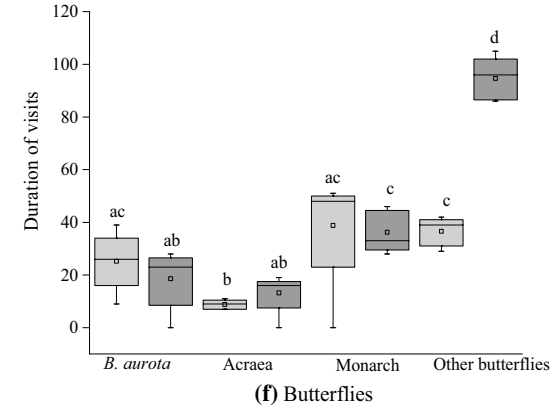
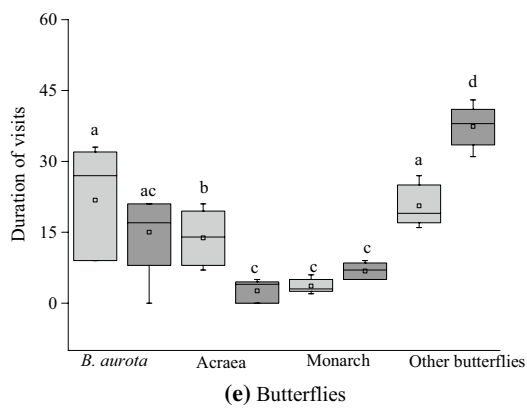
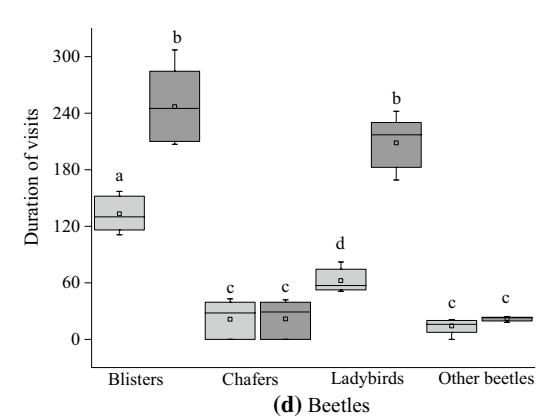
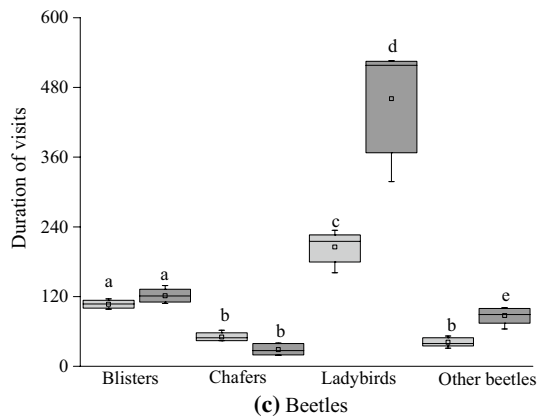
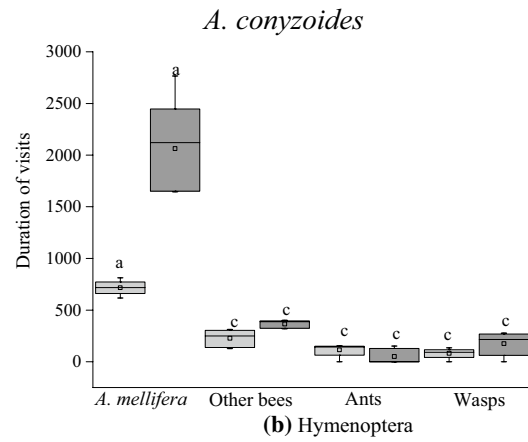
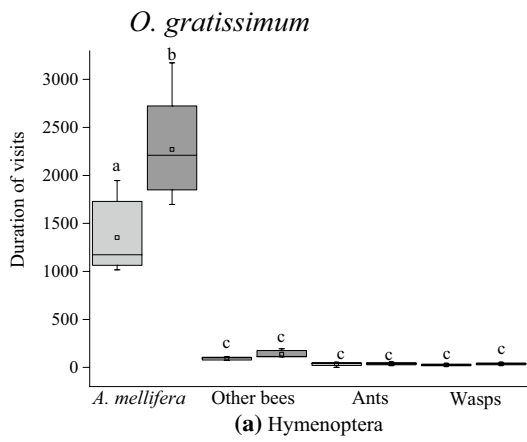


Fig. 4 Duration of visits (in sec) of Hymenoptera (a, b), beetles (c, d), butterflies (e, f), and flies (g, h) to flowers of *O. gratissimum* (left panels) and *A. conyzoides* (right panels) on the invaded (light grey) and uninvaded (grey) sites per 15-min observation period. Boxplots show the median (horizontal line within boxes) and ranges from 25 to 75% quartile, and the tips of the whiskers indicate the 5th and 95th percentiles. Different letters on bars indicate significant differences by Mann–Whitney pairwise test at $p=0.05$

diversity and density of rare or endangered species via multiple means (Brown et al. 2002; Jakobsson et al. 2008; Nielsen et al. 2008).

Our results also suggest that *P. hysterophorus* has the potential to disrupt native plant–pollinator networks, which can have wider-reaching impacts on abundance and diversity of native plants in a habitat (Totland et al. 2006; Lopezaraiza–Mikel et al. 2007; Morales and Traveset 2008; Gibson et al. 2013; Sun et al. 2013). While invasive plants sometimes integrate into the existing flower visitors' networks (Lopezaraiza–Mikel et al. 2007; Aizen et al. 2008; Padrón et al. 2009; Albrecht et al. 2014; Emer et al. 2015), they may disrupt the flow of native pollen through the networks within the recipient ecosystems (Lopezaraiza–Mikel et al. 2007; Chittka and Schürkens 2001; Padrón et al. 2009; Albrecht et al. 2016). In our visitation networks, *P. hysterophorus* interacted with native and introduced co-flowering plants by sharing a wide range of insect flower visitors, some of whom are pollen vectors such as *A. mellifera* and Syrphidae. *Apis mellifera* played a significant role as an integrator of *P. hysterophorus* into flower visitor networks in our study (Padrón et al. 2009; Stiers et al. 2014; Barrios et al. 2016). This generalist flower visitor tended to visit diverse flowers of different plant species including *P. hysterophorus*. However, *A. mellifera* individuals show one of the highest levels of floral constancy of any pollinator (Chittka et al. 1999). We found high nestedness in the uninvaded sites which indicates the presence of more interactions and generalist dominance (Blüthgen et al. 2008), and higher stability of networks in these sites (Ballantyne et al. 2015). As *P. hysterophorus* is a generalist plant (species with many links) which receives both generalist and specialist flower visitors, it could push out specialist plants (species with few links) from the networks by attracting flower visitors away from these plants (Brown et al. 2002; Blüthgen et al. 2008). Low linkage density in invaded sites infers that *P. hysterophorus* decreases plant–insect flower–visitor interactions in these sites (Padrón et al. 2009; Ferrero et al. 2013). Furthermore, its integration into networks reduced native plant–pollinator interactions and therefore led to reduced robustness. The consequences of this could include the disruption of pollination networks, reduced native plant seed set, productivity, and community stability. However,

in our field sites, *P. hysterophorus* did not show a large effect on the visitation network structure.

Since the invasive is facultatively autogamous and anemophilous, it will set seed even without the presence of insect flower visitors (Usharani and Raju 2018). However, it may be drawing pollinators away from plants that need them more than this invasive species. Native plants reliant on pollinators to transport pollen between individuals are more prone to competition for pollination with *P. hysterophorus* than self-compatible plants able to carry out autonomous pollination (Brown et al. 2002; Nielsen et al. 2008). Thus, other plant species, in contrast, will not be able to survive without pollinators. As visitation rate and number of flower visitors to native co-flowering plants are negatively affected in the presence of *P. hysterophorus*, the invasive must be controlled to ameliorate negative impacts on native and established plant communities (Albrecht et al. 2016; Fantinato et al. 2018). Additionally, given other proven allelopathic effects of this species, it is possible that the pollen of *P. hysterophorus* may have traits to which co-flowering plants are not adapted, and may hinder fertilisation due to stigma clogging in native flowers (Chittka and Schürkens 2001; Nielsen et al. 2008; Flanagan et al. 2009; Kaiser-Bunbury and Müller 2009). Such effects have been reported in other invasive species including *Carpobrotus* spp., *Oxalis pes-caprae*, *Lythrum salicaria*, and *Heracleum mantegazzianum* (Brown et al. 2002; Jakobsson et al. 2008; Nielsen et al. 2008; Albrecht et al. 2016). While *A. mellifera* and Syrphidae could conceivably be important pollinators of all three plant species, Melyridae, Meloidae, and Coccinellidae did not act as major flower visitors in our study and are seldom recorded as pollinators. Their visits are likely to be related to either feeding (for instance, on flowers but also on aphids) or mating behaviour (Shimamura et al. 2005). The shorter duration of visits by *A. mellifera*, Syrphidae, other Diptera and some Lepidoptera to flowers of *O. gratissimum* and *A. conyzoides* in invaded quadrats could be due to competition with *P. hysterophorus*. As many Coleoptera (Shimamura et al. 2005) and Diptera (Irvin et al. 1999) are pollen feeders, we anticipate these taxa were attracted to flowers of *P. hysterophorus* due to volume of pollen in our study. Moreover, in this study, the visitation rate of Diptera to flowers of *A. conyzoides* was not strongly affected by *P. hysterophorus* which could be due to their similar flower morphology or a stronger preference for *A. conyzoides* among this taxon, perhaps because of cues such as colour or odour.

Despite the effects of invasive plants being difficult to predict, our study shows that *P. hysterophorus* has potential to displace native plants via competition for pollinator visits. In our study, it exerted a magnet species effect on *A. mellifera* and Syrphidae (Molina-Montenegro et al. 2008; Gibson et al. 2013). However, the impacts could extend further as we do not know its long-term consequences on

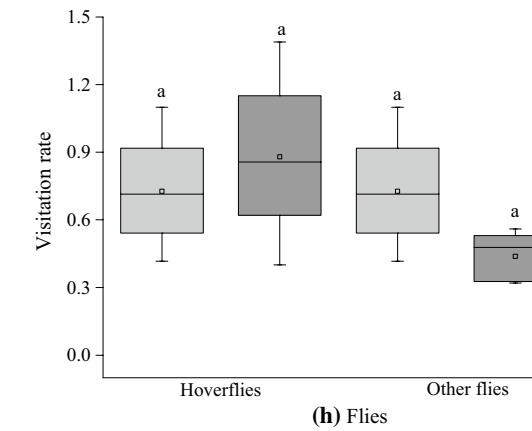
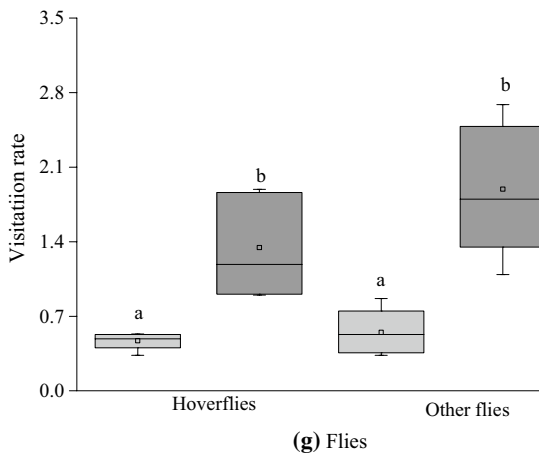
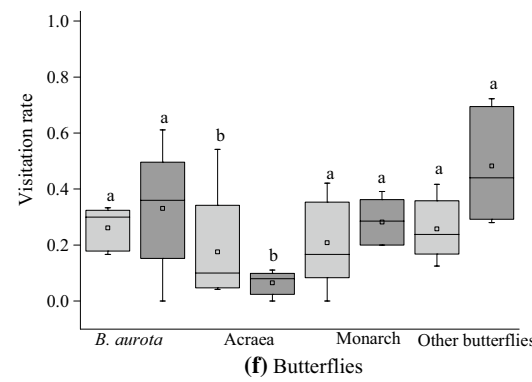
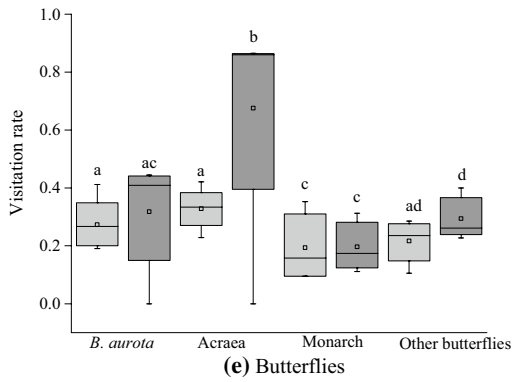
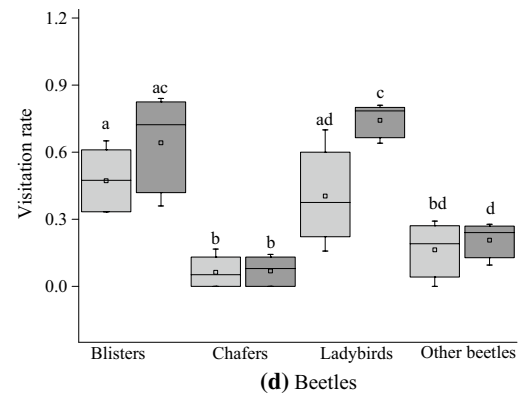
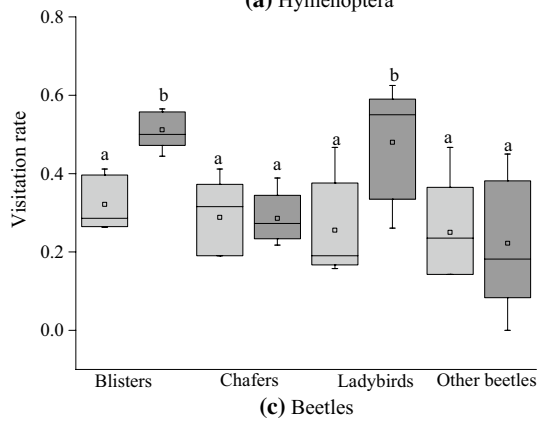
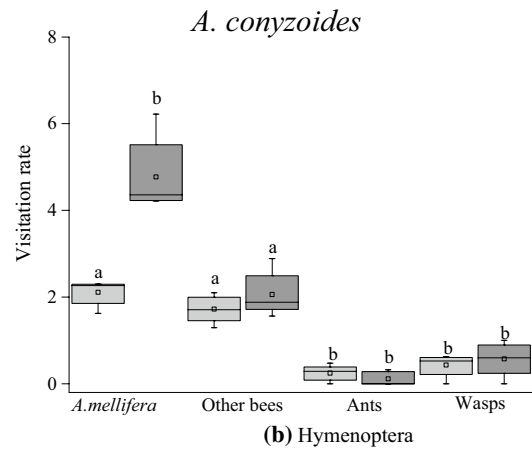
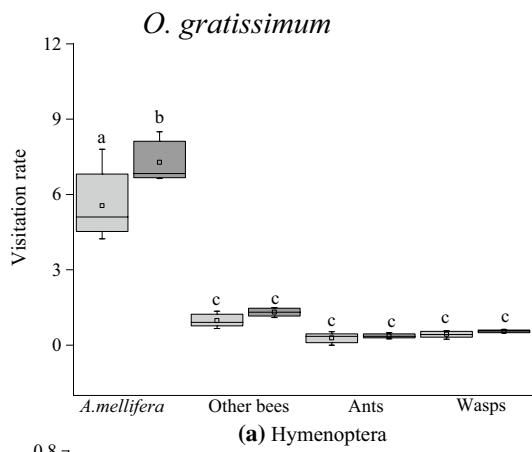


Fig. 5 Visitation rate of Hymenoptera (**a, b**), beetles (**c, d**), butterflies (**e, f**), and flies (**g, h**) to flowers of *O. gratissimum* (left panels) and *A. conyzoides* (right panels) on the invaded (light grey) and uninvaded (grey) sites per 15-min observation period. Boxplots show the median (horizontal line within boxes) and ranges from 25 to 75% quartile, and the tips of the whiskers indicate the 5th and 95th percentiles. Different letters on bars indicate significant differences by Mann–Whitney pairwise test at $p=0.05$

pollinator health and honey quality; other introduced plants with complex chemistry can have pollen or nectar compositions that are deleterious to some pollinator groups (Arnold et al. 2014; Tiedeken et al. 2015). By attracting flower visitors that could otherwise serve as pollinators of native plant species and crops, *P. hysterophorus*, which is rapidly spreading in eastern African ecosystems and crop fields (Witt et al. 2018), could have complex harmful effects on the wider ecosystem. As relatively a high number of generalist pollinators visit *P. hysterophorus*, it is expected to see high seed sets in its existing habitats and the potential to invade more areas by both vegetative and sexual reproductions. Its invasions in crop fields and natural habitats could reduce pollination to native flowering plants and crops, thereby threatening biodiversity, ecosystem services and farmers' livelihoods. Since the invasive continues to spread in Tanzanian habitats, there is potential for it to exert more effects on a wider range of native species.

Conclusion

Parthenium hysterophorus appears to be attractive to flower visitors particularly generalists, and shares flower visitors with other co-flowering plants in Northern Tanzanian semi-natural grassland/scrubland habitat. It has integrated into the plant–pollinator network on sites where it has established, and competes for pollinators with co-flowering plant species, both native and introduced. With its increasing invasion, more studies are required to investigate the impact of *P. hysterophorus* on seed set and development of co-flowering natives, and whether flower visitors transfer alien pollen of *P. hysterophorus* to native flowering species. Moreover, as the plant has complex defensive chemistry (and induces allergic responses in some humans), its adverse effects on wild and managed pollinators, including *A. mellifera*, their brood, honey, and other hive products, should be investigated. Similarly, its allelopathic effects on wild plants' seed sets and pollinator activity should be studied. Both the wild plants and *P. hysterophorus* were visited by a diverse group of flower visitors. The impact of *P. hysterophorus* on visitation rates by flower visitors such as Melyridae, Meloidae, and Coccinellidae may not be important while its effect on potential pollinators such as Apidae and Syrphidae is. This study therefore recommends that eradication and/or management of *P. hysterophorus* is vital to ensure native plants' productivity and community stability. Furthermore, our results contribute to a growing literature showing that invasive–pollinator interactions can significantly affect pollinator visitation behaviour in a recipient ecosystem. Thus, *P. hysterophorus*, which was previously known to exert competitive effects on native plants via allelopathy, has been shown to do so also through competition for flower visitors.

Fig. 6 Visitation web showing plant–flower visitor interactions in invaded and uninvaded plots at Mikuuni (a) and Tengeru (b) study sites. Black boxes represent flower-visiting insects in the upper level, and plants in the lower level, the width of which indicates the number of visits recorded. Grey links indicate plant–flower visitor interactions, and the visitation frequency is represented by the magnitude of interactions (i.e. breadth of the links). Abbreviations for flower-visiting insects are *AM* *Apis mellifera*, *SB* Small bees, *OB* Other bees, *WS* Wasps, *BA* *Balenois aurota*, *ABF* *Acraea* butterflies, *MBF* Monarch butterflies, *OBF* Other butterflies, *HP* Hemiptera, *BT* Blister beetles, *LT* Ladybird beetles, *OT* Other beetles, *HF* Hoverflies, *BL* Blowflies, *BF* Bee flies, *OF* Other flies, whereas plants are *PH* *Parthenium hysterophorus*, *OG* *Ocimum gratissimum*, *AC* *Ageratum conyzoides*, *GC* *Gutierrezia cordifolia*, *IN* *Ipomoea nil*, *LG* *Leucas grandis*, *LN* *Leonotis nepetifolia*, *LM* *Leonotis molis*, *NP* *Nicandra physaloides*, *SS* *Sphaeranthus suaveolens*, *BP* *Bidens pilosa*, *ES* *Emilia* sp., and *ZS* *Zehneria scabra*. NB—bold species are invasive plants to Tanzania

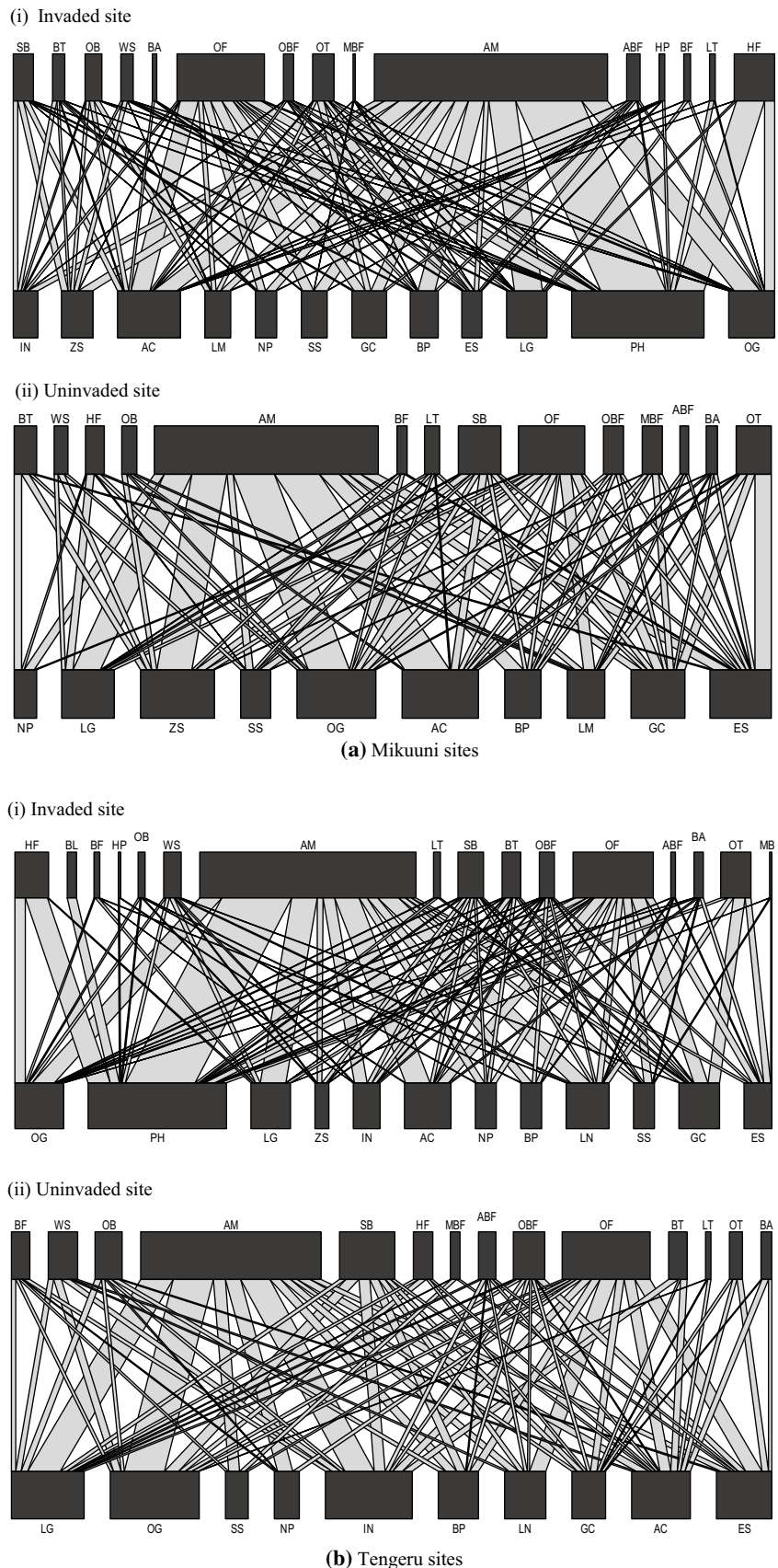


Table 4 Network-level metrics for the invaded and uninvaded study sites based on the number of visits by flower visitors to each plant species

Network-level metrics	Tengeru site		Mikuuni site	
	Invaded	Uninvaded	Invaded	Uninvaded
Connectance	0.5	0.5	0.5	0.5
Nestedness	25.4	31.8	29.7	41.9
Specialisation H'_2 index	0.2	0.2	0.2	0.2
Generality	7.3	6.8	7.6	6.8
Linkage density	6.1	6.5	6.0	6.1
Links per species	3.3	3.2	3.5	3.2

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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