



Original article

Non-native grass invasion associated with increases in insect diversity in temperate forest understory



Judith L. Metcalf*, Sarah M. Emery

Department of Biology, University of Louisville, Louisville, KY 40292, USA

ARTICLE INFO

Article history:

Received 1 March 2015

Received in revised form

21 August 2015

Accepted 22 September 2015

Available online 8 October 2015

Keywords:

Arthropods

NMS

Ordination

Japanese Stiltgrass

Non-native plants

Trophic structure

ABSTRACT

Invasive plants can alter the structure and function of plant communities to such a degree that they can also have significant impacts on the insect communities. Because insects play an important role in many ecosystems, changes in these communities could have important implications, beyond their biodiversity value, for ecosystem function and diversity at other trophic levels. *Microstegium vimineum* is an annual C₄ grass that is invasive in many eastern North American deciduous forests. Because this grass plays an important role in determining the plant community structure in the understory of these forests, it also has the potential to significantly alter understory insect communities. In this study we evaluated the relationship between *M. vimineum* and understory insect communities in a forest reserve in Kentucky, USA. Total insect abundance, richness and diversity showed a positive association with *M. vimineum* presence. Trophic analysis showed significantly higher abundances of herbivores where *M. vimineum* was present. Forb abundance, which serves as the primary food source for herbivorous insects in this system, was lower in sites invaded with *M. vimineum*. Invasion by this non-native was also associated with significant increases in aboveground plant biomass which was nearly 50% greater in invaded sites. These results indicate that the understory insect community may be responding to increased biomass rather than the loss of native forb food resources, which contradicts other studies that have examined relationships between *M. vimineum* invasion and insects. Our results provide evidence that invasive plants can provide benefits for other trophic levels, even when native plant biodiversity is lost.

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1. Introduction

Invasive plant species are considered a major threat to biodiversity and ecosystems worldwide (Mack et al., 2000; Vila et al., 2011). These invasive non-native plants have the potential to alter regional biota, and have been widely shown to impact plant community composition and native plant species abundance (Adams and Engelhardt, 2009; Van Hengstum et al., 2014). Invasive plants can alter the structure and function of plant communities to such a degree that they can also have significant impacts on the insect communities that depend on native vegetation for habitat and food (Adams and Engelhardt, 2009; Litt et al., 2014; Mack and D'Antonio, 2003; Tang et al., 2012; Van Hengstum et al., 2014). The typical reduction in native plant biomass that accompanies invasion often results in a reduction in the abundance and biomass of primary consumers, and consequently their predators, as invasive plants

outcompete native plants (Carpenter and Cappuccino, 2005; Tallamy, 2004; Van Hengstum et al., 2014). For example, Heleno et al. (2008) found a negative relationship between invasive plant cover and total species richness of both plants and insects on Sao Miguel island, part of the Azores archipelago. A number of other studies have also demonstrated a decrease in insect total abundance, species richness and diversity, and trophic and guild structure, particularly for herbivorous insects, in relationship to invasion by non-native plants (Mgobozi et al., 2008; Simao et al., 2010; Wu et al., 2009; Yoshioka et al., 2010).

However, there is often an associated increase in overall productivity that accompanies plant invasion that can have positive effects on certain insects as a result of increased cover, expansion of niche diversity, and micro-climate alterations at ground level (Cebrian et al., 2009; Gratton and Denno, 2003; Siemann, 1998; Strauss, 1987). For example, Emery and Doran (2013) found significant increases in herbivore and pollinator abundances associated with *Gypsophila paniculata* invasion on sand dunes, possibly due to shifts in plant community architecture and floral resources.

* Corresponding author. 352 Spring Street, Ashland, KY 41101, USA.
E-mail address: metcalfjudy@gmail.com (J.L. Metcalf).

Others have found increases in insect communities at multiple trophic levels (Lambrinos, 2000; Mayer et al., 2005; Samways and Moore, 1991; Topp et al., 2008) and in a variety of invaded habitats. Wimp et al. (2010) demonstrated that increases in plant productivity associated with invasion, decoupled from changes in plant community composition, were associated with increased insect species richness at all trophic levels, as well as increased overall diversity of rare species in salt marshes invaded by monoculture stands of *Spartina alterniflora*. It is likely that the various insect groups being studied, as well as the level of invasion and the identity of invading plants being studied contribute to these differences (Simao et al., 2010; Van Hengstum et al., 2014).

In this study, we evaluated the associations between understory insect communities and the invasive grass *Microstegium vimineum* (Trin.) A. Camus. This annual C₄ grass (Poaceae), also known as Japanese Stiltgrass, was accidentally introduced to the U.S. in the early 1900s as packing material (Barden, 1987; Fairbrothers and Gray, 1972), and is a prevalent forest invader throughout the eastern U.S., including in several designated natural areas (Mortensen et al., 2009). It is considered a species of concern due to its ability to thrive in the understories of deciduous forests, often outcompeting native forbs and grasses (Adams and Engelhardt, 2009; Civitello et al., 2008; Flory and Clay, 2009; Flory, 2010; Oswalt et al., 2007; USDA, 2008). *M. vimineum* is an early spring germinating annual that reaches peak biomass in late summer, produces a high volume of seed in early fall and leaves behind a dense mat of litter (Barden, 1987; Hunt and Zaremba, 1992; Redman, 1995). *M. vimineum* has been shown to significantly impact plant community composition, reducing native plant diversity and biomass which could have serious effects on understory insect community structure (Adams and Engelhardt, 2009; Barden, 1987; Civitello et al., 2008; Flory and Clay, 2009; Simao et al., 2010).

The goal of this study was to evaluate the response of the understory insect community to invasion by *M. vimineum* in a deciduous forest reserve in eastern North America. In particular, we ask: (1) Is invasion by *M. vimineum* associated with changes in plant community structure and available biomass? (2) Do sites invaded by *M. vimineum* differ from uninvaded sites in terms of understory insect abundance, biomass and diversity? (3) Do understory insect trophic level and functional group abundance and diversity (predator, parasite, parasitoid, concealed chewer, free-living chewer, free-living sap feeder, pollinator, scavenger/shredder) differ between sites invaded by *M. vimineum* and uninvaded sites?

2. Methods

We conducted this study at the University of Louisville Horner Wildlife Research Forest in Brownsboro, Kentucky, U.S.A. (38:20:27°N, 85:31:53.7°W). This is an 81 ha, second-growth, temperate, deciduous forest with an upland area devoid of any natural permanent water source, and a lowland area bordering a small creek. In May 2010, we established 24 25 m transects, 12 in upland habitats and 12 in lowland habitats. Using a visual estimate of percent cover within each habitat, we located six transects in 'invaded' sites (averaging ~48% *M. vimineum*) and 6 in 'uninvaded' sites (averaging ~4% *M. vimineum*).

2.1. Insect sampling

We collected understory insect samples once per month during two growing seasons (May–October 2010, 2011) using dry pitfall traps and sweep nets. Pitfall trap transects were 20 m in length, with one pitfall trap placed every 5 m along the length of each transect, for a total of 4 pitfall traps per transect. Traps were made using 10.16 cm diameter PVC pipe cut to 10.16 cm long and placed

flush into pre-dug holes in the soil. Traps were set by placing empty 0.24 L plastic cups into the PVC. Pitfall traps did not include any kill liquid to avoid damage to native vertebrates. While some insects may have escaped or been eaten in dry pitfall traps, this method still provides adequate representation of many ground-dwelling invertebrate species (Weeks and McIntyre, 1997). After 48 h, we removed the cups from the PVC, pooled samples, and emptied them into zip-top bags for transport back to the lab. We took two 1 m wide sweep net samples (15 sweeps per transect) through the understory vegetation (approximately 1 m aboveground surface) along each transect, pooled these samples, transferred to zip-top bags, and returned to the lab. We stored all samples at –10 °C until processing. While sweep nets and pitfall traps cannot fully sample the entire insect community in forests (e.g., tree dwellers), they are useful for sampling the groups most likely to be affected by an invasive herbaceous understory species such as *M. vimineum* (e.g., Simao et al., 2010), and represent two common methods for evaluating insect community responses to invasive plants (Van Hengstum et al., 2014).

We identified individual insects to the family level using Johnson and Triplehorn (2005), and assigned them to a trophic group (carnivore, herbivore, omnivore and detritivore) and guild (parasite, parasitoid, predator, concealed chewer, free-living chewer, free-living sap feeder, pollinator, scavenger/shredder) using feeding information found in Marshall (2009) and Gratton and Denno (2005). Samples were then sorted by sampling method, family, site and date, and placed in a drying oven (40 °C) for 48 h and weighed.

2.2. Vegetation and environmental sampling

We collected above-ground standing-crop biomass and litter biomass using two 0.25 m × 0.25 m quadrats, randomly placed along each transect, while ensuring that no location was sampled twice, each month. We clipped live biomass at ground level; litter included tree leaf litter and other non-living plant material rooted or lying on the ground, but excluded woody debris. We separated live *M. vimineum* and litter material from all other plant material, oven dried at 40 °C for 48 h, and weighed.

We established two 'permanent' community plots (1 m²) along each transect (one at each end, on alternating sides) to visually estimate percent cover of *M. vimineum*, forbs, non-*M. vimineum* grasses, sedges, tree seedlings and bare ground for each transect. In 2011, we collected additional data in these community plots on canopy cover (using a Spherical Crown Densimeter), and plant height (measured as the average plant height from five locations in each plot using a standard meter stick).

2.3. Data analysis

We conducted a mixed general linear model with invasion status as a fixed factor, habitat (upland vs lowland) as a random factor, and year and season as covariates on data from the 24 transects to evaluate associations between *M. vimineum* invasion and 1) plant community structure and biomass, 2) insect abundance, biomass, family-level richness, and Shannon diversity and evenness based on abundance values (Shannon, 1948), and 3) individual insect trophic group abundance and biomass after controlling for edaphic and climatic variability. Significant differences in trophic levels were further analysed at the functional guild level. All GLM analyses were completed using *Systat v. 13* (2009).

We used multi-response permutation procedures (MRPP) with a Euclidean distance measure (Zimmerman et al., 1985) to compare insect community composition between invaded and uninvaded sites. MRPP is similar to multivariate analysis of variance

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