Impacts of non-native plant invasion on generalist insect herbivores through habitat modification

(外来植物の侵入がハビタット改変を通じてジェネラリスト植食性昆虫に与える影響)

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Chapter 1 General introduction

General back grounds

Biological invasion is among the current major threats to biodiversity and ecosystem services, which acts synergistically with other "drivers" such as habitat loss, habitat degradation, overexploitation, and climate change (Vitousek et al. 1997; Chapin III et al. 2000; Pejchar and Mooney 2009). Predicting and preventing impacts of plant invasion on native ecosystems are urgent issues (Hobbs and Humphries 1995), because invasive alien plants can form novel basis of ecosystem by replacing native vegetation and fundamentally alter ecosystem functions (Chapin III et al. 2000; Pejchar and Mooney 2009). However, we have poorly understood how non-native plants interact with native biota (Levine et al. 2003), though most of their impacts on biodiversity and ecosystem services are assumed to follow alternation of ecological interactions caused by the invasion resulting in novel biological interactions between non-natives and natives.

Concept of "specialist vs. generalist," which underlies many theories of ecology and evolution, would be a key to evaluate and predict how non-native plant species interacts with native species. That is, whether using narrower portion of a spectrum of resource (such as food and habitat) or not can significantly affect how the species interact with the others, especially, species sharing no evolutionary history, such as aliens.

Native insect herbivores are likely highly sensitive to plant invasions in terrestrial ecosystems, since, as primary consumers, more or less they adapt to a particular type of plants. In addition, insect herbivores play a critical role in transferring energy from plants to higher trophic levels (Tallamy 2004). Thus, understanding responses of a native insect herbivore to invasion leading to a totally new native herbivore-alien plant interaction, having the concept of specificity in mind, is likely to be critically important from a conservation and restoration standpoint.

A caveat here is that the terms “specialist” and “generalist” are used in the diverse definitions depending on authors (Fox and Morrow 1981), especially in the case of food specificity, which has been the most focused resource type. In the thesis, I defined the species that feed on a number of plant genera within ≥1 family as “food generalist”. Although some authors considered that insect herbivores feeding on plant species within two families are substantially specified (Bernays and Graham 1988), we think that our definition is appropriate, at least, in the thesis, because the “food generalists” dealt in the thesis (grasshopper and mirid bug, see below for detail) mainly feed on Poaceae (in some cases, also on Cyperaceae), which is among the most ubiquitous plant group through the world as not only natives, but also aliens (Daehler 1998; Miyawaki and Washitani 2004).

Predicting responses of food generalist insect herbivores and their consequence

Previous studies on the effects of non-native plant species (including exotic trees in plantations) on invertebrates in terrestrial ecosystems have demonstrated that the richness, composition, and abundance of phytophagous insects communities are significantly affected in certain cases. Decrease in species richness and/or abundances of invertebrate guilds have often been reported; richness of species and families (Litt and Steidl 2010), abundance of total phytophagous invertebrates (Gerber et al. 2008; Litt and Steidl 2010; Proches et al. 2008), all phytophagous guilds (Ernst and Cappuccino 2005), and ectophages (with concurrent increases in endophage abundance) (Gratton and Denno 2005).

Others have identified responses of various phytophagous taxa to plant invasion, e.g., abundance decreases or increases in Hemiptera (Chey et al. 1998; Gremmen et al. 1998; Pellens and Garay 1999; Lambrinos 2000; Tsukamoto and Sabang 2005), Lepidoptera (Pellens and Garay 1999; Valtonen et al. 2006; de Groot et al. 2007), Orthoptera (Bock et al. 1986; Samways and Moore 1991; Chey et al. 1998; Mayer et al. 2005; Pawson et al. 2010), Coleoptera (Wardle et al. 1995; Harris et al. 2004; Tsukamoto and Sabang 2005; Topp et al. 2008), seed-feeding ants (French and Major 2001). Burghardt et al. (2009) and Heleno et al. (2009) demonstrated that such bottom-up impacts of non-native plants can cascaded to the upper trophic levels. De Groot et al. (2007), who examined multiple trophic level impacts of *Solidago canadensis* L. invasion into a semi-natural grassland, concluded that butterflies were more susceptible than predaceous carabid beetles. Proches et al. (2008), who examined impact of three Australasian alien trees on richness and abundance of invertebrate communities in South Africa, also showed that only herbivores were significantly impacted. On the other hand, Simao et al. (2010) showed that experimentally introduced *Microstegium vimineum* negatively affected abundance and species richness of predatory arthropods more than those of herbivores, though change of herbivore species composition was unclear.

However, generalizing and predicting how non-native plant impacts native phytophagous insect is rather challenging. Most previous studies have focused solely on the direct negative impacts of non-natives on native biota (Rodriguez 2006), responses of insect herbivores can be both positive and negative; several studies showed negative responses of native butterflies or grasshoppers to non-native plants (e.g. Bock et al. 1986; Samways and Moore 1991; de Groot et al. 2007), whereas others found positive ones (Mayer et al. 2005; Rodriguez 2006).

Nevertheless, we can logically predict that native food specialists should do poorly on alien vegetation, because they should not be appropriately deal with metabolic compounds of aliens as well as natives to which they have adapted (Tallamy 2004; Tallamy and Shropshire 2009). The study by de Groot et al. (2007) indeed showed that butterflies (food specialists) were more negatively affected than hoverflies (food generalists: Note that the words “specialist” and “generalist” in the cited studies were used in more relative sense rather than definition in the thesis mentioned above).

By contrast, we can hardly predict how food generalist insect herbivores respond to non-native plant. Recent meta-analyses and re-analysis of data from past studies have suggested that native herbivores often prefer non-native plant species to natives, which have evolved resistances to them through coevolutionary history (Parker and Hay 2005; Parker et al. 2006). On the other hand, Tallamy et al. (2010), who examined performance of four typical food generalist lepidopteran herbivores on variety of alien plant species, showed that alien plants were unlikely to produce as much generalist insect biomass as the native plants they replaced, though a few exceptions existed. More complicatedly, even studies dealing with similar combination of species showed inconsistent results; invasive alien grasses have been reported to significantly affect grasshoppers both negatively (Bock et al. 1986; Litt and Steidl 2010) and positively (Mayer et al. 2005; Branson and Sword 2009).

A key to understanding inconsistency of responses of food generalists to alien plants would be focusing on processes caused by plant invasion other than food alternation, such as habitat modification. Invasive alien plants often act as autogenic ecosystem-engineer (Jones et al. 1994; Crooks 2002), i.e., their own physical structure forms a novel habitat to herbivores or modified the existent habitat. The ecological importance of such habitat formation or modification for insect herbivores has not been thoroughly studied. From a wider perspective of such types of impacts, two relevant ecological problems can be posed (Note that the word "habitat modification" in the thesis is used in a broad sense; simple change or alternation of land cover were included. Ecologists (e.g. Bruno 2000), however, have frequently been used the word as physical change of habitat causing non-trophic effects, and following trophic effects were excluded in the narrow sense).

First problem is related to the consequences of the degree of habitat requirement. Although food specificity was repeatedly focused in the issues of specialist v.s. generalist, species with wider diet breath are not always generalists along other niche axis; they can have a strict habitat requirement (i.e., habitat specialist). Species with higher habitat specificity are expected to be more sensitive to plant invasion even though the species are food generalists. It is well known particular habitats (e.g. habitats with frequent disturbance such as floodplains and agricultural lands) are highly invasible (Hobbs and Humphries 1995; Bradley et al. 2010). Some herbivores depending on a particular habitat type in floodplains may be vulnerable to plant invasion. However, to my knowledge, vulnerability of native insect herbivores to plant invasion has not yet been examined in relation to habitat specificity. This may be due to that it is challenging to separate trophic from non-trophic effects, since insect herbivores usually use plants as both food and habitat simultaneously. More complicatedly, trophic and non-trophic processes can sometimes interact strongly (Ritchie 2000; Arditi et al. 2005).

Second one is the concern about the effects of spatial patterns of the habitat formed by the non-native plant, which can influence positively and non-linearly population size of insect herbivores that are neither food nor habitat specialists. In general, spatial distribution of the patchy habitats can cause landscape-level effects which cannot be explained by simple summation of area of the patches alone, that is, representing an "emergent property" (Bissonette 1997; King 1997).

For instance, metapopulation theory by Hanski (1999) indicates that habitat patch connectivity resulted in non-linear positive effect on population size of butterfly species (Hanski and Ovaskainen 2000). Invasive alien plant species also form more or less patchy distribution (e.g. Foxcroft et al. 2009), at least, at the early stage of invasion to the area. If their own physical structure form a novel habitat for native insect herbivores and simultaneously becomes a landscape element in the invaded landscape, spatial distribution of the patchy habitats can cause landscape-level effects on the natives.

To my knowledge, the positive multi-level (both landscape and local) effects of a non-native plant species, which may be a relatively small landscape element, on generalist insect herbivores have not been studied. Although local populations of generalist insect herbivores often prefer a particular plant species to the other coexisting plants (Fox and Morrow 1981; Bernays and Graham 1988; Lu et al. 2010), preference of generalist insect herbivores are known to be highly temporal and seasonally variable (Iwao 1971). Therefore, the landscape-level effect on generalist insects by a plant species may have to arise in a relatively shorter time than that on specialist insects to significantly affect their population dynamics. Nevertheless, recent studies (e.g. Malmstrom et al. 2005; Carriere et al. 2006; Branson and Sword 2009) reported that overspill of generalist herbivores from patches of non-native plant species may lead to damage of other native plants or crops (i.e., impact on biodivesity and ecosystem services through apparent competition (Holt 1977)). We would overlook rapid expansion and outbreak of source population of such generalists if the positive landscape-level effect matters.

Scope and outline of the thesis

Based on the current situation of the knowledge on impact of plant invasion on insect herbivores mentioned above, I have investigated the interactions between non-native plants and native generalist insect herbivores to answer the following questions.

(1) Can habitat modification by alien plants negatively affect habitat specialist herbivores as well as food availability changes?

(2) Can spatial amount and connectivity of non-native plant patches affect population dynamics of generalist herbivores?

Examining these questions will contribute to not only appropriate incorporation of non-trophic effect in predicting impacts of plant invasion on invaded ecosystem, but also validating that food generalists with higher habitat requirement can have conservation priorities, and that multi-level and landscape-scale perspectives are important for regulating unbalanced increase of a particular food generalist.

To answer these questions, I dealt with two model systems: weeping lovegrass

Eragrostis curvula (Poaceae) and grasshopper communities in a floodplain and Italian ryegrass *Lolium multiflorum* Lam. (Poaceae) and populations of a mirid bug species *Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae) in an agricultural landscape. Generally, both types of habitats are known to be highly invasible for non-native plant species (Hobbs and Humphries 1995; Bradley et al. 2010). In Japan, in addition to floodplain that is natural "shifting-mosaic" with high spatial heterogeneity (Yoshimura et al. 2005; Washitani 2007), agricultural landscapes, which have been maintained sustainably by traditional human practices (Washitani 2001a), are characterized by fine-grained mosaic of patches of paddies, grasslands, forests and etc. Such a spatial feature makes the systems feasible to be investigated at a relatively small spatial scale.

Following the present chapter in which I have reviewed the need for evaluating impact of plant invasions on native generalist herbivores and provided specific questions (Chapter 1), the following chapters deal with the questions mentioned above. The first question was examined with grasshopper communities in the gravelly floodplain of the Kinu river, central Japan (Chapter 2, 3), and the second with populations of a native pest of rice in the agricultural landscape in Tajiri area, northeast Japan (Chapter 4, 5).

Among floodplain phytophagous insects, grasshoppers are typical food generalists (Chapman 1990). Among Japanese grasshoppers, there are habitat specialists dependent on a variety of specific habitats (Japanse Society of Orthoptera 2006). Therefore, I investigated a relationship between habitat specificity of grasshopper species and their response to invasion of weeping lovegrass *E. curvula*, one of the most invasive alien grass in the gravelly floodplains of Japan (Muranaka and Washitani 2004; Study Group on Impacts and Managements of Alien Species 2010) (Chapter 2).

It is challenging to directly examine whether or not the effect of habitat modification is among important mechanisms for dynamics of insect herbivore in the invaded ecosystem, because separating trophic effects from the non-trophic effect is rather difficult. However, *Eusphingonotus japonicus*, a representative habitat specialist grasshopper in the gravelly area of the floodplain, provide us an opportunity to examine importance of non-trophic process, since the gravelly area, among the most invasible habitat for weeping lovegrass (Muranaka and Washitani 2004; Study Group on Impacts and Managements of Alien Species 2010), is covered by only sparse vegetation in its original state (Thus, structural importance of native plants is low). I examined the relationship between trophic and non-trophic effects of weeping lovegrass invasion on *E. japonicus* through combination of field survey, field observations, and laboratory experiments (Chapter 3).

In the Chapter 4, I examined the facilitation of mirid bug species *S. rubrovittatus* by Italian ryegrass *L. multiflorum*, a non-native meadow grass which is commonly cultivated and naturalized throughout Japan (Miyawaki and Washitani 2004). *S. rubrovittatus* is known to be a native generalist herbivore which uses heading grasses and sedges as food and habitat (i.e. host). Italian ryegrass was suspected to contribute to the recent expansion of damage to rice by the bug through apparent competition (Ono et al. 2007).

Consequently, landscape level effects of patches of Italian ryegrass on the density of *S. rubrovittatus* were reported in the Chapter 5, because survey mentioned previous chapter can confirm that the agricultural landscape in the Tajiri area of Osaki City, Miyagi Prefecture, northern Japan, where the small meadows of Italian ryegrass are patchily distributed, is appropriate system to examine the positive landscape effect of non-native plant species on a native generalist.

In the brief concluding chapter (Chapter 6), I summarized the conclusions of the studies mentioned to predict more general impacts of plant invasion on insect herbivores, biodiversity and ecosystem services.

Chapter 2 Impacts of weeping lovegrass (*Eragrostis curvula*) invasion on native grasshoppers: responses of habitat generalist and specialist species

Introduction

As mentioned in chapter 1, inconsistent reported responses of native food generalists to plant invasion (e.g. Bock et al. 1986; Samways and Moore 1991; Mayer et al. 2005; Parker and Hay 2005; de Groot et al. 2007) are among obstacles for predicting the impacts of plant invasion on biodiversity. Plant invasion can cause not only trophic effects on native herbivores through competitive exclusion of native food plants, but also non-trophic effects through habitat modification. Food generalists depending on limited habitat types are hypothesized to be sensitive to plant invasions. However, correlation between sensitivity to plant invasion and habitat specificity of food generalist insect herbivores has not been fully understood, even though habitat specialists can have high conservation value (e.g., Reich 1991).

Weeping lovegrass (*Eragrostis curvula* (Schrad.) Nees) is an alien perennial grass native to South Africa. The species was introduced to Japan (mostly via North America) after World War II to prevent soil erosion (Osada 1989). Since then, this grass has been rapidly occupying space in river floodplains throughout Japan (Miyawaki and Washitani 2004).

Among ecosystems, floodplains appear to be readily invaded by alien plants species (Hobbs and Humphries 1995; Planty-Tabacchi and Tabacchi 1996). This is likely due to increases in resource availability mediated by flood disturbance and enhanced dispersal of invader propagules by river flows (Richardson et al. 2007). Flooding results in open spaces with sparse vegetation and concomitantly reduced levels of competition and increased susceptibility to plant invasion (Richardson et al. 2007).

Floodplains along the middle reaches of rapidly flowing rivers in Japan have extensive gravelly areas with sparse vegetation (Yoshimura et al. 2005); these gravelly areas are highly invasible habitats (Washitani 2001b). The Kinu River is a typical fast flowing river along which gravelly areas near channels are covered by sparse vegetation. These gravelly areas provide habitat for a number of endangered plants and animals endemic to such environments, e.g., *Aster kantoensis* Kitami, *Ixeris tamagawaensis* (Makino) Kitami*,* and *Eusphingonotus japonicus* (Muranaka and Washitani 2004; Tochigi Prefecture 2005). There are also riparian grasslands comprising native species such as Japanese silver grass (*Miscanthus sinensis* Andersson), cogon grass (*Imperata cylindrica* (L.) Raeusch. var. *koenigii* (Retz.) Pilg.), and Japanese lawn grass (*Zoysia japonica* Steud.) in less disturbed areas at higher elevations along the river bank. Weeping lovegrass forms dense tussocks, mostly in areas of sparse vegetation (Muranaka and Washitani 2001), and occupies habitats suitable for endangered plant species endemic to gravelly floodplains (Muranaka and Washitani 2001; Washitani 2001b). The National Censuses on River Environments, which are periodic surveys of fauna and flora conducted by the Ministry of Land, Infrastructure, Transport, and Tourism, Japan (hereafter, “MLIT”), reported that the weeping lovegrass-dominated vegetation area in the Kinu River floodplains increased >10-fold between 2002 and 2006 (unpublished data).

Among floodplain phytophagous invertebrates, grasshoppers (Acrididae) are typical food generalists; no Japanese grasshopper species is known to feed exclusively on a single plant genus (Chapman 1990). Furthermore, among the Japanese representatives of the Acrididae, there are species dependent on a variety of specific habitats (Japanese Society of Orthoptera 2006). Thus, grasshoppers are suitable candidates for examining the influences of weeping lovegrass invasion on herbivores that are food-generalists but habitat-specialists.

To examine the hypothesis that grasshopper species with specific habitat preferences are more impacted by weeping lovegrass invasion than habitat generalists, we investigated relationships between alien grass coverage and abundances of grasshopper species in two contrasting habitats (gravelly areas and riparian grasslands) in the Kinu River gravelly floodplain.

Materials and methods

Study area

The study was conducted on the gravelly floodplain along the middle reaches of the Kinu River, central Japan (36°41′N, 139°56′E; Fig. 2.1). Disturbance by flooding has zoned the vegetation types along the river channels in the study site into gravelly areas with sparse vegetation (“gravelly area”) and native riparian grassland (“grassland”). For our purposes, the extents of original vegetation types before weeping lovegrass invasion were those indicated on a map compiled by the National Censuses on River Environments in 2002 when weeping lovegrass stands were relatively scarce (MLIT, River Bureau, River Environment Division 2004). Among the vegetation types shown on this map, “natural bare area”, “vegetation area dominated by *Artemisia capillaris* Thunb. or *Anaphalis margaritacea* (L.) Benth. et Hook.f. subsp. *yedoensis* (Franch. et

Sav.) Kitam." (both are typical species of gravelly floodplains (Muranaka and Washitani 2004)), and "open water" (at the MLIT census time) were subsumed into the category "original gravelly areas" (immediately before the invasion of weeping lovegrass). The other vegetation types (mainly consisting of "vegetation area dominated by monocotyledonous herbs" and "vegetation area dominated by annual herbs") on the map were subsumed into the category "original native grasslands".

Ensuring that coverage of weeping lovegrass did not differ between habitat types, we set up 53 sampling plots (100 m^2 each) with varying coverage of weeping lovegrass 89-94 km upstream of the Tone River confluence (within ca. 1.9 km^2 of the study site, 1.3 km^2 were gravelly areas and 0.55 km^2 grasslands) in 2006. The distance between plot centers was 1.45 ± 1.21 km (mean ± SD). Alcohol-based felt pens and stakes were used to mark the plots for relocation at each census. Geographic coordinates of plots were also recorded using GPS (as a precautionary measure). Fourteen and 39 sampling plots were assigned to original gravelly and native grassland categories, respectively. Only one sampling plot was in the area dominated by weeping lovegrass in 2002, and we classified the plot as native grassland because it was almost completely surrounded by "native grassland" areas.

Vegetation characteristics

Each sampling plot was surveyed for vegetation composition from 29 May to 15 June and from 13 October to 10 November 2006. During these spring and fall samplings, we placed 12 subplots (1 × 1 m) in each sampling plot; total vegetation cover (including weeping lovegrass) and weeping lovegrass cover were recorded on a percentage basis. Percent coverage was averaged over subplots and census times for each plot. We used “native cover” (total coverage of plants other than weeping lovegrass) as an index of native plant coverage.

Census of grasshoppers

Grasshoppers belong to a relatively large, conspicuous (Samways and Moore 1991) taxon and are easily identified since only 45 Acrididae species (excluding Melanoplinae species, which mainly inhabit forests or alpine grasslands) are known in Japan (Japanese Society of Orthoptera 2006). In addition, among the Japanese grasshoppers are species endemic to open habitats on gravelly floodplains, such as *Eusphingonotus japonicus* (Takeuchi and Fujita 1998), and those inhabiting grasslands, such as *Gonista bicolor* and *Mongolotettix japonicus* (Japanese Society of Orthoptera 2006). Common species like *Acrida cinerea*, which may inhabit urban areas, were also included in the study (Japanese Society of Orthoptera 2006). Thus, we predicted that grasshopper species would show relationships between dependence on a particular habitat type and the impact of weeping lovegrass invasion.

We conducted periodic censuses of the Acrididae in 53 sampling plots. The censuses were conducted from 10:00 to 17:00 at quarterly intervals (25 May–15 June, 3–11 August, 21–30 September, and 12–17 November 2006) on days with no or moderate wind and without measurable precipitation. Mean monthly temperature in the city of Utsunomiya, ca. 10 km from the study area, varied between 11.4 and 26.3°C during the censuses (Japan Meteorological Agency 2008). At each census, we recorded the abundances of each species of Acrididae sighted or caught in an insect net (50 cm in diameter) during a 15-min period. This census method is known as the “timed count” and has high fidelity in plots with low densities of grasshoppers (Gardiner et al. 2005).

Atractomorpha lata (Pyrgomorphidae) was also recorded, because the Pyrgomorphidae is closely related to the Acrididae, and there are similar life histories in the two families. Captured insects were released immediately after species identification except in cases where immediate identification was difficult. Nymphs that could not be identified to species were recorded at the genus or higher taxonomic level. Identification was based on the Japanese Society of Orthoptera (2006).

Prior to statistical analyses, abundance data from the four census dates were summed for each species in each sampling plot.

Statistical analyses

To categorize each grasshopper species by degree of dependence on gravelly areas with sparse vegetation, we applied a generalized linear model with a negative binomial error distribution. The explanatory variable was the original habitat type (gravelly areas: 0, grasslands: 1), and the response variable was the abundance of each grasshopper species (recorded in ≥ 5 plots). Species were grouped into "gravel-area species" or "grassland species" depending on whether they were significantly ($p < 0.05$ by χ^2 likelihood ratio test) associated with the original gravelly areas or the original native grasslands (hereafter habitat specialist). Species not significantly associated with either habitat type were categorized as "common" (i.e., habitat generalist).

To analyze relationships between abundance of grasshopper species and coverage of weeping lovegrass, we used Zero Inflated Poisson (ZIP) regression (see Martin et al. 2005) as an appropriate treatment for abundance data with many zero values. ZIP regression can model count data as a mixture of a point mass at zero (modeled by the logistic part of the ZIP model) and a Poisson distribution (modeled by the Poisson part of the ZIP model). The explanatory variable of the Poisson part was weeping lovegrass coverage, and no variable was set in the logistic part (i.e., only the intercept was estimated). The response variable for the regression was the abundance of each species (recorded in ≥ 5 sampling plots). We compared odds of species that were significantly negatively affected by the coverage of weeping lovegrass between habitat specialist and generalist using Fisher's exact test. We defined the significance on the basis of p-value ($p < 0.05$) in ZIP model for the species. In addition, for each species, maximum percent coverage of weeping lovegrass among plots (where the species was present) was examined as "the threshold coverage of weeping lovegrass." Differences of the threshold coverage between specialist and generalist were compared with use of the unpaired Student's t-test. All statistics were computed using R 2.4.0 for Windows (http://cran.r-project.org/). For ZIP analysis, the *zicounts* package version 1.1.4. (Mwalili 2005) was used.

Results

Impact on vegetation

Vegetation characteristics of the census plots are given in Table 2.1. ANOVA showed that while total vegetation coverage differed between habitat types ($F_{1,51} = 21.99$, $p < 0.001$), the cover of weeping lovegrass did not ($F_{1,51} = 0.032$, $p = 0.85$).

In the gravel-area plots, total vegetation coverage was positively related to weeping lovegrass cover ($r = 0.98$, $t_{12} = 16.7$, $p < 0.001$), while native cover was not significantly correlated with weeping lovegrass cover ($r = 0.29$, $t_{12} = -1.04$, $p > 0.05$). In the grassland plots, total vegetation coverage was not correlated with weeping lovegrass cover ($r = 0.18$, $t_{37} = 1.11$, $p > 0.05$), but native cover was negatively related to weeping lovegrass cover ($r = 0.60$, $t_{37} = –4.56$, $p < 0.001$).

Impact on grasshoppers

We recorded 997 individuals of 15 species of Acrididae, including one unidentified species. One species of Pyrgomorphidae was identified during the census (Appendix 2.1).

Twelve species were recorded in ≥ 5 plots. Of these, *Locusta migratoria* ($p = 0.011$) and *Eusphingonotus japonicus* ($p = 0.012$) were significantly more abundant in the original gravelly area and were categorized as gravel-area species. *Shirakiacris shirakii* ($p = 0.005$), *Gonista bicolor* ($p = 0.001$), and *Mongolotettix japonicus* ($p = 0.003$) were significantly more abundant in original native grasslands and were categorized as grassland species. These five species were also defined as habitat specialist. The remaining seven species were not significantly associated with either habitat type and were categorized as common species i.e., habitat generalist.

The abundances of seven species (two gravel-area species, three grassland species, and two common species) showed significantly negative relationships with weeping lovegrass coverage (Table 2.2). Two-sided Fisher's exact test ($p = 0.028$) showed that the significantly larger portion of habitat specialist was significantly negatively related to coverage of weeping lovegrass. The threshold coverage (Appendix 2.1) were not significantly different between habitat generalist and specialist ($t_{10} = -0.36$, $p = 0.73$).

Discussion

The significant difference in susceptibility to the alien grass invasion between habitat specialist and generalist grasshoppers were revealed in our study, which supports the hypothesis that grasshopper species with specific habitat preferences are more impacted by weeping lovegrass invasion than habitat generalists.

Among the habitat specialists, two taxa were categorized as gravel area species: *Eusphingonotus japonicus*, which is a habitat specialist in gravelly areas of Japanese floodplains (Takeuchi and Fujita 1998), and *Locusta migratoria*, which prefers open habitats with sparse vegetation for basking and laying eggs (Price 1991). Abundances of both species declined significantly with increasing weeping lovegrass coverage. Although the threshold coverage was not different between habitat specialist and generalist probably due to presence of the grassland species occurring at plots with the relatively denser weeping lovegerass stand, *Eusphingonotus japonicus* had the lowest threshold of weeping lovegrass coverage among the seven species showing significant negative relationships with weeping lovegrass. This suggested that the endemic grasshopper was the most susceptible to invasion by this plant. Native cover, which likely indicates abundance of food resources rather than favorable habitat structure for food-generalist grasshoppers specialized to open areas, was independent of weeping lovegrass coverage in the gravelly plots. However, total vegetation cover was highly correlated with weeping lovegrass cover in these plots. This suggests that the decrease in open habitat driven by weeping lovegrass invasion causes decreases in gravel-area species abundances.

Weeping lovegrass may also have negatively affected all of the three grassland species, viz. *Gonista bicolor*, which likely depends on native grass species such as cogon grass, *Shirakiacris shirakii*, which appears to be associated with heterogeneous habitats consisting of tall and short grasses such as Japanese silver grass and Japanese lawn grass (Yoshioka, personal observation), and *Mongolotettix japonicus*, which was reported to prefer tall grasses such as Japanes silver grass (Japanese Society of Orthoptera 2006), respectively. Such negative responses of grasshoppers in grasslands are partly congruent with the findings of Bock et al. (1986). The negative relationship between native cover and weeping lovegrass cover suggests that for grassland species there are simultaneous decreases in both food and habitat following invasion. However, it is not clear that weeping lovegrass is an unsuitable food for the three food generalist grasshopper species considered to consume a wide range of Poaceae species (Japanese Society of Orthoptera 2006; Yoshioka, personal observation). It is more probable that microhabitat or habitat structure formed by monoculture stands of the alien are unsuitable for grasshoppers.

Oxya yezoensis and *Oedaleus infernalis* were the only habitat generalist species negatively affected by weeping lovegrass. The former species were known to rather prefer wetter habitat such as paddy fields (Japanese Society of Orthoptera 2006) and were observed relatively close to water in the gravelly areas and riparian grasslands in the study area. Stands of weeping lovegrass may too dry for the species. *O. infernalis* were relatively common in the study areas, but is known to prefer relatively open and short grassland (Japanese Society of Orthoptera 2006). Thus extremely dense coverage by the alien grass might be avoided by the species.

Although weeping lovegrass had negative impacts on both gravel-area and grassland species, the threshold weeping lovegrass coverage reducing the abundance of the grassland species tended to be higher than that of *Eusphingonotus japonicus*.

Furthermore, populations of species dependent on open habitats (e.g., *E. japonicus*) are profoundly affected by invasion because open habitats provide an empty niche for the invader and are thus highly invasible.

An analysis of vegetation maps of 8.3 km^2 of Kinu River middle reaches (including our study area) revealed that 1.0 km^2 (17.8%) of the gravel areas was replaced by dense stands of weeping lovegrass, while only 0.24 km^2 (9.1%) of riparian grasslands were replaced by the invasive grass between 2002 and 2006 (K. Ichinose, personal communication). *E. japonicus* is endemic to Japan and listed in 24 prefectural red data books (Association of Wildlife Research and EnVision 2007). Invasion of weeping lovegrass into riparian gravelly areas may be among the most important factors threatening this grasshopper. Since 2002, restoration of gravelly areas by removal of weeping lovegrass has been conducted for the conservation of endemic plant species in the Kinu River floodplain (Muranaka and Washitani 2004). This process will also promote conservation of gravel area-specific grasshoppers such as *E. japonicus*.

Weeping lovegrass is less invasive in native grasslands, which are less disturbed than gravelly floodplain areas. Thus, populations of grassland grasshopper species such as *Gonista bicolor, Shirakiacris shirakii* and *Mongolotettix japonicus* are unlikely to decline over the short term in response to this invasion. However, it is essential to have a long-term perspective, because increasing propagule pressure from adjacent habitats suitable for alien species (gravelly areas, in this case) may promote increases of the species in habitats that are not necessarily suitable (Didham et al. 2007). Furthermore, *G. bicolor* and *S. shirakii* are the most commonly listed grassland species in prefectural red data books, i.e., in fourteen and fifteen of 47 Japanese prefectures, respectively (Association of Wildlife Research and EnVision 2007).

Among herbivores, specialists dependent on particular plant species for food resources (e.g., butterflies) are more affected by plant invasions than other species (de Groot et al. 2007). We found that even polyphagous herbivores (such as grasshoppers) were also affected significantly by plant invasion when their habitats were highly invasible. Hence, dependence on disturbance-dominated habitats and food specificity should both be flagged as indicative traits in evaluating impacts of plant invasion on native herbivores.

Table 2.1 Vegetation characteristics of the census plots.

		All plots (n = 53)	Gravel–area (n = 14)	Grassland (n = 39)
Total vegetation coverage (%)	mean ± SD	52.5 ± 28.0	27.1 ± 22.7	61.7 ± 24.0
	range	2.25 – 89.2	2.25 – 81.3	2.50 – 89.2
Coverage of weeping lovegrass (%)	mean ± SD	16.6 ± 22.2	15.7 ± 23.6	16.9 ± 22.0
	range	0 – 79.4	0 – 72.5	0 – 79.4

Table 2.2 Zero-Inflated Poisson regressions of the abundance of each grasshopper species on coverage by *E. curvula.*

Species	Group[a]	Intercept1[b]	Interceptp[c]	Coefficient[d]	P-Value[e]
Locusta migratoria L.	gravel-area*	-0.677	1.187	-0.018 (0.007)	0.008
Eusphingonotus japonicus (Saussure)	gravel-area*	0.739	2.713	-0.097 (0.017)	< 0.001
Shirakiacris shirakii (Bolívar)	grassland*	1.288	2.396	-0.061 (0.015)	< 0.001
Gonista bicolor (Thunberg)	grassland*	0.263	2.877	-0.028 (0.004)	< 0.001
Mongolotettix japonicus (Bolívar)	grassland*	0.821	1.784	-0.012 (0.005)	0.021
Atractomorpha lata (Motschoulsky)	common	1.202	1.637	-0.056 (0.029)	0.055
Patanga japonica (Bolívar)	common	1.485	1.561	-0.026 (0.015)	0.080
Oxya yezoensis Shiraki	common	1.393	1.472	-0.018 (0.008)	0.032
Acrida cinerea (Thunberg)	common	-0.475	1.272	0.005 (0.004)	0.293
Glyptobothrus maritimus (Mistshenko)	common	2.051	-1.846	0.157 (n.a.)	n.a.
Gastrimargus marmoratus (Thunberg)	common	0.860	1.114	-0.028 (0.017)	0.095
Oedaleus infernalis Saussure	common	0.619	1.568	-0.015 (0.007)	0.037

[a] '*' was added to the habitat specialist species

[b] Intercepts of the logistic part of the ZIP model.

[c] Intercepts of the Poisson part of the ZIP model.

[d] Coefficients of the Poisson part of the ZIP model. S.E. was showed in parentheses

[e] P values of the coefficients of the Poisson part based on z statistic.

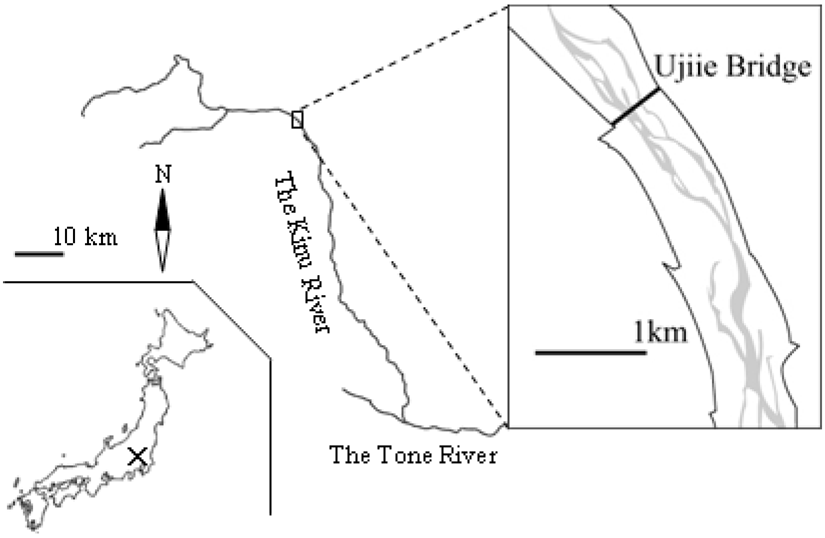


Fig. 2.1 The location of the study area.

Appendix 2.1 Grasshopper taxa recorded

	Total abundance	Recorded plots	Threshold coverage by *E. curvula*[a]
Gravel-area species			
Acrididae			
Locusta migratoria L.	88	32	71.5
Eusphingonotus japonicus (Saussure)	143	14	29.4
Grassland spesies			
Acrididae			
Shirakiacris shirakii (Bolívar)	70	10	45
Gonista bicolor (Thunberg)	273	23	79.4
Mongolotettix japonicus (Bolívar)	76	16	79.4
Common spesies			
Pyrgomorphidae			
Atractomorpha lata (Motschoulsky)	40	10	71.5
Acrididae			
Patanga japonica (Bolívar)	31	9	71.5
Oxya yezoensis Shiraki	33	10	79.4
Acrida cinerea (Thunberg)	125	32	72.5
Glyptobothrus maritimus (Mistshenko)	8	6	22.3
Gastrimargus marmoratus (Thunberg)	35	13	68.3
Oedaleus infernalis Saussure	68	18	71.5
Group was undefined			
Acrididae			
Oxya japonica (Thunberg)	2	2	0.33
Mecostethus parapleurus (Hagenbach)	1	1	39.8
Trilophidia japonica Saussure	1	1	0
Acrididae sp.	3	2	0
Total	997		

[a] Maximum % coverage by *E. curvula* in plots where the species was present.

Nomenclatures and arrangement within group follow *Orthoptera of the Japanese Archipelago in Color* (Japanese Society of Orthoptera 2006)

Chapter 3 Invasion of weeping lovegrass reduces native food and habitat resource of *Eusphingonotus japonicus* (Saussure)

Introduction

Although the results of previous studies (Chapter 2, see also Yoshioka et al. 2010a) suggested that habitat specialists are vulnerable to ecosystem-engineering non-native plants, it is difficult to examine whether or not non-trophic effects play a critical role in the response of the insect herbivores to invasive plants, since most of insect herbivores (even food generalists) use plants as both food and habitat. Predicting resultant impacts may also be difficult if the directions of trophic and non-trophic effects of plant invasions are not the same in such cases where food generalists prefer exotic to native plants (Parker and Hay 2005; Rodriguez 2006). It is also conceivable that trophic and non-trophic processes can compounded to resulting complex interactions (Ritchie 2000; Arditi et al. 2005). However, separating these processes is important for understanding the incongruous responses of food generalist herbivores to alien plants (Bock et al. 1986; Samways and Moore 1991; French and Major 2001; Mayer et al. 2005; Rodriguez 2006; de Groot et al. 2007).

Floodplains along the middle reaches of rapidly flowing rivers in Japan exhibit extensive gravelly areas with sparse vegetation (Yoshimura et al. 2005) inhabited by a number of endemic and endangered plant and insect species (Takenaka et al. 1996; Muranaka and Washitani 2004; Washitani 2007; Yoshioka et al. 2010a). Floodplains are also known to be among the most susceptible habitats to invasive plants (Hobbs and

Humphries 1995; Planty-Tabacchi and Tabacchi 1996; Richardson et al. 2007), and the gravelly floodplains of Japan are no exception (Washitani 2001b; Muranaka and Washitani 2004).

Weeping lovegrass *Eragrostis curvula* (Schrad.) Nees, a perennial grass native to South Africa, is an aggressive invader in the gravelly floodplains in Japan (Muranaka and Washitani 2004; Committee for investigating the Effects of and Countermeasures against Riparian Exotic Species 2009). This alien grass, when introduced, spreads rapidly by developing conspicuous dense tussocks, altering the gravelly areas with previously sparse vegetation to monospecific, long-lasting grasslands (Muranaka and Washitani 2004). In addition to competitive exclusion of endemic riparian herbs (Matsumoto 2000; Muranaka and Washitani 2001), decreased populations of *Eusphingonotus japonicus* (Saussure) (Orthoptera: Acrididae), an endangered grasshopper endemic to such habitats, have been reported (Yoshioka et al. 2010a).

E. japonicus is almost entirely dependant on gravelly areas with sparse vegetation as habitat (Takeuchi and Fujita 1998). On the other hand, *E. japonicus* has been reported to feed on a wider range of plants belonging to different families, including Poaceae (Uchida 2005; Suda personal observation; Yoshioka personal observation). Thus, creating unattractive habitat structure for the grasshopper by the grass invasion may be a major cause of the impact (Yoshioka et al. 2010a). However, it is possible that endemic riparian herbs, originally dominant in gravelly areas, are a more important food resource, because weeping lovegrass is a C4 plant (Sage and Monson 1999), which is thought to be more difficult to chew than most native riparian herbs, which tend to be C3 plants (Ehleringer and Monson 1993). Thus, invasions of weeping lovegrass may negatively impact *E. japonicus* through two presumable mechanisms:

habitat modification and/or food limitation. Conversely, if weeping lovegrass can be used as a food resource, we would expect it to exhibit the positive effect of increasing food resources for the grasshopper.

We examined the relationship between invasive weeping lovegrass and *E. japonicus* using field observations and laboratory experiments to address the following questions: 1) What are the major food resources of *E. japonicus* in its native habitat? 2) Does *E. japonicus* prefer endemic herb species to weeping lovegrass and/or can it feed on weeping lovegrass? 3) How do the combined abundances of weeping lovegrass and endemic herb species, potentially important food resource, affect that of *E. japonicus*?

Materials and Methods

Study area

The Kinu River is a major tributary of the Tone River in the center of the Kanto Plain, Central Japan (see Chapter 2 for detail). The middle reach of the river exhibits the typical rapid flow of Japanese rivers. However, aggressive invasion of weeping lovegrass to the gravelly floodplains (i.e., > 10-fold increase of the weeping lovegrass-dominated vegetation area between 2002 and 2006) has been observed (the Ministry of Land, Infrastructure, Transport of Japan unpublished data).

The study was conducted on the floodplain along the middle reaches (36° 41’ N, 139° 56’ E) approximately 87.5-94.5 km upstream of the Tone River confluence (containing totally c.a. 2.5 km^2 of the gravelly areas), where endemic and endangered plant species remain, but are seriously threatened by the invasion of weeping lovegrass

(Muranaka and Washitani 2004). Within the study area, weeping lovegrass has been reported to exclude three endemic Compositae species: *Aster kantoensis* Kitami., *Ixeris tamagawaensis* (Makino) Kitami., and *Anaphalis margaritacea* (L.) Benth. et Hook.f. subsp. *yedoensis* (Franch. et Sav.) Kitam (Muranaka and Washitani 2001). Now the population of biennial *Aster kantoensis* was extremely reduced (Washitani 2001b; Muranaka and Washitani 2004). In the city of Utsunomiya, approximately 10 km from the study area, the mean monthly temperatures in August and September 2006 and August and September 2007, when the study were conducted, were 26.3°C, 21.9°C, 27.2°C and 23.6°C, respectively (Japan Meteorological Agency 2009).

Patterns of feeding behavior and microhabitat use of *E. japonicus* in the field

To examine the major food resources and microhabitat usage of *E. japonicus*, observations of feeding behavior were conducted for 19 days (from August 22 to September 9, 2006) from 10:00 to 18:00 within an area where weeping lovegrass had not invaded yet (total plant coverage = 1.83%, coverage of weeping lovegrass = 0%, coverage of *Ixeris tamagawaensis* = 0.83%, coverage of *Anaphalis margaritacea* = 0.92%, coverage of other plants = 0.17%). Note that the site was bordered by an extensive stand of weeping lovegrass and a grasshopper could readily enter the stand.

When an adult female *E. japonicus* was sighted, we observed the individual for as long as possible from a distance of 2-3 m. Using the one-zero sampling method at 1-min intervals, we recorded start and end times of two types of behaviors: feeding and resting on plants. This temporal resolution of recording was assumed appropriate because previous works on Acrididae (sensu Eades and Otte 1997) showed that gaps between feeding bouts were longer than 1 min (Simpson 1990; Chambers et al. 1996).

Data for all individuals observed (for > 0.5 h) were pooled. A continuous sequence of minutes when feedings were observed was defined as a unit of “relative feeding frequency”. In other words, a sequence of observation time was separated by minutes when feeding were not observed. Then, relative feeding frequencies of individual plant species was counted as a simple index for usage frequency of each plant species. The percentage of time spent resting on any plants out of the total observation time was also calculated as an index of microhabitat use.

Food preference/consumption tests

The preference for, and consumption of, weeping lovegrass as a food was examined by two types of laboratory experiments: a test where the grasshopper was provided with an endemic herb and weeping lovegrass simultaneously, and another test in which the grasshopper was only given weeping lovegrass (hereafter referred to as the “preference test” and “potential consumption test”, respectively) in late September 2007.

Two days before the tests, weeping lovegrass, *Ixeris tamagawaensis*, and *E. japonicus* were collected from the study area. The grasshoppers were individually maintained without feeding in columnar mesh cages (20 cm height × 35 cm diameter; Versatile net, Okazaki, Japan) for 24 h before the experiments at 25/20°C (12.5 h day/11.5 h night), simulating the thermal conditions in the field. The experimental plants were kept in pots filled with water to prevent wilting. At the start of the tests, the grasshoppers were individually exposed to the plant materials.

For the preference test, grasshoppers were allowed to feed on the grass and/or herb provided as cut plants of nearly equal wet weight (1 ± 0.0050 g) placed inside the cages. The plants were placed in sponges typically used for flower arrangements (Oasis, Smithers-Oasis Japan, Japan) to retain turgidity. For each replication, plant position (right side or left side) was randomized. In total, 12 grasshoppers (6 males, 6 females) were used in the experiment.

After 24 h, plants were withdrawn and desiccated for 3 days at 70°C. The dry masses of the plants after testing (W_f) were determined using an electric balance (AG285, Mettler Toledo, Switzerland). The initial dry mass before the test (W_i) was estimated using the regression formula of dry mass by wet mass (W_{wi}: *I. tamagawaensis*: $W_i = 0.19 \times W_{wi}$, $R^2 = 0.90$; weeping lovegrass: $W_i = 0.46 \times W_{wi}$, $R^2 = 0.91$). The regression coefficients were estimated using the data from 12 samples of each plant species (0.1-1.0050 g wet mass) exposed to the same conditions in the preference test. The dry mass consumption by *E. japonicus* was calculated as W_i-W_f. For the potential consumption test, the possibility of consumption of weeping lovegrass was examined by providing *E. japonicus* with the grass alone (1 ± 0.0050 g wet mass × 2) under the same experimental conditions as the preference test.

To statistically test the null hypothesis that the dry mass consumption of weeping lovegrass and that of *I. tamagawaensis* in the preference test were equal, an F-statistic was calculated, using Roa's method (1992), as corrected by Manly (1993). The 95% confidence interval of the dry mass consumption of weeping lovegrass in the potential consumption test was calculated. The consumption data for two male *E. japonicus* that died during each test were not analyzed. Statistical analyses of the collected data for 10 individuals in each test were conducted using R 2.6.1 for Windows.

Effects of coverage of weeping lovegrass and endemic plants on *E. japonicus*

abundance

We set up 22 sampling plots (10×10 m each) within the study area in 2007. Half of the plots were placed in typical gravelly areas with sparse vegetation at the early stage of weeping lovegrass invasion, while the other 11 were set within dense stands of the alien grass. We selected these plots because the coverages of *Ixeris tamagawaensis* and *Anaphalis margaritacea* were not highly correlated with weeping lovegrass coverage. The distance between individual plot centers was 2262 ± 1647 m (mean ± SD). Alcohol-based felt pens and stakes were used to mark the corners of the plots for relocation. The geographic coordinates of the plots were recorded using GPS.

The censuses were conducted from 10:00 to 18:00 from August 1-14, 2007, with the exception of days with measurable precipitation and/or strong wind. During each census, we recorded the abundances of adult *E. japonicus* sighted or caught in an insect net (50 cm in diameter) until no new individuals were counted for 10 min. The census was conducted for 60-90 min per sampling plot. Captured insects were released immediately after the census was complete.

The vegetation composition was studied at each sampling plot from June 29 to July 15, 2007. We placed five subplots (1×1 m) in the form of a quincunx (as on dice) within each sampling plot, and total vegetation cover (including weeping lovegrass) as well as the individual coverage of weeping lovegrass, *Ixeris tamagawaensis*, and *Anaphalis margaritacea* were recorded on a percentage basis. The percentage coverage of each plant species was averaged over the subplots. We also summed the cover of *Ixeris tamagawaensis* and that of *Anaphalis margaritacea*, hereafter referred to as "endemic herb cover" and used that as an index of the amount of stable food resources for *E. japonicus*.

Multiple linear regression analysis was used to analyze the relationships between the abundance of grasshopper species and the coverage of weeping lovegrass, as well as the coverage of endemic herbs and their interactions. The explanatory variables were weeping lovegrass cover and endemic herb cover. We also added the interaction "weeping lovegrass cover × endemic herb cover" to the explanatory variables to examine whether weeping lovegrass could affect the availability of other plant species. The response variable for the regression was the abundance of *E. japonicus*. Normality of residuals was confirmed by Shapiro-Wilk test ($p > 0.05$). All statistical analyses were conducted using R 2.6.1 for Windows (http://cran.r-project.org/).

Results

Major food resource and microhabitat use of *E. japonicus*

The behavior of nine individual *E. japonicus* was observed for 2240 min in total. The observation times for each individual ranged from 0.9-7 h. Almost all individuals fed on plant materials alone and only one individual was observed to nibble a dead body of a cricket (*Teleogryllus infernalis*; Saussure, 1877). The relative feeding frequency on each plant species is shown in Figure 3.1. *E. japonicus* fed most frequently on the two dominant endemic herbs *I. tamagawaensis* and *A. margaritacea*. Total time spent resting on any plants out of the total observation time was only 20 min. The percentage of time spent resting on plants was only 0.89%. Additionally, no individual was observed moving into the weeping lovegrass stand bordering the observation area.

Preference/consumption of weeping lovegrass by *E. japonicus*

During the preference test, *E. japonicus* consumed 0.062±0.047 g dry mass of *I. tamagawaensis*, but never consumed weeping lovegrass ($F_{1/10}$ = 22.1, p = 0.00084). Similarly, no consumption of weeping lovegrass was observed during the potential consumption test. Although the sample size (N = 10) was small, the variation in response was also low. Thus small sample size did not affect statistical power.

Effects of weeping lovegrass and endemic plant coverage on the abundance of *E. japonicus*

Within the study plots where the effects of plant coverage on the abundance of grasshoppers were examined, the weeping lovegrass coverage reached 83% in the stand, while those of *I. tamagawaensis* and *A. margaritacea* were only 5.6 and 11%, respectively (Table 3.1). Welch's two sample t-test showed that the total vegetation cover was significantly differed ($t_{11.064}$ = -9.93, $p < 0.001$) between weeping lovegrass-dominated plots (56.95 ± 16.60%) and non weeping lovegrass dominated plots (5.96 ± 3.83%) due to the weeping lovegrass coverage (51.09 ± 14.79% and 0.36 ± 0.54% in dominated and non-dominated plots, respectively). The weeping lovegrass coverage was statistically independent from that of *I. tamagawaensis* (r = -0.39 t_{20} = -1.9, p-value = 0.071) and *A. margaritacea* (r = -0.18; t_{20} = -0.83, p-value = 0.42).

We recorded 59 individuals of *E. japonicus* in total. The abundance of *E. japonicus* was significantly negatively associated with weeping lovegrass coverage, weeping lovegrass coverage × endemic herb coverage, and significantly positively related to endemic herb coverage (Table 3.2, Fig. 3.2).

Discussion

We observed that *E. japonicus* mainly fed on endemic riparian herbs. Our laboratory experiments also showed that *E. japonicus* preferred *I. tamagawaensis* and that it never consumed weeping lovegrass even if no alternative food plant was available. Thus, an invasion of weeping lovegrass does not mean increased food resources for *E. japonicus*, but may instead result in food deficiency, through the indirect effect of competitive exclusion of edible herbs (Muranaka and Washitani 2001).

The field census revealed that the abundance of *E. japonicus* was positively related to the endemic riparian herb cover in the plots where weeping lovegrass had not yet dominated. Weeping lovegrass had a strong negative effect on *E. japonicus* even when the riparian herbs were relatively abundant.

E. japonicus exhibits a gravelly color and morphology, which is not cryptic on plants (Japanese Society of Orthoptera 2006), and thus individuals rarely land on plants when they jump or fly (Tottori prefecture 2002). These traits suggest that habitat modification from sparse riparian to dense alien vegetation will lead to avoidance of the grass stands by the grasshopper, regardless of the presence or absence of food plants. The extremely short periods of time spent on plants during our observations support this hypothesis. The interacting effects of habitat modification and food limitation indicated by the multiple linear regression analysis might also reflect access restriction to endemic herbs by weeping lovegrass, because vegetative structure is known to be the major determinant of microhabitat selection of grasshoppers (Anderson 1964).

Although habitat avoidance is non-lethal for an individual grasshopper, it will cause serious effects at the population level, through habitat loss and population isolation. Previous examinations (Haynes and Cronin 2003; Cronin and Haynes 2004) revealed the behavior of a food specialist leafhopper was altered by the dominance of an exotic plant, which significantly impacted the metapopulation dynamics. In addition, we have never observed predation of *E. japonicus* in the grass stands throughout the study time, and competition with common species seems unlikely to seriously affect grasshoppers (Evans 1992).

Generally, herbivores that have specific host plants are significantly affected by plant invasion (e.g., Valtonen 2006; de Groot et al. 2007). However, there is no information available with respect to which type of effects, i.e., trophic or non-trophic, play a more important role for a food generalist herbivore. French and Major (2001) showed that an invasive alien tree, *Acacia saligna*, negatively impacted seed-feeding ants in fynbos. Consequently, they found that the ants preferred the seeds of the alien as well as of native related species. Neverthless, trophic processes remain a possible explanation for the results of their study (i.e., less diverse food in the invaded habitat could cause negative effects). Conversely, we were able to separate the trophic and non-trophic effects of invasive plants, as well as show that the latter effect can be detrimental to an herbivore even before an alien plant affects native food source.

If plant invasions alter both habitat structure and food availability for herbivores, they can have serious negative impacts on the herbivore population even if the alien is edible. In addition, such ecosystem engineering effect may more rapidly occur than native food resource limitation by aliens, because competitive exclusion takes relatively long time to be realized (Sax et al. 2007). Thus, evaluating the rapid effects of habitat modification is essential for predicting the impacts of plant invasions on herbivores, which have shown incongruous responses to exotic plants (Bock et al.

1986; Samways and Moore 1991; French and Major 2001; Mayer et al. 2005; Parker and Hay 2005; Rodriguez 2006; de Groot et al. 2007). On the other hand, from the point of restoration, selective removal of non-native plants may be more effective than indiscriminate eradication by machine if native plants to be concerned remain in the restoration-target area. In the part of our study area, selective removal of weeping lovegrass by hand has periodically been conducted for the conservation of endemic plant species (Ichinose unpublished data). Our study endorsed that such a restoration program will also be effective for gravel area-specific insects such as *E. japonicus*. Incorporating interaction of habitat modification (non-trophic effects) and food limitation (trophic effects) by non-native plants will contribute to the conservation and restoration of native herbivores, and thereby native ecosystems.

Table 3.1 Vegetation characteristics in the census plots.

	Average ± SD	(min, max)
Total plant coverage (%)	31.45 ± 28.62	(0.6, 91)
Weeping lovegrass coverage (%)	25.73 ± 27.90	(0, 83)
Coverage of *I. tamagawaensis* (%)	0.97 ± 1.56	(0, 5.6)
Coverage of *A. margaritacea* (%)	1.56 ± 2.71	(0, 11)

Table 3.2 Result of multible regression analysis

	Coefficient	SE	t value	p value	
Intercept	2.7	0.94	2.9	0.010	*
Weeping lovegrass cover	-0.047	0.021	-2.2	0.044	*
Endemic herb cover	0.72	0.20	3.6	0.0018	**
Weeping lovegrass cover × endemic herb cover	-0.018	0.0061	-3.0	0.0082	**

Signif. codes: ‘**’ p value < 0.01 ‘*’ p value < 0.05

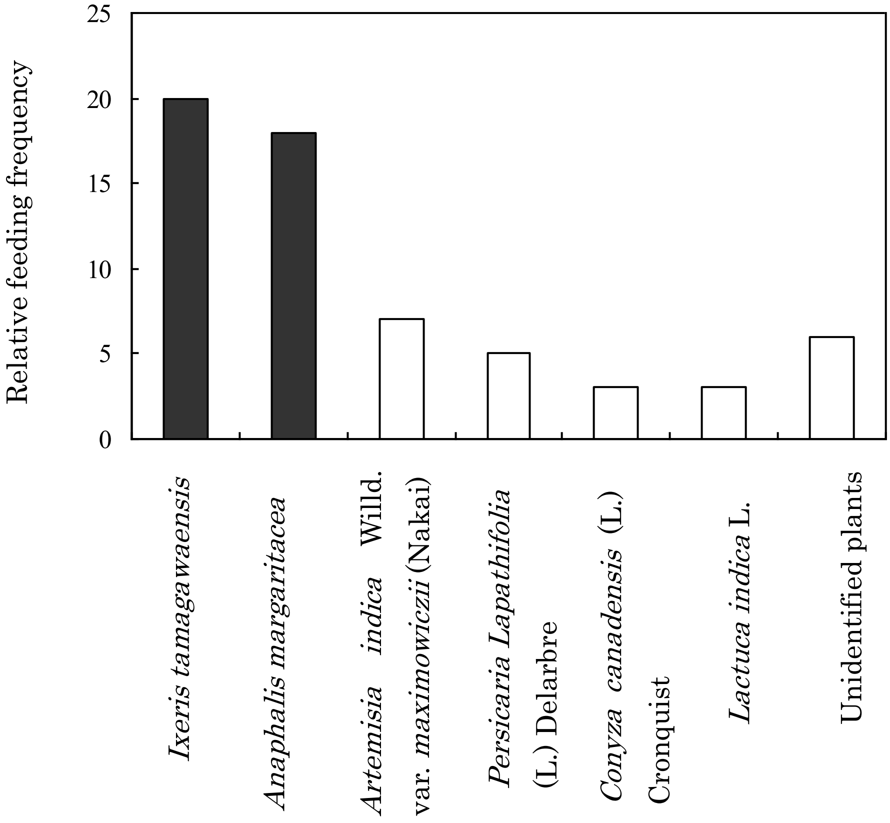


Fig. 3.1 Relative feeding frequency of individual plant species

A unit of relative feeding frequency is defined as a continuous sequence of minutes when feedings were observed. Frequency of feeding on native riparian herbs was shown by black bars and that of other ruderal plants was by white bars.

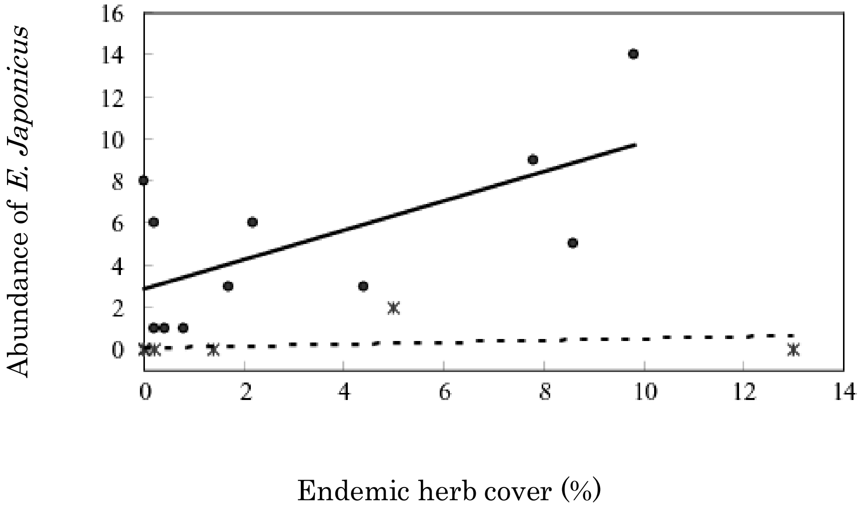


Fig. 3.2 The relationship between the abundance of *E. japonicus* and the endemic cover

Filled circles represent data in the non weeping lovegrass-dominated plots (n = 11). Asterisks represent data in the weeping lovegrass-dominated plots (n = 11). Regression lines for each treatment are shown; a solid line is for non weeping lovegrass dominated plots (R^2 = 0.41) and a dashed line is for weeping lovegrass-dominated plot (R^2 = 0.071).

Chapter 4 Facilitation of a native pest of rice, *Stenotus rubrovittatus*, by the non-native *Lolium multiflorum* in an agricultural landscape

Introduction

Most previous studies on impacts of plant invasion have focused solely on the direct negative impacts of non-natives on native biota as showed in the previous chapters. However, some recent studies have suggested that native food generalist insect species can prefer non-native plants (Parker and Hay 2005), and hence are facilitated by them through provision of a trophic subsidy or a novel habitat, or both (Rodriguez 2006). A few studies on natural ecosystems have revealed the negative impacts of invasive alien plants on native plants through apparent competition (Holt 1977) by facilitating native herbivores to inflict more damage to native than to alien plants (Branson and Sword 2009; Malmstrom et al. 2005; Orrock et al. 2008).

In agricultural landscapes, analogous problems can arise, in which a non-native plant facilitates native pests of a crop. Some studies (Carriere et al. 2006; Iwao 1971; Redak et al. 2004; Tillman et al. 2009) have unintentionally reported that certain non-native crops can provide a habitat for or a source of the pest of other crops. This problem are not only directly related to ecosystem services (crop production), but also indirectly, but seriously, to biodiversity through increased usage of pesticide as a countermeasure. Therefore, significance of positive effects of non-native plants including crops on food generalist insects in agricultural landscapes should be investigated to understand the impacts of non-native plants on biodiversity and ecosystem services. However, little information is available on whether non-native plants including crops can provide new exploitable resources for pests of other crop plants and thereby lead to increased pest population sizes than ever.

Currently, one of the most serious economic threats to rice (*Oryza sativa* L., Poaceae) cultivation in Japan is the discoloration of grains caused by mirid bugs including the sorghum plant bug *Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae) (Kiritani 2007). *S. rubrovittatus* damages the grains of rice, causing discoloration, and therefore leading to a severe economic loss to farmers under the current national regulation system for rice quality, which is based almost exclusively on the appearance of grains. Although *S. rubrovittatus* is native to Japan, the economic damage caused by the species has increased throughout the Japanese archipelago in the past few decades (Hayashi and Nakazawa 1988; Okutani-Akamatsu et al. 2007).

Stenotus rubrovittatus is known to prey on the ears of various species of Poaceae and Cyperaceae and reproduces on them at least three times during a year (Hayashi and Nakazawa 1988; Kashin et al. 2009; Nagasawa 2007). Given that Poaceae and Cyperacea are ubiquitous in the agricultural landscapes, the bug is generalist species which is unlikely to be constrained by both food and habitat. However, the mirid bug invades rice paddies only when the heading of rice occurs in summer. In addition, they rarely reproduce in the paddies (Takeuchi et al. 2005). Thus, the change in land-use from paddies to meadows and fallow fields, which has been encouraged by the rice acreage reduction policy practiced since 1970, may have resulted in an increase in novel source habitats of the mirid bug (Hayashi and Nakazawa 1988; Kiritani 2007).

Italian ryegrass *Lolium multiflorum* Lam. (Poaceae), a non-native pasture grass common today in meadows of Japan, has been suspected to be the most favorable host of *S. rubrovittatus* (Hayashi and Nakazawa 1988; Nagasawa 2007). However, the relative importance of Poaceae and Cyperaceae species in and around paddies as the host of the polyphagous bug remains to be examined at the landscape level.

This study examined whether the newcomer, *L. multiflorum*, facilitates population growth of *S. rubrovittatus* more effectively than resident plants that have a relatively long history in the agricultural landscape of Japan. First, in a large-scale field survey with many replications, we measured densities of the mirid bug together with abundances of its potential hosts (Poaceae and Cyperaceae) in fields and meadows that had been converted from paddies. Based on the censuses, we evaluated the seasonal population dynamics of *S. rubrovittatus* at the stage prior to the immigration to paddies, which is known to occur in mid-August or later (Hayashi and Nakazawa 1988; Ono 2006; Takada personal observation). We then analyzed the dependency of *S. rubrovittatus* density on the abundance of individual Poaceae and Cyperaceae species to identify the most important host plants for source populations of *S. rubrovittatus* in the paddy landscape.

Materials and methods

Study site

The study was conducted in the paddy landscape of the city of Osaki, Miyagi Prefecture, northern Japan (38º37'N, 141º07'E). Annual precipitation in the city is 1126 mm and the mean temperatures in June, July, and August 2008 were 18.5, 22.6, and 22.5ºC respectively (Japanese Meteorology Agency 2010).

Stenotus rubrovittatus is the most abundant and influential arthropod pest of paddies in the region (Kashin et al. 2009; Ono 2006). The agricultural landscape in the study region consists mainly of paddies, fallow fields, meadows converted from paddies, and small scattered woodland patches. In the meadows, *L. multiflorum* is sown in autumn or early spring and harvested for forage in the middle of June. The mowed grass then rapidly regrows and is harvested again in late July. However, the timing of the second harvest is highly variable depending on weather conditions because farmers prefer drying the mowed grass in the sun before collecting it from the meadow. Thus, in rainy summers, some meadows can remain unmowed until early August, when rice plants are heading. After summer, when *L. multiflorum* has senesced, most meadows are dominated by weeds such as *Echinochloa* spp.

Field surveys

We conducted periodic censuses of *S. rubrovittatus* and its host plants in the meadows and fallow fields over three seasons in 2008 (8–16 June, 26 June–5 July, and 1–9 August), which correspond to *S. rubrovittatus* life cycle stages, i.e., the early adult phase of the overwintering generation, the peak of the adult phase of the overwintering generation, and the peak of the first generation, respectively (Ono 2006).

Censuses were performed at a large number of sampling plots (215, 174, and 194 for the first, second, and third census, respectively) within a 20 km^2 area of the study site to cover sites dominated by a variety of species of Poaceae and Cyperaceae. Each sampling plot was established near the center of a meadow or fallow field (i.e., one plot per meadow or field). Although most plots were surveyed in all three census periods, some additional plots were surveyed only in particular census periods to cover representative plant species in each census period. The position coordinates of the plots were measured using a global positioning system (GPS) and an agricultural land use map compiled by the local government. The distances to the nearest neighbor plot in the first, second, and third census were 91 ± 69, 102 ± 75, and 102 ± 79 m (mean ± SD), respectively. The area of the individual meadows and fallow fields ranged from approximately 60 to 20,000 m^2.

The censuses took place from 09:00 to 17:00. At each census season, the densities of adult *S. rubrovittatus* were examined through net sampling by performing 20 sweeps with a 36-cm-diameter insect net in each plot. This sampling method covers ca. 20 m^2 (Takai et al. 1965). Given the relatively small disturbed area, sufficient sampling intervals, and high density of the mirid bug, the impact of sampling on the next sampling should be negligible.

The second census coincided with the occurrence of the nymph of the first generation; thus, the density of nymphs of Miridae was also examined to confirm that the mirid bug reproduces in the plot rather than temporarily aggregating there. The nymph of *S. rubrovittatus* is difficult to distinguish from those of other mirid bugs such as *Trigonotylus caelestialium* (Kirkaldy) (Hemiptera: Miridae) and *Stenodema calcarata* (Fallén) (Hemiptera: Miridae). Nevertheless, *S. rubrovittatus* is the most dominant mirid species in the region, and the censused density of nymphs may approximate the dynamics of the species (Kashin et al. 2009).

We measured the abundance of ears of each species of Poaceae and Cyperaceae by counting the number of ears within a 0.2×6 m^2 quadrat established near the plot. Vegetation height was measured at nine regularly spaced points within each quadrat. These height measurements were averaged over each plot. For the meadow plots, we recorded whether the meadow has been mowed recently.

Statistical analyses

To analyze the relative importance of each species of Poaceae and Cyperaceae as a host plant for *S. rubrovittatus* in each season, we applied a generalized linear model with a negative binomial error distribution. The explanatory variables were the abundance of ears of each Poaceae and Cyperaceae species (recorded in ≥ 10 plots), latitude, longitude, and vegetation height. Latitude and longitude can be used to remove potential confounding effects of spatial autocorrelations, whereas vegetation height can remove those due to physical structures of plants independent of species. The response variable was the density of adult *S. rubrovittatus*.

Model selection was conducted by comparing candidate models consisting of all possible combinations of the ear abundance of Poaceae and Cyperaceae species using Akaike's information criterion (AIC) to obtain the best model of the mirid bug–host relationship (i.e., the model with the lowest AIC value). Other explanatory variables (latitude, longitude, and height) were added to all candidate models. Thus, the model selection should show relatively conservative results. Although model selection with "all possible models" has a risk of selecting an inappropriate model as a result of data-dredging unless the candidate models are meaningful biologically (Burnham and Anderson 2002), the Poaceae and Cyperaceae species analyzed here (see Table 4.1) should give biologically-meaningful variables because all of the species are relatively abundant in the landscape and these species or their congeners were observed to be sucked by *S. rubrovittatus*, except for *Elymus. tsukushiensis* (Hayashi and Nakazawa 1988; Takada personal observation; Yoshioka personal observation). Given the wide diet breadth of *S. rubrovittatus*, all of these species should be analyzed. The tolerances of each explanatory variable were sufficiently high (> 0.51, > 0.60, > 0.58 in the first, second, and third census, respectively). Before analysis, all of the explanatory variables were centered and scaled (dividing by SD) so that their effects could be compared.

The relationship between the abundance of ears and mirid nymph density in the second census (early summer: from the end of June to early July) was analyzed in the same way.

All statistical analyses were performed using R for Windows 2.11.1 (R Development Core Team 2010). Spatial autocorrelation of residuals of the best models were also checked by Moran's I correlograms (Legendre and Legendre 1998; Dormann et al. 2007), which plot Moran's I for ten 200m-wide distance classes. Moran's I and its p-value based on 10000 times permutations were computed by ncf package in the R, and the significance level was corrected by the method of Bonferroni.

Results

Seasonal dynamics of *S. rubrovittatus* and its potential hosts

In the first census performed in mid-June, we caught 1.2 ± 2.6 *S. rubrovittatus* adults per plot (mean ± SD) in 20 sweeps of an insect net. In the second and third censuses, performed from the end of June to early July and in early August, 4.7 ± 9.9 and 14.9 ± 44.3 adults were recorded, respectively.

We caught 4.8 ± 25.5 mirid nymphs per trial in the second census. The majority of nymphs were considered to be *S. rubrovittatus* because adult densities of *T. caelestialium* and *S. calcarata* were much lower (1.5 ± 6.9 and 1.2 ± 2.3 in the second census, and 3.5 ± 10.3 and 1.8 ± 7.9 in the third census, respectively) than those of *S.*

rubrovittatus, as mentioned above.

In the first, second, and third censuses, seven, seven, and six taxa of potential hosts, respectively, were recorded in ≥ 10 plots (Table 4.1). Ears of a few plant species including Italian ryegrass were observed in all census seasons.

The most important host for *S. rubrovittatus* before the heading of rice

Model selection revealed relationships between densities of *S. rubrovittatus* and the abundance of potential host species (Table 4.2; Appendix 4.1, 4.2). In the best models (the models with lowest AIC values in each census) for the first census, the abundance of ears of *L. multiflorum* was not related to density of the mirid bug. However, it was positively correlated (the lower limit of the 95% confidential interval of the coefficient >0) with mirid density in the second and third censuses. None of the other plant species had a coefficient with a 95% confidential interval with a lower limit greater than zero throughout the seasons. The mirid nymphs in the second census were also positively correlated with the abundance of *L. multiflorum* ears (Table 4.3). The effects of *L. multiflorum* ears in the best models were consistent with those of other candidate models with ΔAIC (difference in AIC from best model) ≤ 10 (Appendix 4.1, 4.2). No significant values of Moran's I was also detected from the residuals of the best models for the second and third seasons.

Although the mirid bug density differed between plots dominated by *L. multiflorum* (i.e., plots in meadows and a small proportion of fallow fields) and others, the difference in maximum density was not as great in the second census (Fig. 4.1A). However, the adult bug density in plots dominated by *L. multiflorum* became extremely high by the third census, unless the plots had been mowed (Fig. 4.1B).

Discussion

The seasonal dynamics of *S. rubrovittatus* revealed in this study were consistent with those of previous reports (e.g., Hayashi and Nakazawa 1988; Ono 2006); adult density rapidly increased until early August. This high adult density just before the heading of rice would enhance the overspill of the mirid bugs to nearby paddies. This is consistent with the observation by Ono et al. (2007) that damage to rice tended to be negatively related to the distance from Italian ryegrass meadows.

Our statistical analyses demonstrated that *L. multiflorum* was the only plant species that showed the highest effect on the density of *S. rubrovittatus* adults irrespective of census season; i.e., the abundance of *L. multiflorum* was positively related to the density of both the adults of the overwintering and the first generations, although mowing the grass could suppress the local density of the bugs. The positive relationship between *L. multiflorum* and mirid nymphs in the second census suggests that the grass can enhance population growth (i.e., reproductive numerical response) of the mirid bug rather than only cause temporal aggregation of adult bugs. Thus, not only the high nutritional performance of the grass as a food, as expected from oviposition preference (Gripenberg et al. 2010; Nagasawa 2007), but also the temporal stability of the grass as a host may be the reason for the outbreak of the first generation.

Several weed species in fallow fields were also found to be positively related to the density of *S. rubrovittatus*. Nevertheless, our results robustly showed that the meadows of *L. multiflorum* were the most important stable habitat for the mirid bug, whereas the other weed species in the fallow fields were ephemeral hosts because none of them significantly positively affected the mirid bugs through seasons, and, thus, would contribute less to the population growth of the bug before the colonization of rice paddies.

This study clearly demonstrated that a newly introduced non-native grass provided the mirid bug *S. rubrovittatus* with a new exploitable resource, which is contributable to increased seasonal paddy colonization by the bug. Although previous studies have suggested that one crop can be a source of pests for another crop (Carriere et al. 2006; Redak et al. 2004; Tillman et al. 2009), to our knowledge, the present study is the first to clearly show that a newcomer plant can become the most important source of a native pest of other crop species.

The reason why the mirid bug preferred a non-native plant over native hosts remains to be clarified. One possibility is temporal complementarity; abundant ears of Italian ryegrass may be available for the bug in the season when native hosts are relatively unavailable or unstable. If this is the case, harvest practice may also play a role. In addition, the regrowth of Italian ryegrass might make a high-nitrogen meristem available for the bug. Another non-exclusive explanation is that Italian ryegrass may be a close relative of the native hosts of the bug and thus may share important phytochemicals that mediate host recognition in this bug. However, there is no native *Lolium* in Japan (Osada 1989). Hori (2009) examined the olfactory response of *S. rubrovittatus* to panicles of rice (Poaceae) and spikelets of *Scirpus juncoides* (Cyperaceae) experimentally, and showed that both significantly attracted the bug to the same degree. Thus, phytochemicals may not adequately explain the strong preference of the bugs for Italian ryegrass.

Numerous potential pests may exist in agricultural ecosystems. For example, the removal of natural enemies using insecticides can cause outbreaks of potential pests, i.e., “resurgence” (Ripper 1956). In this study, we demonstrated that the introduction of just one non-native plant species can cause an outbreak of a native potential pest of another crop plant. It is also conceivable that apparent competition between non-natives and native weeds coupling with allochthonous inputs of the non-native plant propagule may also promote spread of the non-native through an agricultural ecosystem, although this may not be the case in our study system, in which naturalized Italian ryegrass was not as dominant.

The introduction of plant species that may facilitate native polyphagous herbivores should be prevented as a precaution, but predicting such species may be difficult. Several plant traits may be the key to such potential interactions (e.g., Orrock et al. 2010). To date, many studies on the relationships between traits of non-native species and their invasiveness have been published (van Kleunen et al. 2010), but relationships between these traits and the non-native plant’s interactions with native animals and apparent competition should be studied more extensively.

In the case of an “apparent competition” between non-native and crop plant species, such as revealed here, landscape-level perspectives are needed; conventional pest management (application of insecticides to individual infested fields) cannot prevent new immigrants from source populations. Area-wide pest management, including appropriately timed removal or mowing of the source habitat, is certainly more effective. Quantifying the spatiotemporal dynamics of metapopulations of polyphagous pests and their hosts will be essential to the planning of such pest control strategies (Carriere et al. 2006). Accumulation of such empirical landscape-scale data will also contribute to adequately predicting the impact of non-native plants on biodiversity through facilitation of generalist insects.

Table 4.1 Poaceae and Cyperaceae species used as candidate explanatory variables in model selection

Poaceae and Cyperaceae species [a]	Abundance of ear (mean ± SD)		
	The first census	The second census	The third census
Carex neurocarpa Maxim. (Cyperaceae)	3.64 ± 20.2	0.822 ± 4.37	1.08 ± 6.20
Schoenoplectus juncoides (Roxb.) Palla (Cyperaceae)	-	-	3.21 ± 16.5
Agrostis clavata Trin. subsp. *matsumurae* (Hack. ex Honda) Tateoka (Poaceae)	-	1.12 ± 9.45	-
Agrostis gigantea Roth (Poaceae)	-	-	1.20 ± 6.74
Alopecurus aequalis Sobol. (Poaceae)	53.6 ± 188	30.9 ± 125	1.16 ± 6.34
Anthoxanthum odoratum L. (Poaceae)	2.84 ± 17.1	0.511 ± 2.56	-
Echinochloa spp. (Poaceae) [b]	-	-	0.61 ± 2.99
Elymus tsukushiensis Honda var. *transiens* (Hack.) Osada (Poaceae)	0.237 ± 1.30	1.08 ± 6.99	-
Glyceria ischyroneura Steud. (Poaceae)	1.28 ± 7.43	-	-
Lolium multiflorum Lam. (Poaceae)	32.7 ± 123	61.5 ± 143	41.7 ± 124
Poa trivialis L. (Poaceae)	3.42 ± 12.0	2.89 ± 10.8	-

[a] Species recorded in ≥ 10 plots are shown.

[b] *Echinochloa crus-galli* (L.) P.Beauv. (Poaceae) and *Echinochloa oryzicola* (Vasing.) Vasing. (Poaceae)

Table 4.2 The best generalized linear model relating the abundance of ears of Poaceae and Cyperaceae to the density of adult *S. rubrovittatus*.

Census period	Poaceae and Cyperaceae species and covariate	Standard partial regression coefficient	
		Estimate ± S.E.	95% C.I [a]
The first census	*Anthoxanthum odoratum*	-0.24 ± 0.15	[-0.54, 0.059]
	Poa trivialis	0.22 ± 0.14	[-0.047, 0.49]
	longitude	0.15 ± 0.20	[-0.25, 0.54]
	latitude	-0.11 ± 0.20	[-0.51, 0.28]
	height	0.83 ± 0.16	[0.53, 1.1]
The second census	*Alopecurus aequalis*	0.22 ± 0.12	[-0.023, 0.45]
	Anthoxanthum odoratum	0.28 ± 0.12	[0.042, 0.52]
	Elymus tsukushiensis	-0.47 ± 0.37	[-1.2, 0.25]
	Lolium multiflorum	0.62 ± 0.13	[0.37, 0.87]
	Poa trivialis	-0.70 ± 0.25	[-1.2, -0.21]
	longitude	-0.24 ± 0.16	[-0.55, 0.069]
	latitude	-0.47 ± 0.16	[-0.79, -0.16]
	height	0.53 ± 0.14	[0.25, 0.81]
The third census	*Carex neurocarpa*	-0.51 ± 0.32	[-1.1, 0.11]
	Schoenoplectus juncoides	0.21 ± 0.17	[-0.12, 0.54]
	Echinochloa spp.	0.32 ± 0.17	[-0.010, 0.65]
	Lolium multiflorum	1.4 ± 0.17	[1.0, 1.7]
	longitude	-0.30 ± 0.22	[-0.74, 0.14]
	latitude	-0.63 ± 0.22	[-1.1, -0.20]
	height	0.87 ± 0.19	[0.51, 1.2]

[a] 95% Wald Confidential Intervals

Table 4.3 The best generalized linear model relating the abundance of ears of Poaceae and Cyperaceae to the density of Miridae nymphs in the second census.

Poaceae and Cyperaceae species and covariate	Standard partial regression coefficient	
	Estimate ± S.E.	95% C.I [a]
Alopecurus aequalis	0.58 ± 0.13	[0.33, 0.83]
Anthoxanthum odoratum	0.18 ± 0.13	[-0.075, 0.44]
Lolium multiflorum	0.61 ± 0.13	[0.35, 0.87]
longitude	-0.25 ± 0.18	[-0.59, 0.092]
latitude	-0.39 ± 0.17	[-0.74, -0.051]
height	0.66 ± 0.15	[0.38, 0.95]

[a] 95% Wald Confidential Intervals

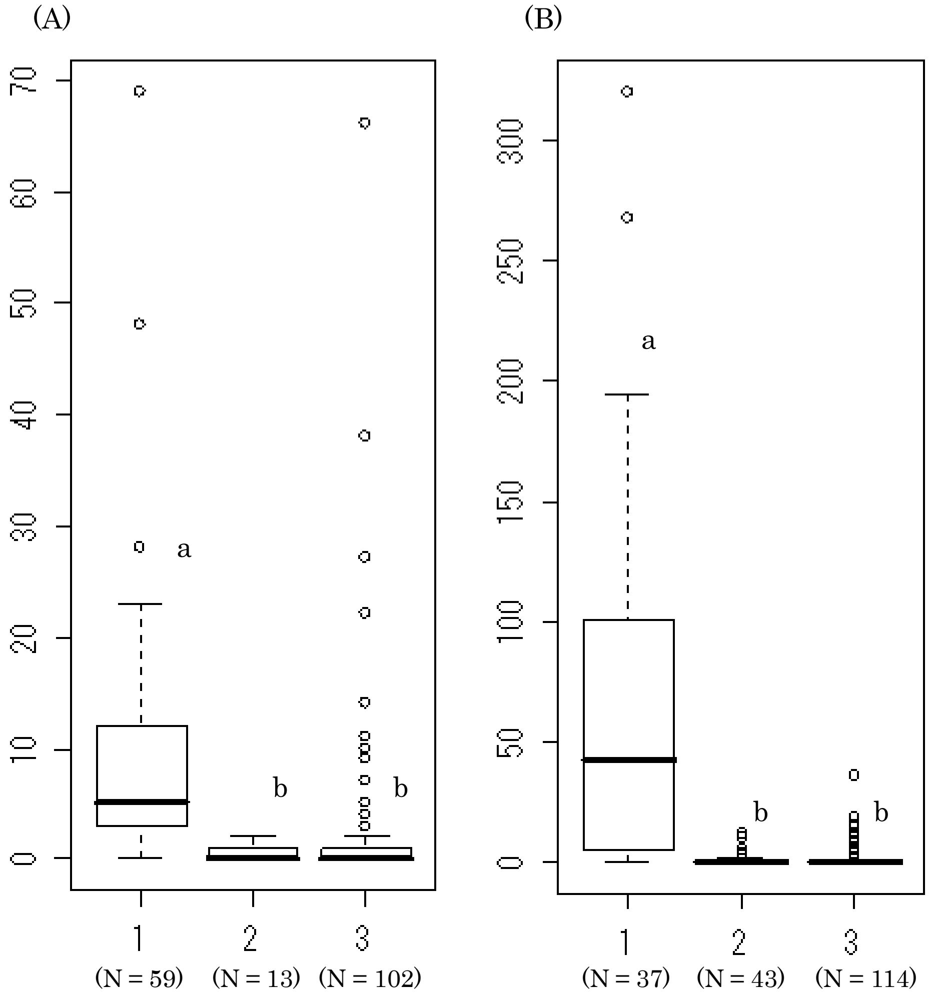


Fig. 4.1 Box plot of the density of adult *Stenotus rubrovittatus* in the (A) second and (B) third censuses at (1) plots with *L. multiflorum* dominance (> 10% coverage of heading *L. multiflorum*); i.e., meadows and a minor part of fallow fields), (2) plots within mowed meadows, and (3) those within other fallow fields. Different lowercase letters indicate significant (P < 0.05) differences in density, based on the Wilcoxon rank sum test with the Bonferroni correction.

Appendix 4.1 AIC and coefficients of the explanatory variables (the names of each plant species correspond to the effects of ear abundance of the species) in the candidate models that explain the density of adult *Stenotus rubrovittatus* in the (a) first, (b) second, and (c) third censuses. Only models within 10 AIC units of the most parsimonious model in each census period are shown.

(a) The first census

AIC	*Carex neurocarpa*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Glyceria ischyroneura*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
564.34	-	-	-0.24	-	-	-	0.22	0.15	-0.11	0.83	-0.091
564.53	-	-	-	-	-	-	0.23	0.17	-0.066	0.73	-0.068
565.42	-	-	-	-	0.12	-	0.22	0.14	-0.072	0.69	-0.077
565.46	-	-	-0.23	-	0.11	-	0.21	0.12	-0.12	0.79	-0.097
565.51	-	0.17	-0.23	-	-	-	0.23	0.12	-0.15	0.81	-0.099
565.56	-	0.18	-	-	-	-	0.24	0.14	-0.11	0.71	-0.077
565.92	-	-	-0.28	-	-	0.16	0.23	0.15	-0.10	0.77	-0.094
566.11	-0.088	-	-0.25	-	-	-	0.22	0.17	-0.097	0.87	-0.093
566.13	-	0.21	-	-	0.13	-	0.23	0.091	-0.12	0.65	-0.089
566.18	-	-	-0.28	-	-	-	-	0.068	-0.14	0.91	-0.052
566.29	-	-	-0.25	-0.037	-	-	0.22	0.14	-0.11	0.84	-0.091
566.35	-	0.19	-0.21	-	0.12	-	0.22	0.078	-0.16	0.75	-0.11
566.42	-0.062	-	-	-	-	-	0.23	0.19	-0.055	0.76	-0.069
566.45	-	-	-	-	-	0.073	0.24	0.17	-0.059	0.70	-0.068
566.52	-	-	-	-0.021	-	-	0.24	0.17	-0.066	0.74	-0.068
566.81	-	-	-	-	-	-	-	0.085	-0.095	0.80	-0.024
566.85	-	0.19	-0.27	-	-	0.20	0.24	0.11	-0.14	0.72	-0.10
566.95	-	-	-0.26	-	0.11	0.17	0.22	0.12	-0.10	0.72	-0.10
567.01	-	-	-0.25	-	0.12	-	-	0.054	-0.13	0.84	-0.062
567.12	-0.11	-	-0.24	-	0.11	-	0.21	0.15	-0.098	0.83	-0.10
567.22	-0.085	-	-	-	0.12	-	0.22	0.16	-0.058	0.72	-0.079
567.28	-	-	-	-	0.12	0.096	0.23	0.14	-0.063	0.64	-0.078
567.31	-	-	-	-	0.14	-	-	0.069	-0.083	0.73	-0.038
567.32	-	0.20	-	-	-	0.13	0.25	0.13	-0.099	0.64	-0.079
567.32	-	-	-0.23	-0.065	0.11	-	0.21	0.11	-0.12	0.79	-0.098
567.34	-	-	-	-0.053	0.12	-	0.22	0.13	-0.075	0.69	-0.078
567.41	-0.060	0.16	-0.24	-	-	-	0.22	0.13	-0.14	0.84	-0.10
567.49	-	0.17	-0.24	-0.028	-	-	0.23	0.11	-0.15	0.81	-0.099
567.49	-	0.22	-0.25	-	0.13	0.22	0.23	0.066	-0.15	0.64	-0.11
567.50	-	0.16	-0.27	-	-	-	-	0.037	-0.18	0.88	-0.059

(a) continued

AIC	*Carex neurocarpa*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Glyceria ischyroneura*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
567.54	-0.031	0.17	-	-	-	-	0.24	0.15	-0.10	0.72	-0.078
567.56	-	0.18	-	-0.011	-	-	0.24	0.14	-0.11	0.71	-0.077
567.70	-	0.23	-	-	0.14	0.17	0.24	0.081	-0.11	0.56	-0.092
567.74	-0.079	-	-0.29	-	-	0.15	0.23	0.17	-0.087	0.81	-0.096
567.84	-0.11	-	-0.29	-	-	-	-	0.097	-0.12	0.96	-0.056
567.89	-	-	-0.28	-0.029	-	0.15	0.23	0.14	-0.10	0.78	-0.094
568.00	-	0.18	-	-	-	-	-	0.051	-0.14	0.77	-0.032
568.03	-	-	-0.30	-	-	0.099	-	0.066	-0.14	0.87	-0.053
568.04	-	0.19	-0.24	-	0.14	-	-	0.01	-0.18	0.81	-0.072
568.06	-0.051	0.20	-	-	0.14	-	0.23	0.10	-0.11	0.67	-0.090
568.06	-	0.21	-	-0.046	0.14	-	0.23	0.083	-0.12	0.65	-0.090
568.10	-0.084	-	-0.25	-0.023	-	-	0.22	0.17	-0.099	0.88	-0.093
568.11	-	-	-0.28	-0.046	-	-	-	0.063	-0.14	0.92	-0.053
568.15	-	0.21	-	-	0.15	-	-	0.025	-0.13	0.70	-0.049
568.18	-0.076	0.18	-0.22	-	0.12	-	0.21	0.099	-0.15	0.78	-0.11
568.24	-	0.19	-0.22	-0.058	0.13	-	0.22	0.068	-0.17	0.75	-0.11
568.36	-0.058	-	-	-	-	0.065	0.24	0.19	-0.049	0.73	-0.069
568.41	-0.060	-	-	-0.011	-	-	0.23	0.18	-0.055	0.76	-0.069
568.44	-	-	-	-0.017	-	0.070	0.24	0.17	-0.060	0.70	-0.068
568.52	-0.13	-	-0.27	-	0.13	-	-	0.087	-0.11	0.90	-0.067
568.62	-0.085	-	-	-	-	-	-	0.11	-0.080	0.83	-0.026
568.68	-0.097	-	-0.27	-	0.12	0.16	0.22	0.14	-0.088	0.76	-0.10
568.77	-	-	-0.28	-	0.13	0.12	-	0.051	-0.12	0.80	-0.064
568.78	-	-	-	-0.030	-	-	-	0.082	-0.095	0.80	-0.024
568.80	-0.042	0.18	-0.28	-	-	0.19	0.24	0.12	-0.13	0.74	-0.10
568.81	-	-	-	-	-	-0.012	-	0.085	-0.096	0.80	-0.024
568.84	-	0.19	-0.27	-0.015	-	0.20	0.24	0.11	-0.14	0.73	-0.10
568.85	-	-	-0.26	-0.055	0.11	0.16	0.22	0.11	-0.11	0.72	-0.10
568.86	-	-	-0.26	-0.069	0.13	-	-	0.044	-0.13	0.85	-0.063
568.98	-0.11	-	-	-	0.15	-	-	0.096	-0.064	0.77	-0.041
569.02	-0.10	-	-0.24	-0.057	0.12	-	0.21	0.13	-0.10	0.83	-0.10
569.11	-0.078	-	-	-	0.13	0.086	0.23	0.15	-0.051	0.67	-0.080
569.15	-0.081	-	-	-0.047	0.13	-	0.22	0.15	-0.061	0.72	-0.080
569.21	-	-	-	-0.056	0.14	-	-	0.060	-0.086	0.74	-0.039
569.21	-	-	-	-0.047	0.12	0.089	0.23	0.13	-0.067	0.65	-0.078
569.22	-	0.18	-0.30	-	-	0.13	-	0.030	-0.18	0.83	-0.061
569.29	-	-	-	-	0.14	0.027	-	0.068	-0.081	0.72	-0.038

(a) continued

AIC	*Carex neurocarpa*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Glyceria ischyroneura*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
569.30	-0.087	0.15	-0.28	-	-	-	-	0.063	-0.16	0.93	-0.062
569.31	-0.018	0.19	-	-	-	0.13	0.25	0.14	-0.095	0.65	-0.079
569.32	-	0.20	-	-0.002	-	0.13	0.25	0.13	-0.099	0.64	-0.079
569.40	-0.056	0.16	-0.24	-0.019	-	-	0.22	0.13	-0.14	0.84	-0.10
569.41	-0.055	0.21	-0.26	-	0.13	0.21	0.23	0.082	-0.14	0.67	-0.12
569.43	-	0.22	-0.25	-0.044	0.13	0.21	0.23	0.058	-0.16	0.65	-0.12
569.45	-	0.16	-0.27	-0.037	-	-	-	0.033	-0.18	0.89	-0.060
569.54	-0.030	0.17	-	-0.006	-	-	0.24	0.14	-0.10	0.72	-0.078
569.58	-	0.21	-0.28	-	0.15	0.16	-	0.0029	-0.17	0.73	-0.075
569.66	-	0.23	-	-0.034	0.14	0.16	0.24	0.075	-0.11	0.57	-0.093
569.67	-0.032	0.22	-	-	0.14	0.16	0.24	0.090	-0.10	0.58	-0.093
569.72	-0.11	-	-0.31	-	-	0.089	-	0.094	-0.12	0.92	-0.057
569.73	-0.08	-	-0.29	-0.017	-	0.15	0.23	0.17	-0.089	0.81	-0.096
569.75	-0.11	0.17	-0.25	-	0.14	-	-	0.043	-0.15	0.85	-0.075
569.81	-0.11	-	-0.29	-0.031	-	-	-	0.093	-0.13	0.97	-0.056
569.92	-	0.19	-0.24	-0.061	0.14	-	-	0.0044	-0.18	0.81	-0.073
569.92	-0.056	0.17	-	-	-	-	-	0.067	-0.12	0.80	-0.033
569.97	-	-	-0.31	-0.041	-	0.094	-	0.061	-0.14	0.88	-0.054
569.99	-	0.18	-	-	-	0.034	-	0.049	-0.13	0.75	-0.032
569.99	-0.078	0.19	-	-	0.16	-	-	0.047	-0.11	0.73	-0.051
569.99	-	0.17	-	-0.020	-	-	-	0.049	-0.14	0.78	-0.033
569.99	-0.047	0.20	-	-0.043	0.14	-	0.23	0.096	-0.11	0.67	-0.091
570.03	-	0.22	-	-	0.16	0.090	-	0.018	-0.13	0.65	-0.050
570.07	-	0.21	-	-0.048	0.16	-	-	0.017	-0.13	0.70	-0.050
570.09	-0.073	0.18	-0.22	-0.053	0.13	-	0.22	0.089	-0.15	0.78	-0.11
570.33	-0.13	-	-0.29	-	0.14	0.11	-	0.083	-0.10	0.85	-0.068
570.35	-0.056	-	-	-0.007	-	0.065	0.24	0.18	-0.050	0.73	-0.069
570.40	-0.13	-	-0.27	-0.062	0.14	-	-	0.077	-0.11	0.91	-0.068
570.60	-0.093	-	-0.27	-0.049	0.12	0.16	0.22	0.13	-0.092	0.76	-0.10
570.61	-0.082	-	-	-0.017	-	-	-	0.10	-0.081	0.84	-0.026
570.61	-0.087	-	-	-	-	-0.025	-	0.11	-0.081	0.85	-0.026
570.64	-	-	-0.28	-0.062	0.13	0.11	-	0.041	-0.13	0.81	-0.065
570.78	-	-	-	-0.031	-	-0.017	-	0.082	-0.097	0.81	-0.024
570.80	-0.041	0.18	-0.28	-0.010	-	0.19	0.24	0.12	-0.13	0.75	-0.10
570.90	-0.11	-	-	-0.051	0.15	-	-	0.087	-0.067	0.78	-0.042
570.98	-0.11	-	-	-	0.15	0.012	-	0.095	-0.063	0.77	-0.041
571.05	-0.075	-	-	-0.042	0.13	0.080	0.23	0.15	-0.054	0.68	-0.080

(a) continued

AIC	*Carex neurocarpa*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Glyceria ischyroneura*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
571.07	-0.076	0.16	-0.31	-	-	0.12	-	0.054	-0.16	0.87	-0.063
571.19	-	0.17	-0.30	-0.029	-	0.13	-	0.027	-0.18	0.84	-0.062
571.20	-	-	-	-0.055	0.15	0.019	-	0.060	-0.084	0.73	-0.039
571.28	-0.082	0.15	-0.28	-0.026	-	-	-	0.059	-0.16	0.93	-0.062
571.31	-0.018	0.19	-	0.001	-	0.13	0.25	0.14	-0.095	0.65	-0.079
571.35	-0.052	0.21	-0.26	-0.041	0.13	0.21	0.23	0.074	-0.14	0.68	-0.12
571.37	-0.090	0.20	-0.28	-	0.15	0.15	-	0.031	-0.15	0.78	-0.078
571.50	-	0.21	-0.28	-0.050	0.15	0.16	-	-0.0044	-0.17	0.74	-0.076
571.63	-0.030	0.22	-	-0.033	0.14	0.16	0.24	0.084	-0.11	0.58	-0.093
571.64	-0.10	0.17	-0.26	-0.057	0.15	-	-	0.034	-0.16	0.86	-0.076
571.70	-0.10	-	-0.32	-0.028	-	0.087	-	0.090	-0.12	0.93	-0.057
571.90	-0.069	0.21	-	-	0.16	0.077	-	0.039	-0.11	0.68	-0.052
571.91	-0.053	0.17	-	-	-	0.024	-	0.065	-0.12	0.78	-0.033
571.92	-0.053	0.17	-	-0.012	-	-	-	0.066	-0.12	0.80	-0.033
571.92	-0.076	0.19	-	-0.045	0.16	-	-	0.039	-0.12	0.73	-0.052
571.97	-	0.22	-	-0.042	0.16	0.083	-	0.012	-0.13	0.66	-0.051
571.98	-	0.18	-	-0.017	-	0.031	-	0.048	-0.13	0.76	-0.033
572.23	-0.13	-	-0.29	-0.057	0.14	0.10	-	0.074	-0.11	0.86	-0.069
572.60	-0.083	-	-	-0.019	-	-0.027	-	0.10	-0.083	0.85	-0.027
572.90	-0.11	-	-	-0.051	0.15	0.0047	-	0.087	-0.067	0.78	-0.042
573.06	-0.073	0.16	-0.31	-0.021	-	0.12	-	0.051	-0.16	0.87	-0.063
573.29	-0.089	0.19	-0.29	-0.048	0.15	0.15	-	0.023	-0.15	0.79	-0.078
573.85	-0.068	0.20	-	-0.040	0.17	0.070	-	0.033	-0.11	0.69	-0.052
573.91	-0.051	0.17	-	-0.011	-	0.022	-	0.064	-0.12	0.79	-0.033

(b) the second census

AIC	*Carex neurocarpa*	*Agrostis clavata*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
778.85	-	-	0.21	0.28	-0.47	0.62	-0.70	-0.24	-0.47	0.53	1.0
778.91	-	-	0.23	0.30	-	0.66	-0.83	-0.25	-0.46	0.48	1.0
779.19	-0.23	-	0.22	0.29	-	0.63	-0.82	-0.23	-0.45	0.52	1.0
779.58	-	-	-	0.26	-0.53	0.59	-0.68	-0.24	-0.48	0.56	1.0
779.99	-	0.10	0.22	0.28	-0.68	0.63	-0.68	-0.26	-0.49	0.53	1.0
780.00	-	-	-	0.29	-	0.64	-0.81	-0.25	-0.47	0.51	1.1
780.02	-0.25	-	-	0.28	-	0.60	-0.80	-0.22	-0.46	0.55	1.0

(b) continued

AIC	*Carex neurocarpa*	*Agrostis clavata*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
780.27	-0.15	-	0.21	0.28	-0.30	0.61	-0.72	-0.23	-0.46	0.54	1.0
780.78	-	0.039	0.23	0.30	-	0.67	-0.83	-0.26	-0.47	0.48	1.0
780.81	-	0.10	-	0.26	-0.73	0.60	-0.66	-0.26	-0.50	0.56	1.0
780.84	-0.24	0.063	0.22	0.29	-	0.64	-0.81	-0.24	-0.46	0.52	1.0
780.93	-0.16	-	-	0.26	-0.32	0.58	-0.70	-0.23	-0.47	0.58	1.0
781.55	-0.15	0.092	0.22	0.28	-0.40	0.62	-0.70	-0.25	-0.48	0.54	1.0
781.74	-0.26	0.057	-	0.28	-	0.61	-0.80	-0.23	-0.47	0.55	1.0
781.93	-	0.031	-	0.29	-	0.64	-0.81	-0.25	-0.48	0.51	1.1
782.30	-0.16	0.087	-	0.26	-0.42	0.59	-0.68	-0.25	-0.49	0.57	1.0
783.79	-	-	0.20	0.21	-0.62	0.65	-	-0.21	-0.49	0.49	1.1
784.20	-	-	-	0.20	-0.66	0.62	-	-0.20	-0.50	0.52	1.1
784.65	-	0.12	0.21	0.21	-0.81	0.66	-	-0.23	-0.52	0.49	1.1
785.17	-	0.11	-	0.20	-0.85	0.63	-	-0.23	-0.52	0.52	1.1
785.51	-	-	-	-	-0.65	0.45	-0.43	-0.27	-0.63	0.67	1.1
785.58	-0.093	-	0.20	0.21	-0.53	0.64	-	-0.20	-0.49	0.50	1.1
785.93	-0.11	-	-	0.19	-0.55	0.62	-	-0.19	-0.50	0.53	1.1
785.96	-	-	0.18	-	-0.62	0.46	-0.42	-0.28	-0.64	0.65	1.1
786.48	-0.094	0.11	0.21	0.21	-0.65	0.65	-	-0.23	-0.51	0.50	1.1
786.57	-	-	-	-	-0.72	0.51	-	-0.24	-0.61	0.62	1.1
786.69	-	0.11	-	-	-0.86	0.46	-0.42	-0.30	-0.65	0.67	1.1
786.85	-0.17	-	-	-	-0.46	0.44	-0.45	-0.26	-0.62	0.69	1.1
786.91	-	-	0.22	0.23	-	0.71	-	-0.21	-0.50	0.42	1.2
786.95	-	-	0.18	-	-0.69	0.52	-	-0.24	-0.61	0.60	1.1
786.96	-0.11	0.11	-	0.20	-0.66	0.63	-	-0.22	-0.52	0.53	1.1
787.07	-	0.11	0.18	-	-0.83	0.47	-0.41	-0.30	-0.66	0.65	1.1
787.11	-0.29	-	-	-	-	0.45	-0.54	-0.26	-0.63	0.66	1.1
787.14	-0.24	-	0.21	0.22	-	0.67	-	-0.19	-0.48	0.46	1.1
787.36	-0.16	-	0.17	-	-0.45	0.45	-0.44	-0.27	-0.63	0.67	1.1
787.54	-0.28	-	0.18	-	-	0.46	-0.53	-0.26	-0.64	0.65	1.1
787.59	-	0.11	-	-	-0.92	0.51	-	-0.26	-0.63	0.62	1.1
787.64	-	-	-	0.21	-	0.69	-	-0.21	-0.51	0.45	1.2
787.65	-0.26	-	-	0.20	-	0.65	-	-0.18	-0.49	0.49	1.2
787.68	-	-	-	-	-	0.48	-0.53	-0.29	-0.65	0.61	1.2
787.89	-	0.12	0.18	-	-0.89	0.53	-	-0.27	-0.63	0.60	1.1
787.92	-	-	0.19	-	-	0.50	-0.52	-0.30	-0.66	0.60	1.1
788.16	-0.17	0.092	-	-	-0.55	0.45	-0.43	-0.28	-0.65	0.68	1.1
788.22	-0.12	-	-	-	-0.59	0.50	-	-0.22	-0.60	0.63	1.1

(b) continued

AIC	*Carex neurocarpa*	*Agrostis clavata*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	intercept
788.44	-	-	-	0.18	-0.79	-	-0.55	-0.24	-0.56	0.77	1.1
788.59	-0.16	0.10	0.18	-	-0.54	0.46	-0.42	-0.29	-0.65	0.66	1.1
788.64	-0.11	-	0.17	-	-0.57	0.51	-	-0.23	-0.60	0.61	1.1
788.75	-0.26	0.068	0.21	0.22	-	0.68	-	-0.20	-0.49	0.45	1.1
788.77	-	0.042	0.22	0.23	-	0.72	-	-0.22	-0.50	0.42	1.2

(c) The third census

AIC	*Carex neurocarpa*	*Schoenoplectus juncoides*	*Agrostis gigantea*	*Alopecurus aequalis*	*Echinochloa spp.*	*Lolium multiflorum*	longitude	latitude	height	intercept
827.93	-0.51	0.21	-	-	0.32	1.4	-0.30	-0.63	0.87	1.2
828.08	-0.58	-	-	-	0.39	1.3	-0.35	-0.55	0.89	1.3
828.85	-	0.24	-	-	0.25	1.4	-0.30	-0.63	0.83	1.3
829.46	-	-	-	-	0.30	1.3	-0.37	-0.53	0.84	1.3
829.65	-0.53	0.24	-	-0.11	0.35	1.4	-0.30	-0.64	0.88	1.2
829.89	-0.49	0.22	-0.039	-	0.31	1.4	-0.30	-0.63	0.88	1.2
830.07	-0.56	-	-0.026	-	0.39	1.3	-0.35	-0.55	0.89	1.3
830.07	-0.59	-	-	-0.022	0.41	1.3	-0.35	-0.54	0.89	1.3
830.48	-	0.23	-0.13	-	0.24	1.4	-0.30	-0.63	0.84	1.3
830.63	-	0.26	-	-	-	1.3	-0.27	-0.56	0.86	1.3
830.69	-	0.26	-	-0.088	0.26	1.4	-0.30	-0.63	0.84	1.3
830.78	-0.36	0.24	-	-	-	1.3	-0.27	-0.56	0.92	1.3
831.04	-	-	-0.14	-	0.30	1.3	-0.37	-0.53	0.85	1.3
831.43	-	-	-	0.036	0.29	1.3	-0.36	-0.54	0.84	1.3
831.50	-0.40	-	-	-	-	1.2	-0.33	-0.46	0.96	1.4
831.62	-0.51	0.24	-0.036	-0.11	0.34	1.4	-0.29	-0.64	0.88	1.2
831.64	-	-	-	-	-	1.2	-0.34	-0.46	0.89	1.4
832.06	-0.57	-	-0.024	-0.019	0.40	1.3	-0.35	-0.55	0.89	1.3
832.12	-	0.25	-0.16	-	-	1.3	-0.27	-0.56	0.87	1.3
832.32	-	0.26	-0.13	-0.088	0.25	1.4	-0.30	-0.63	0.84	1.3
832.55	-0.34	0.25	-0.10	-	-	1.2	-0.27	-0.56	0.93	1.3
832.60	-	0.27	-	-0.039	-	1.3	-0.27	-0.56	0.87	1.3
832.74	-0.36	0.26	-	-0.048	-	1.3	-0.27	-0.56	0.92	1.3
833.02	-	-	-0.14	0.036	0.29	1.3	-0.36	-0.54	0.85	1.3
833.08	-	-	-0.16	-	-	1.2	-0.34	-0.46	0.91	1.4
833.21	-0.39	-	-	0.12	-	1.2	-0.32	-0.48	0.94	1.3

(c) continued

AIC	*Carex neurocarpa*	*Schoenoplectus juncoides*	*Agrostis gigantea*	*Alopecurus aequalis*	*Echinochloa spp.*	*Lolium multiflorum*	longitude	latitude	height	intercept
833.25	-	-	-	0.14	-	1.2	-0.33	-0.48	0.88	1.4
833.29	-0.38	-	-0.091	-	-	1.2	-0.33	-0.47	0.96	1.3
834.08	-	0.27	-0.16	-0.040	-	1.3	-0.27	-0.56	0.88	1.3
834.50	-0.34	0.26	-0.10	-0.048	-	1.2	-0.26	-0.56	0.93	1.3
834.70	-	-	-0.16	0.14	-	1.2	-0.33	-0.48	0.89	1.4
834.99	-0.37	-	-0.092	0.12	-	1.2	-0.32	-0.48	0.95	1.3

Appendix 4.2 AIC and coefficients of the explanatory variables (the names of each plant species correspond to the effects of ear abundance of the species) in the candidate models that explain the density of mirid nymphs in the second census. Only models within 10 AIC units of the most parsimonious model in each census period are shown.

AIC	*Carex neurocarpa*	*Agrostis clavata*	*Alopecurus aequalis*	*Anthoxanthum odoratum*	*Elymus tsukushiensis*	*Lolium multiflorum*	*Poa trivialis*	longitude	latitude	height	Intercept
675.71	-	-	0.58	0.18	-	0.61	-	-0.25	-0.39	0.66	0.73
676.08	-	-	0.60	0.17	-	0.59	0.22	-0.24	-0.44	0.55	0.72
676.46	-	-	0.62	-	-	0.53	0.27	-0.27	-0.54	0.59	0.74
676.65	0.15	-	0.63	0.18	-	0.64	0.25	-0.28	-0.48	0.46	0.71
676.74	-	-	0.61	-	-	0.56	-	-0.29	-0.51	0.73	0.76
676.86	0.11	-	0.60	0.19	-	0.64	-	-0.28	-0.41	0.62	0.72
677.13	-	-	0.60	0.19	0.11	0.64	-	-0.24	-0.40	0.61	0.73
677.18	-	0.10	0.59	0.18	-	0.62	-	-0.27	-0.41	0.66	0.73
677.32	0.13	-	0.65	-	-	0.57	0.30	-0.30	-0.58	0.52	0.73
677.51	-	0.10	0.62	0.17	-	0.60	0.22	-0.26	-0.46	0.54	0.71
677.92	-	-	0.61	0.17	0.065	0.61	0.20	-0.24	-0.44	0.53	0.72
677.94	-	0.092	0.64	-	-	0.54	0.27	-0.29	-0.57	0.58	0.73
678.15	0.10	-	0.62	-	-	0.58	-	-0.31	-0.53	0.70	0.75
678.16	0.14	0.090	0.64	0.18	-	0.65	0.26	-0.29	-0.49	0.46	0.70
678.27	-	0.092	0.62	-	-	0.57	-	-0.31	-0.53	0.73	0.75
678.39	-	-	0.62	-	0.085	0.58	-	-0.28	-0.52	0.70	0.75
678.39	0.11	0.091	0.61	0.19	-	0.65	-	-0.30	-0.43	0.61	0.72
678.44	-	-	0.63	-	0.026	0.54	0.26	-0.27	-0.55	0.58	0.74
678.45	0.11	-	0.61	0.19	0.084	0.66	-	-0.27	-0.42	0.58	0.72
678.64	0.14	-	0.63	0.18	0.014	0.64	0.25	-0.27	-0.47	0.46	0.71
678.65	-	0.094	0.61	0.19	0.10	0.65	-	-0.26	-0.42	0.61	0.72
678.87	0.13	0.085	0.67	-	-	0.58	0.30	-0.32	-0.60	0.51	0.72
679.30	0.14	-	0.65	-	-0.024	0.57	0.31	-0.30	-0.58	0.52	0.73
679.38	-	0.095	0.62	0.17	0.055	0.62	0.20	-0.26	-0.46	0.52	0.71
679.74	0.090	0.087	0.64	-	-	0.59	-	-0.33	-0.55	0.69	0.75
679.92	0.090	-	0.64	-	0.066	0.60	-	-0.31	-0.54	0.67	0.75
679.93	-	0.091	0.64	-	0.016	0.55	0.27	-0.29	-0.57	0.58	0.73
679.96	-	0.089	0.64	-	0.079	0.59	-	-0.30	-0.54	0.69	0.75
680.02	0.10	0.089	0.62	0.20	0.079	0.67	-	-0.29	-0.43	0.58	0.72
680.15	0.14	0.089	0.64	0.18	0.0075	0.65	0.25	-0.29	-0.49	0.46	0.70
680.84	0.13	0.087	0.66	-	-0.031	0.57	0.32	-0.32	-0.60	0.51	0.72
681.54	0.083	0.085	0.65	-	0.061	0.60	-	-0.33	-0.55	0.67	0.74

Chapter 5 Landscape effect of a non-native grass on source population of a native generalist mirid bug

Introduction

Non-native plant invaders may not only negatively affect, but also facilitate some generalist insect herbivores through provision of trophic subsidy and/or novel habitat (Rodriguez 2006), and thus exert indirect negative impacts (i.e. apparent competition *sensu* Holt (1977)) on native plants and/or crops (Malmstrom et al. 2005; Carriere et al. 2006; Branson and Sword 2009; see also Chapter 4). Therefore, facilitation of native generalist herbivores by non-native plants and their dynamics may be an essential issue to predict whole impacts of non-native plant invasion on biodiversity and ecosystem services.

The impact of facilitation of native generalist herbivores by non-native plants is better to be considered at landscape level, because stands of non-native plants can act as novel habitat patches for native insects (Jones et al. 1994; Crooks 2004; Rodriguez 2006). If so, spatial distribution of the patches can cause landscape-level effects of a plant invader on population size of the herbivore which cannot be explained by simple summation of area of the patches alone, as "emergent property" (Bissonette 1997; King 1997). For instance, metapopulation theory by Hanski (1999) demonstrates that habitat patch connectivity resulted in non-linear positive effect on population size of butterfly species (Hanski and Ovaskainen 2000). However, to our knowledge, the positive multi-level (both local and landscape) effects of non-native plants on generalist herbivores have not yet been reported.

Although generalist herbivore insect may prefer a particular plant species (Fox and Morrow 1981; Bernays and Graham 1988; Lu et al. 2010), their preference are highly temporal and seasonally variable (Iwao 1971). Therefore, the positive landscape-level effect on generalist insects by a plant species may have to arise in a relatively shorter time than that on specialist insects to significantly affect their population dynamics because generalists may interact with the plant during only a small part of their life cycles. Nevertheless, we would overlook rapid expansion and outbreak of source population of generalists which can damage other native plants or crops if such a landscape-level effect matters.

Agricultural landscape in Japan, characterized by highly heterogeneous mosaic of cropland and various non-crop land vegetation (Washitani 2001a; Katoh et al. 2009), provides research opportunity to examine the landscape-level effect of non-native plant species introduction and/or invasion on generalist herbivores. In Japan, the rice acreage reduction policy practiced since 1970 caused a prevailing trend in land-use change from paddies to meadows or fallow fields (Hayashi and Nakazawa 1988; Kiritani 2007). Italian ryegrass *Lolium multiflorum* Lam. (Poaceae), a non-native meadow grass has been a common forage crop in such meadows (Hayashi and Nakazawa 1988). Uncultivated fallows can also become source habitats of generalist herbivores because they were frequently invaded by non-native weeds including naturalized meadow grasses.

Lolium multiflorum is known to be the most important source host for a generalist mirid bug, sorghum plant bug *Stenotus rubrovittatus* (Matsumura) (Hemiptera: Miridae)(Chapter 4), which is currently one of the most serious economic pest to rice (*Oryza sativa* L., Poaceae) in Japan (Kiritani 2007). *S. rubrovittatus* is known to predate the ears of various species of Poaceae and Cyperaceae and reproduces on them at least three times during a year (Hayashi and Nakazawa 1988; Kashin et al. 2009). Although *Stenotus rubrovittatus* show an opportunistic strategy (i.e., polyphagy and multivoltine), the bugs exhibit marked preference for ears of *L. multiflorum* from early to mid summer (Chapter 4). On the other hand, the species occurs in rice paddies only in the short period when rice heads in mid summer (Takeuchi et al. 2005). They rarely reproduce in the paddies (Takeuchi et al. 2005), but are assumed to overspill to rice fields from proximal meadows and fallows. Therefore, meadows can be regarded to be population sources, while paddies, sinks for the bug.

Discoloration of the rice grains caused by the bugs leads to a severe economic loss to farmers under the current national regulation system for rice quality, which is based almost exclusively on the appearance of grains. From the economic point of view, the damage by the bugs is a particularly serious problem and effective pest management is urgently needed especially in areas practicing biodiversity-friendly agricultures with no or reduced insecticide applications (Washitani 2007).

The present study aimed to determine whether or not local abundance of host plant (local-level factor) as well as spatial characteristic of a heterogeneous agricultural landscape, specifically amount and/or connectivity of meadow patches dominated by non-native *L. multiflorum* (landscape-level factor) affects density of *S. rubrovittatus* in their source habitat at the stage prior to the immigration to paddies.

First, we surveyed spatial distribution of meadows dominated by *L. multiflorum*, uncultivated fallows and woodlands as landscape-level factors in an area of Osaki City, Miyagi Prefecture, northern Japan, where biodiversity-friendly farming without or with reduced agrichemicals have been practiced. Second, we measured density of the mirid bug at the fallows and meadows in early August, together with abundances of its potential hosts (Poaceae and Cyperaceae) as local-level factors. Then, we analyzed relationships between density of *S. rubrovittatus* and the local/landscape-level factors.

Materials and methods

Study area

The study was conducted in Tajiri area of Osaki City, Miyagi Prefecture, northern Japan (38º37'N, 141º07'E) where pioneering biodiversity-friendly agricultures have been practiced (see also Chapter 4). The landscape of the area mainly consists of paddies, uncultivated fallows, meadows converted from paddies, and small patches of woodlands. The annual precipitation of the city in 2008 is 1,126 mm and the mean temperature in June, July, August was 18.5, 22.6, and 22.5º C respectively (Japanese Meteorology Agency http://www.jma.go.jp/jma/index.html).

L. multiflorum has been cultivated throughout Japan as common foraging crop, and also naturalized as invasive alien species (Miyawaki and Washitani 2004). The species is also the most common meadow grass cultivated in the meadows of the study area. Patch size of these Italian ryegrass meadows is within the range of patch size of naturalized non-native plants, and much smaller than an modern arable field (c.a. 20 ha in Europe and 200 ha in U.S.A by Nyffeler and Sunderland (2003)), because average patch size of arable field in the area is quite a small (less than a few ha). *S. rubrovittatus* is the most abundant and influential arthropod pest in paddies in the region (Kashin et al.

2009; Chapter 4).

In the meadows, *L. multiflorum* is sown in autumn or early spring and harvested for forage in the middle June, but the mowed grass rapidly regrows and is harvested again in late July. The timing of the second harvest is highly variable according to weather conditions, because farmers prefer drying the mowed grass in the sun before collecting them from the meadow (Yoshioka personal observation). Thus, in the year with rainy summer, some meadows can remain unmowed until early-mid August, when rice plants begin to head and the bugs seasonally colonize into paddy fields. After summer, most of the meadows were dominated by weeds such as *Echinochloa* spp. as well as in uncultivated fallow fields because most *L. multiflorum* has been senescent.

In the uncultivated fallows, sedges and grasses such as *Carex ueurocarpa* Maxim. (Cyperaceae), *Schoenoplectus juncoides* (Roxb.) Palla (Cyperaceae), *Agrostis gigantea* Roth (Poaceae), *Echinochloa* spp. (Poaceae), and a small amount of naturalized *L. multiflorum* are heading in early August. Thus, they can also act as habitats for *S. rubrovittatus* before colonization into paddies.

Landscape structure

We conducted field survey to assess the current spatial distribution of landscape elements of the study area in the middle of May and from the end of July to the middle of August. The map of agricultural land use of the study area and information on crop rotation compiled by the local government were used as supplement.

We identified five categories of land patch: paddy fields, Italian ryegrass meadows, fallows, woodland patches, and others. Italian ryegrass meadows were defined as the patches where percent coverage of heading *L. multiflorum* > 10% at either survey time. Most of the meadows were converted from paddy fields due to the rice acreage reduction policy. The meadows were subdivided into two categories according to whether they had been mowed in the end of July: "unmowed meadows" and "mowed meadows". The data collected were mapped using software packages ArcGis 9 (ESRI Inc., Redlands, CA, USA) and Hawth's Analysis Tool (http:// www.spatialecology.com.).

Field sampling

We conducted field censuses of *S. rubrovittatus* and their host plants in the meadows and fallow fields from 1 August to 9 August in 2008. The season corresponds to the peak population density of the bug of the annual first generation before seasonal dispersion into paddies (Kashin et al. 2009; Chapter 4). The census was performed at 194 sampling plots (37 in unmowed meadows, 43 in mowed meadows, and 114 in fallows, respectively) within a 20 km^2 area of the study area to cover the sites dominated by various Poaceae and Cyperaceae species. Each census plot was set at the nearly center of a meadow or fallow field. The distance to nearest neighbor plots in each census was 102 ± 79 m (mean ± SD), respectively. The area of the individual meadows and fallow fields ranged from ca.60 to 20000 m^2.

The daily censuses were started at 9:00 and ended at 17:00. The densities of adult *S. rubrovittatus* were measured through net sampling with 20 sweeps using a 36-cm diameter insect net in each plot.

We also measured the abundance of ears of each Poaceae and Cyperaceae species by counting the number within a 0.2×6 m^2 quadrate set near the plot. The vegetation heights were also measured at nine regularly spaced points within the quadrate. These height measurements were averaged over each plot. For the meadow plots, we recorded whether the meadow has been mowed recently or not.

In addition, these sampling data were also used for the research on host usage of *S. rubrovittatus* in the study area (see also Chapter 4 for detail).

Statistical analyses

To analyze the effect of local and landscape factors on *S. rubrovittatus*, we applied a generalized linear model with a negative binomial error distribution. The fact that the bug density in unmowed meadow was much higher than those of fallow fields and mowed meadows (Chapter 4) suggested mechanisms determining the density can be different among the habitat types. Thus, we analyzed the data in unmowed meadows and the data in fallow fields separately. The data in mowed meadows were not analyzed because the density of bugs was negligible (Chapter 4) and thought to be not the habitat of the mirid bug.

The models includes the bug density as a responsible variable and three landscape factors (unmowed meadow, fallow, and woodland area surrounding the census plots), and within-plot factors (vegetation height and ear abundance of each Poaceae and Cyperaceae species which were recorded in ≥ 10 plots in each habitat type; *L. multiflorum* in mowed meadow plots and *C. ueurocarpa, S. juncoides*, *A. gigantea*, *Echinochloa* spp., and *L. multiflorum* in fallow plots, respectively) as independent variables. Among the landscape factors, surrounding woodland assumed to be a potential dispersion barrier for the bug inhabiting grasslands, but the others are assumed to be source habitats of the bugs. The latitude and longitude of study plots were also included in the models as independent variables in order to separate effects of unexpected geographical trends.

The spatial extent at which landscape factors should be extracted is not clear, so we generated a buffer circle with a given radius (100, 200, 300, 400, 500, 600, and 700 m) around each sampling plot and then calculated proportions of the areas of the three landscape elements within the buffer area using GIS. The previous work by Carriere et al. (2006), in which the density of a mirid bug *Lygus hesperus* in cotton fields were affected by landscape elements within 750 m, at most, from the focal cotton fields, supports that the range of buffer in this study (100-700 m) would appropriate for examining *in situ* spatial scale for mirid bug dispersal. In particular, unmowed meadow and fallow areas in a buffer were expected to be the measure of connectivity of potential habitats (Molianen and Nieminen 2002) for the mirid bugs. However, area of a patch where a sampling plot exists rather than patch connectivity may play a role if unmowed meadow area in a buffer affected the bug density in the ummowed meadow plot (or fallow area in a buffer affected the density in the fallow plot). In order to deal with such cases (Appendix 5.1), we also analyzed the model with a patch area instead of surrounding patch area within a buffer.

Then, model selection by comparing candidate models consisting of all possible combinations of explanatory variables using AIC (Akaike Information Criteria) was conducted in each size of buffer in order to obtain the best model (i.e. the model with the lowest AIC value). The values of within-field factors were unique to each field, which was unchanged with buffer size. Although model selection with “all possible models” has a risk of selecting an inappropriate model as a result of data-dredging unless the candidate models are meaningful biologically (Burnham and Anderson 2002), our previous studies (Chapter 4) showed that these explanatory variables are sufficiently biologically-meaningful. Before analysis, all of the explanatory variables were centered and scaled (dividing by SD) so that their effects could be compared.

In order to clarify a short-time landscape level change of meadow status (i.e., unmowed meadow in early August) rather than long-time landscape structure directly affects the bug density, the similar analysis in which area of unmowed meadows in buffers were replaced with that of all Italian ryegrass meadows (including both unmowed and mowed) was also conducted in the same way if a significant effect of surrounding unmowed meadow area was detected. Spatial structure of all Italian ryegrass meadows through a year are expected to be longer-term index of connectivity of source habitat of *S. rubrovittatus*. Hence, presence of a short-time landscape effect would be supported if the best models with unmowed meadow area show the better fitting (lower AIC values) than those with all Italian meadow area.

All statistical analyses were performed using R for Windows 2.11.1 (R Development Core Team 2010). For the best models, tolerances of independent variables were checked. Spatial autocorrelation of residuals of the best models were also checked by Moran's I correlograms (Legendre and Legendre 1998; Dormann et al. 2007), which plot Moran's I for ten 200 m-wide distance classes. Moran's I and its p-value based on 10000 times permutations were computed by *ncf* package in the R, and the significance level (5%) was corrected by the method of Bonferroni.

Results

Choice of spatial scale for the models with good performance

Model selection revealed that the buffer with a radius of 200m minimized AIC values of the model in the unmowed meadow plots (Fig. 5.1), while the 300m-radius buffer minimized the values in fallow plots (Fig. 5.2). These AIC values were considerably lower (ΔAIC > 2) than that of the most parsimonious models with no landscape factors included i.e., 0 m-radius buffers models (AIC = 378.05 and 262.13 in the meadows and fallow plots, respectively). Tolerances of each selected variables were sufficiently high (> 0.76) in the both most parsimonious models. No significant values of Moran's I was also detected from the residuals of the best models.

Factors affecting the bug density in unmowed meadow plots

In the most parsimonious model for bug density in the unmowed meadow plot with the 200m-radius buffer, the density was highly correlated with the unmowed meadow area around the plot and the ear abundance of *L. multiflorum* (Table 5.1). The direction of the coefficients of the two factors was consistently maintained in the other candidate models with the 200 m-radius buffer with ΔAIC < 2 (Table 5.1). The best model with the 300 m-radius buffer also showed that the two factors positively affected the bug density.

The effect of the unmowed meadow area around the plot could reflect the area of the patch where the sampling plot itself exists rather than summed patch area reflecting patch connectivity. However, the model with the patch area of the focal unmowed meadow instead of summed unmowed meadow area within a 200m radius buffer showed higher AIC value (379.97) and the 95% confidential interval of the coefficients of patch area overlapped zero ([-0.30, 0.53]). Thus, the effect of surrounding unmowed meadow area would be related to habitat isolation rather than habitat loss.

Factors affecting the bug density in fallow plots

The mirid bug density in the fallow plots was also positively correlated to the unmowed meadow area within the 300 m-radius buffer (Table 5.2). The direction of the coefficients of the factors was maintained in the other candidate models with the 300 m-radius buffer with ΔAIC < 2. Some within-plot factors (the ear abundance of *S. juncoides*, *Agrostis gigantea*, *Echinochloa* spp., and *L. multiflorum*) also positively affected the density. The surrounding unmowed meadow area within the 400, 500, and 700 m-radius buffer also positively (the lower limit of 95% confidential interval of the coefficient > 0) correlated with the bug density.

Models with all Italian ryegrass meadow area instead of unmowed meadow area

The models concerning the bug density both in the unmowed meadow plots and the fallow plots with summed area of Italian ryegrass meadow including both mowed and unmowed showed generally poorer fitting than the models with summed unmowed meadow area (Figs. 5.1, 5.2). In particular, the most parsimonious model in the fallow plots with summed unmowed meadow area had quite lower AIC value (ΔAIC < 2) than the most parsimonious model with summed area of Italian ryegrass meadow including both mowed and unmowed (Fig. 5.2)

Among the models for the bug density in unmowed meadow plots with summed area of Italian ryegrass meadow including both mowed and unmowed as an explanatory variable, no landscape factors were selected in the best model except models with the 100 m-radius buffer, in which positive effect of summed area of Italian ryegrass meadow including both mowed and unmowed, which is moderately correlated to summed unmowed meadow area whithin 200 m buffer ($r^2 = 0.70$), was selected. The model selection for the fallow plots with summed area of Italian ryegrass meadow including both mowed and unmowed showed that the effects of the summed surrounding area of Italian ryegrass meadow including both mowed and unmowed had trends similar to that of the summed surrounding unmowed meadows (data not shown).

Discussion

Local and landscape-level effect of Italian ryegrass meadows

This study demonstrated that not only local factors (abundance of *L. multiflorum*), but also a landscape factor, i.e., the surrounding unmowed meadow area, significantly positively affects the bug density both in the unmowed meadow plots and the uncultivated fallow plots. Thus, *L. multiflorum* were suggested to significantly influence on the generalist bug density at both local and landscape levels although other grass and sedge species had also significant influences. This positive multi-level effect of unmowed meadow patches on the bug density suggests that increase of surrounding unmowed meadow area would cause non-linear increase of the bug abundance (i.e. density × area) in a focal patch and also that of the whole metapopulation.

Effective spatial scale for the performance of models on the density of the mirid bug in the meadows and fallows (200-300 m) was not so different from that for the bug abundance in organic paddy fields (300-400 m, Takada et al. in review) and the reported case of a moderately heterogeneous agricultural landscape of Arizona (Carriere et al. 2006).

Although the model for the bug density of the unmowed meadow plot with summed Italian ryegrass meadow area including both mowed and unmowd within 100m buffer also showed relatively low AIC value, it was inconsistent with models at the other spatial scale and with the result of the previous studies (Takada et al. in review; Carriere et al. 2006). In addition, summed Italian ryegrass meadow area including both mowed and unmowed within 100 m buffer was moderately correlated to summed unmowed meadow area within 200 m buffer, thus its correlation to bug density may be spurious. Therefore, unmouwed meadow area would explain the pattern more appropriately, which suggest that the effect of habitat connectivity on population dynamics may have reflected a relatively short-time phenomenon. Other studies on short-lived (more than one generation per year) animals inhabiting agricultural landscape also have reported quite a short-term (within a generation) negative effect of habitat fragmentation on a planthopper seasonally specialized to oat (Grilli and Bruno 2007) and on a harvest mice inhabit fallow patches (Kuroe et al. 2010).

Possible mechanisms of the short-term landscape-level effect

There are not a few explanations for causes of the short-time-scale (within a generation) positive effect of habitat area and/or connectivity on insect density. One possible explanation is a combination effect of resource concentration hypothesis (Root 1973; Connor et al. 2000) and decreasing mortality rate during dispersal in a metapopulation (Hanski et al. 2000; Matter et al. 2004). Phytophagous insects are likely to move from small to large habitat patches (Root 1973) at relatively small spatial scale (Haynes and Crist 2009), while increasing of dispersion in small habitat patches of fragmented landscape leads to higher mortality due to increase of time spent in unsuitable habitats (i.e. "matrix" in a metapopulation (Hanski 1999)). It has been reported that the increase of time spent in matrix cause rapidly sharp decrease of metapopulation size of a specialist leaf hopper (Cronin and Haynes 2004) in a short time. In our study area, spiders (Kobayashi et al. in submission) and frogs (Iwabuchi personal communication) in the paddy fields (i.e., matrix for *S. rubrovittatus* in the first generation) were observed to prey on the bugs. They may contribute to mortality of the bugs during dispersal to some degree.

On the other hand, enemies hypothesis (Root 1973), which suggest that generalist predators tend to be denser in smaller patches, can also predict a positive effect of habitat area on herbivores. However, vote-counting of response of arthropods to vegetation diversity revealed this hypothesis is less likely than resource concentration hypothesis, because monophagous herbivores tends to decrease more remarkably than polyphagous in the plot with high vegetation diversity, which cannot be explained by the enhanced predation of generalist predator (Andow 1991).

If dispersal of the mirid bugs is the major factor determining the emergent pattern observed in the present study, it is plausible that even generalist herbivores can be subjected to immediate regulation by spatial amount and connectivity of preferable non-native plant patches, even though they are known to be rather resistant to habitat fragmentation (Ockinger et al. 2010). This would be not unique to *S. rubrovittatus*, but be common to generalist insect herbivores, because most of them locally and/or temporarily exhibit clear preference for one or few particular host plants (Fox and Morrow 1981; Bernays and Graham 1988; Lu et al. 2010). In addition, our study suggested that such a positive emergent effect can arise at finer landscape scale (within a few ha), and these can be caused by establishment and dominance of a non-native plant even in a small part of a landscape.

Implication for pest management in invaded agricultural landscapes

We can also draw the implication for pest management from the results. Not a few studies on apparent competition (e.g. Carriere et al. 2006; Orrock et al. 2008; Branson and Sword. 2009) reported “overspill of pests” from source population in patches of alien plants to sink population in patches of natives or crops. Investigating dispersion of pests from sources to sinks should be essential for management, because damages of natives or crops *per se* occur in the sink habitats. However, in such cases, appropriate management of source population should be more effective than intensive management of sink population. If habitat area and/or connectivity among source patches matters as partly shown in the present study, fragmentation of patches of the plant species at an appropriate spatial scale and timing is expected to be effective to decrease source population of the pest, especially in the case where it is unrealistic to remove all source patches. In order to design landscape-oriented pest control, we should recognize spatial connectivity among source patches in addition to connectivity between source (non-natives) patches and sink (natives or crops) patches which the previous studies (Carriere et al. 2006; Orrock et al. 2008; Oliver et al. 2009) often focused.

Table 5.1 The best five generalized linear model explaining the density of adult *Stenotus rubrovittatus* in meadows in the model selection with 200 m-radius buffers

AIC	Selected variables	Coefficient	95% C.I.[a]
375.79	Ear abundance of *Lolium multiflorum*	0.66	[0.26, 1.0]
	Unmowed meadow area within 200 m buffer	0.43	[0.015, 0.85]
	Latitude	-0.68	[-1.1, -0.28]
377.11	Ear abundance of *Lolium multiflorum*	0.59	[0.17, 1.0]
	Unmowed meadow area within 200 m buffer	0.37	[-0.038, 0.78]
	Vegetation height	0.20	[-0.19, 0.60]
	Latitude	-0.66	[-1.1, -0.26]
377.28	Ear abundance of *Lolium multiflorum*	0.67	[0.28, 1.1]
	Unmowed meadow area within 200 m buffer	0.43	[0.022, 0.85]
	Fallow area within 200 m buffer	-0.14	[-0.51, 0.23]
	Latitude	-0.65	[-1.1, -0.25]
377.60	Ear abundance of *Lolium multiflorum*	0.63	[0.24, 1.0]
	Unmowed meadow area within 200 m buffer	0.44	[0.027, 0.86]
	Latitude	-0.69	[-1.1, -0.28]
	Longitude	-0.089	[-0.48, 0.30]
377.64	Ear abundance of *Lolium multiflorum*	0.66	[0.27, 1.1]
	Unmowed meadow area within 200 m buffer	0.43	[0.013, 0.84]
	woodland area within 200 m buffer	-0.084	[-0.48, 0.31]
	Latitude	-0.73	[-1.2, -0.29]

[a] 95% Wald Confidential Intervals

Table 5.2 The best five generalized linear model explaining the density of adult *Stenotus rubrovittatus* in fallows in the model selection with 300m-radius buffers

AIC	Selected variables	Coefficient	95% C.I.[a]
257.62	Ear abundance of *Agrostis gigantea*	0.55	[0.15, 0.95]
	Ear abundance of *Echinochloa* spp.[b]	1.3	[0.87, 1.7]
	Ear abundance of *Lolium multiflorum*	0.60	[0.20, 0.99]
	Ear abundance of *Schoenoplectus juncoides*	0.57	[0.17, 0.98]
	Unmowed meadow area within 300 m buffer	0.77	[0.31, 1.2]
	Longitude	-0.67	[-1.2, -0.10]
258.79	Ear abundance of *Agrostis gigantea*	0.54	[0.15, 0.94]
	Ear abundance of *Echinochloa* spp.	1.3	[0.89, 1.7]]
	Ear abundance of *Lolium multiflorum*	0.47	[0.064, 0.88]
	Ear abundance of *Schoenoplectus juncoides*	0.60	[0.19, 1.0]
	Unmowed meadow area within 300 m buffer	0.72	[0.25, 1.2]
	Latitude	-0.29	[-0.91, 0.33]
	Longitude	-0.84	[-1.5, -0.15]
259.09	Ear abundance of *Agrostis gigantea*	0.59	[0.19, 0.99]
	Ear abundance of *Echinochloa* spp.	1.3	[0.85, 1.7]
	Ear abundance of *Lolium multiflorum*	0.59	[0.20, 0.99]
	Ear abundance of *Schoenoplectus juncoides*	0.58	[0.17, 0.98]
	Unmowed meadow area within 300 m buffer	0.74	[0.28, 1.2]
	Vegetation height	0.20	[-0.27, 0.67]
	Longitude	-0.69	[-1.3, -0.11]
259.12	Ear abundance of *Agrostis gigantea*	0.58	[0.15, 1.0]
	Ear abundance of *Carex neurocarpa*	-0.26	[-1.1, 0.60]
	Ear abundance of *Echinochloa* spp.	1.4	[0.96, 1.8]
	Ear abundance of *Lolium multiflorum*	0.60	[0.20, 0.99]
	Ear abundance of *Schoenoplectus juncoides*	0.56	[0.15, 0.97]
	Unmowed meadow area within 300 m buffer	0.77	[0.31, 1.2]
	Longitude	-0.65	[-1.2, -0.071]
259.36	Ear abundance of *Agrostis gigantea*	0.53	[0.12, 0.93]
	Ear abundance of *Echinochloa* spp.	1.2	[0.79, 1.6]
	Ear abundance of *Schoenoplectus juncoides*	0.59	[0.18, 1.0]
	Unmowed meadow area within 300 m buffer	0.59	[0.13, 1.0]
	Latitude	-0.57	[-1.2, 0.033]
	Longitude	-1.1	[-1.8, -0.40]

[a] 95% Wald Confidential Intervals

[b] *Echinochloa crus-galli* (L.) P. Beauv. (Poaceae) and *Echinochloa oryzicola* (Vasing.) Vasing. (Poaceae)

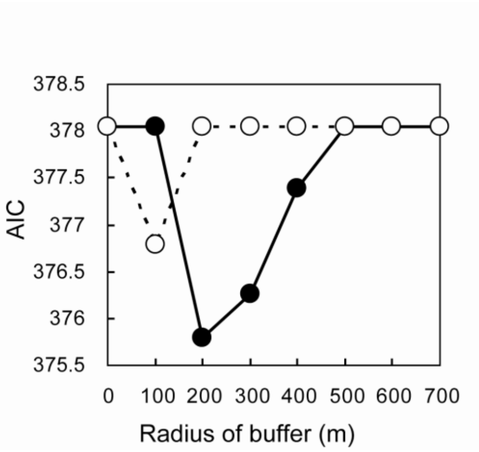


Fig. 5.1 The minimum AIC values of the models explaining density of *Stenotus rubrovittatus* at unmowed plots in each radius of buffer: the values of models including unmowed meadow area as one of the candidate independent variables are shown by filled circles, while those of models including all Italian ryegrass meadow area, instead of unmowed meadow area, as one of the candidate explanatory variables are shown by open circles

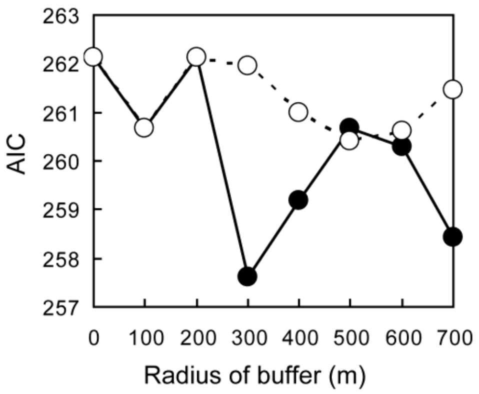
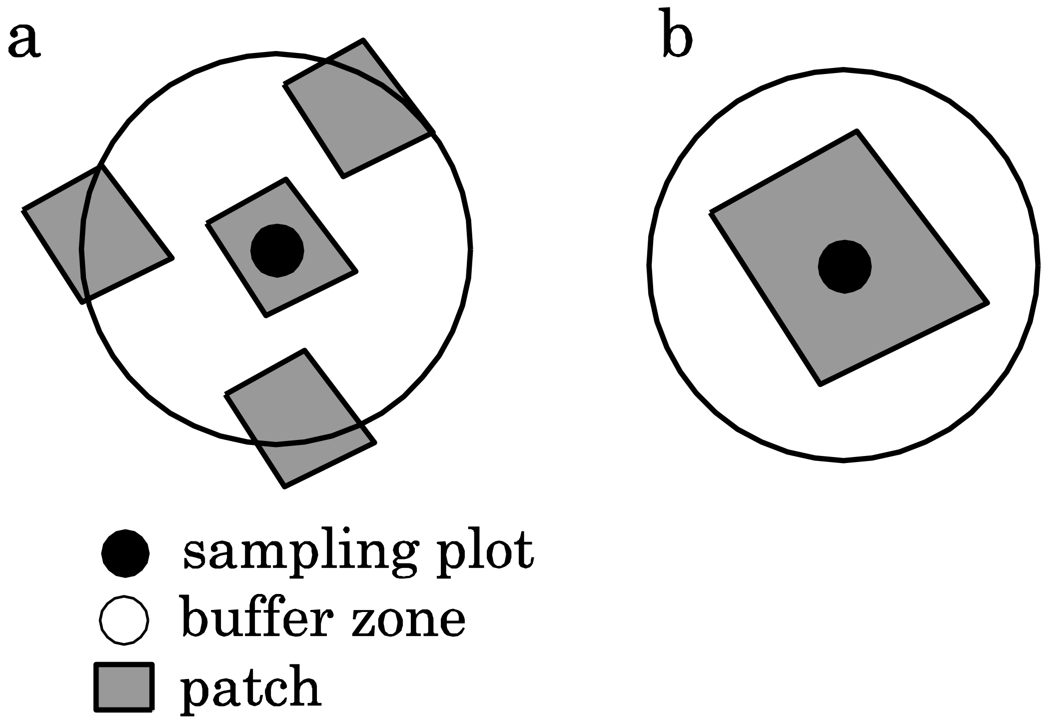


Fig. 5.2 The minimum AIC values of the models explaining density of *Stenotus rubrovittatus* at fallow plots in each radius of buffer: the values of models including unmowed meadow area as one of the candidate independent variables are shown by filled circles, while those of models including all Italian ryegrass meadow area, instead of unmowed meadow area, as one of the candidate explanatory variables are shown by open circles



Appendix 5.1 Area of the meadows (or fallows) in a buffer zone can reflect both connectivity between a sampling plot and surrounding patches (a) and area of a patch where a sampling plot exists (b).

Chapter 6 Conclusion

The results of my investigation compiled into the present thesis demonstrated that habitat modification by invasion of non-native plant species can substantially affect communities and populations of native generalist insect herbivores.

In the Chapter 2 & 3, the hypothesis that habitat modification by alien plants can negatively affects habitat specialist herbivores was supported. In the community of grasshoppers in a gravelly floodplain, disproportionately negative responses to coverage of weeping lovegrass were observed for the species with stricter habitat requirement (Chapter 2, see also Yoshioka et al. 2010a). Physical structure of dense tussock of weeping lovegrass was demonstrated to be avoided by habitat specialist, *Eusphingonotus japonicus*, whether its native food resources have remained or not (Chapter 3, see also Yoshioka et al. 2010b).

In the Chapter 4 & 5, the hypothesis that spatial structure of non-native plant patch can affect dynamics of population of generalist herbivores was supported. Italian ryegrass was confirmed to be the most preferable host for a generalist mirid bug *Stenotus rubrovittatus* in the agricultural landscape (Chapter 4) and not only its local abundance, but also its spatial amount and connectivity were suggested to positively affect the population density of the mirid bug (Chapter 5).

These novel findings about interactions between native insect herbivores and non-native plants may provide two important perspectives which are likely to contribute to predicting impacts of invasive alien species.

Perspectives suggested

First, it is possible that effects of habitat modification by non-native species can be more important than trophic effects (exclusion of native food resource) for spatial distribution of habitat specialists, especially in habitats maintained by frequent disturbances. Although ecosystem engineering by invasive alien species can cause critical impacts on invaded ecosystems (Matsuzaki et al. 2009), trophic and non-trophic effects of plant invasion have been insufficiently separated in the previous studies.

In the thesis, however, I suggested the possibility that habitat modification of weeping lovegrass causes negative impacts on spatial distribution of individual habitat specialist grasshoppers much more rapid than competitive exclusion of native plants, which generally takes a time longer than their generation times (Sax et al. 2007). This effect may be caused by behavioral avoidance of invaded patches and therefore non-lethal at the individual level, but will substantially affect population size of the insect herbivore through decrease of available habitat area. If the invaded habitat type is originally more frequently disturbed, hence more invasible, the impacts of invasive alien plant on habitat specialists will become more remarkable. These characteristic of habitat modification effects by non-native plant should be incorporated in the prediction of impacts of invasive alien species and determination of conservation priority.

Second, landscape-level perspective should also matter if the non-native plant facilitates populations of a particular native generalist insect herbivore. The majority of previous studies focused on negative impacts of invasive alien plants on biodiversity only within patches of the aliens because plants are basically sessile. However, several studies suggested that non-native plants facilitate food generalist insect herbivores, leading to indirect negative effects on allopatric native or crop plants (Branson and Sword 2009; Malmstrom et al. 2005; Orrock et al. 2008). In the present thesis (Chapter 4, 5), we suggested that even patches of non-native plants themselves can interact with each other and cause non-linear effects on population size of a particular food generalist insect herbivore. These results suggest that focusing solely local-level effects of non-native plants can overlook outbreak of a particular food generalist.

The results also suggest effective tactics which can be applicable to conservation and restoration. Metapopulation approaches i.e., distinguishing between source populations and sink populatins and/or fragmenting populations of non-native species or pests facilitated by them can also be useful for efficiently controlling outbreak of pests, even though they are generalists (Chapter 4, 5).

Applications of spatially-explicit metapopulation theory have been oriented to conservation of endangered species (Harrison 1991), though its spatially-implicit origin (Levins 1969) was assumed to be applied to pest management. The theory should be applied more to inhibit self-propagating threats to biodiversity such as invasive alien species and facilitated pests (Note that outbreak of pest can indirectly threat biodiversity and ecosystem services through intensified usage of insecticides).

Problems left to be explored

Further empirical studies should be done in order to examine whether the suggestions from my study have validity and generality, because we investigated only two systems for a limited time. These two study systems showed negative and positive effects of non-native plants to food generalist insect herbivores, respectively. At this time, however, we have poorly understood whether generalist insect herbivores which specify to neither food nor habitat (e.g. *S. rubrovittatus*) are likely to be facilitated by non-native plant or not. Parker and Hay (2005) suggested that native generalist herbivores can prefer non-native plants because non-natives have not evolved a particular resistance to them. On the other hand, Tallamy et al. (2010) suggested that non-natives are unlikely to facilitate generalist herbivores than natives because generalists often locally adapted to particular plant species. Harvey et al. (2010) mentioned that the effect of an evolutionary "lottery" (i.e., stochasticity) will determine whether native generalists can use invasive alien plants.

Nevertheless, further studies on ecological or physiological traits of insects and plants would make response of generalist herbivores more predictable. In addition, interactions with the other drivers such as climate change (Walther et al. 2009; Bradley et al. 2010) and other invasive alien species (Simberloff & Von Holle 1999; Kawakami et al. 2009; Chiba 2010) should not be overlooked in the prediction of actual outcome.

Furthermore, studies considering a longer time scale might predict another scenario driven by non-native plants. For insects with short generation time, possibility of rapid evolution (Yoshida et al. 2003) should be considered. Recent studies showed that some native insect herbivore became adapted to non-native plant and even speciated at ecological time scales (Strauss et al. 2006; Vellend et al. 2007). Studies with an evolutionary ecological viewpoint would be needed for predicting medium to long-term change brought by non-native plants. For instance, concept of niche conservatism: the retention of niche-related ecological traits over time (*sensu* Wiens et al. 2010), may contribute to predicting not only whether a food specialist will adapt to invasive alien plant, but also whether food generalist preadapting to non-native plants will specialized to the species. Examining the relationship between phylogeny of herbivores and their response to a non-native plant may be a first step for such studies. Note that the phylogenetic approach is beyond our study purpose and difficult to deal with in our study systems, because the approach needs well-established phylogenetic trees or replications of genera or families. Regrettably, the grasshopper community in our study system can not meet the requirement.

Nevertheless, it is undoubtable that plant invasion with habitat modification can change species composition of insect herbivores quite rapidly through behavioral responses. Testing applicability of these perspectives obtained in the thesis to solve the problems of non-native species in the changing world would make a certain contribution not only to conservation and restoration, but also to develop novel or more general ecological knowledge.

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