The battle for suburbia: Japanese stilt-grass vs. garlic mustard – and deer

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Abstract

Background/Questions/Methods

Fragmented, suburban forests are essential for biodiversity and ecosystem services, and they offer many human communities a connection to nature. However, these forests are challenged by the dual problem of overabundant deer and invasion by multiple, potentially interacting non-native plant species. Two dominant herb layer invaders in eastern forests are garlic mustard (*Alliaria petiolata*) and Japanese stilt-grass (*Microstegium vimineum*). We have established a well-replicated factorial field experiment with all combinations of staged, novel invasions of one, both, or neither species, and exclusion or presence of deer (with fences), across six suburban New Jersey forests (224 4x4 m plots). These forests differ in ambient deer pressure, but all are in an area with about 30 deer/km2. We have measured invasion success as percent cover since the seed additions in November 2012, in order to test whether these species invade as 'passengers' on the ecosystem change caused by overabundant deer, and to determine if they facilitate each other's invasion, setting the stage for a possible 'invasional meltdown' scenario.

Results/Conclusions

Initial recruitment of the two species among and within forests was highly variable. We added equal numbers of seeds to each addition plot, but recruitment of garlic mustard in the first summer ranged from 0-188 plants per plot, and 13-605 for Japanese stilt-grass; it clearly dominated the initial invasion phase. Fewer garlic mustard plants recruited in forests with more leaf litter, which explained 68% of the variation, but it did not explain stilt-grass recruitment. By the Spring 2015 census, stilt-grass percent cover averaged 4% in the three forests with lower deer pressure (measured as percent foliage cover in the shrub layer) and 12% in those with higher deer pressure. Garlic mustard cover in Spring 2015 averaged only about 1.4% and 0.6% in the forests with lower and higher deer pressure, respectively. Greater soil water potential predicted greater cover, particularly for stilt-grass, but only in the forests with higher deer pressure. Canopy gap fraction was higher in forests with lower deer pressure, but had little influence on cover. The only detectable effect on each other's cover was that in the plots where garlic mustard also was added, stilt-grass cover was less when protected from deer. These relatively early-stage results lend support to the hypothesis, for stilt-grass only, that invasion of suburban forests follows a passenger model of ecosystem change. It also points to a hierarchical model of competition between co-occurring invasive species, rather than facilitation.

Introduction

- Suburban forests are important as a main reservoir for biodiversity, and because they provide access to nature for many people in densely populated regions.
- These forests are under pressure from overabundant deer and multiple invasive species. Their ecological interactions in suburban forests are not well understood, but may be key **drivers** of plant community structure.
- We are experimentally investigating the recruitment and invasive success of two non-native, herbaceous plants, *Microstegium vimineum* (Japanese stilt-grass) and *Alliaria petiolata* (garlic mustard), under varying ambient deer pressure, in/out of deer fences, with/without each other, and in response to a range of environmental factors.
- Garlic mustard is a dominant species in the herb layer in the spring and early summer, while Japanese stilt-grass (a C_4 species) is more dominant in late summer and fall. This temporal separation may allow them to avoid intensive competition with each other, while benefiting each other by suppressing native species. This could lead to an **invasional meltdown**, in which multiple invasive species facilitate each other's invasion and effects.
- Overabundant deer leave the shrub and herb layer barren, which may open niche space for non-native species like garlic mustard and Japanese stilt grass to invade as **passengers** on such an ecosystem change. However, it also is possible that deer could consume invasive plants or trample them, ultimately slowing their invasion.

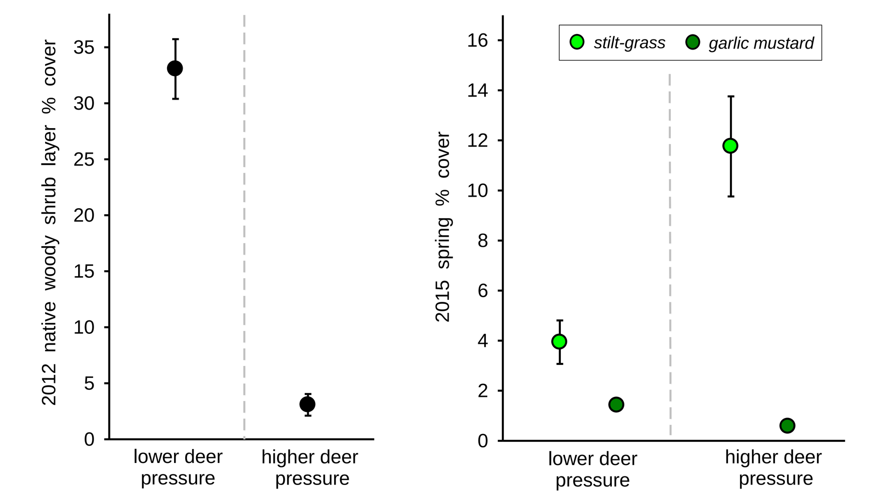
Methods

- Factorial experiment, replicated in six suburban forests in central New Jersey, a region with ~ 30 deer/km², but three forests have lower deer pressure and three have higher deer pressure.
- Forty 16m² plots in each forest (a few lost to Hurricane Sandy), with 5 reps of 8 treatment combinations: equal invasive seed addition (stilt-grass, garlic mustard, both, neither; added late fall 2012) X deer fence (yes/no; installed early spring 2013).
- Deer pressure measured by percent native woody foliage in shrub layer at each plot, with 'forest secchi' method, by sighting on a 1 m² board with 16 squares and counting the number intercepted by foliage.
- Every spring and fall since 2013: percent cover of all species in the herb layer, estimated from 16 0.25m² quadrats per plot.
- Throughout the course of the experiment: measurements of many other biotic and abiotic variables, including
  - soil water potential (fall 2014), averaged two samples/plot, measured in a bench-top water potential meter (WP4, Decagon Devices).
  - canopy gap fraction (summer 2015), digitized with ImageJ from high quality, fish-eye lens photos taken with iPhone 5 and iPodTouch 5.

Results

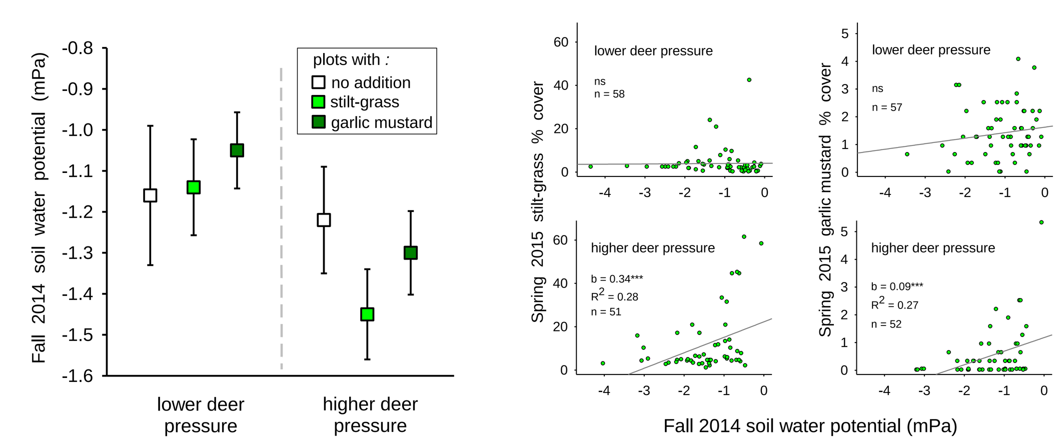
1 Initial recruitment in Spring 2013 was highly variable among forests and plots, and was overall greater for stilt-grass (13 – 605 plants / plot) than for garlic mustard (0 – 188 plants / plot).

2 Deer pressure - Three forests experience lower deer pressure and three higher deer pressure, shown by shrub cover. Stilt-grass established more in forests with higher deer pressure; garlic mustard establishment was very low and not influenced by deer pressure.
(Means ± se; number of plots from left to right: 120, 120, 59, 58 , 53, 54)

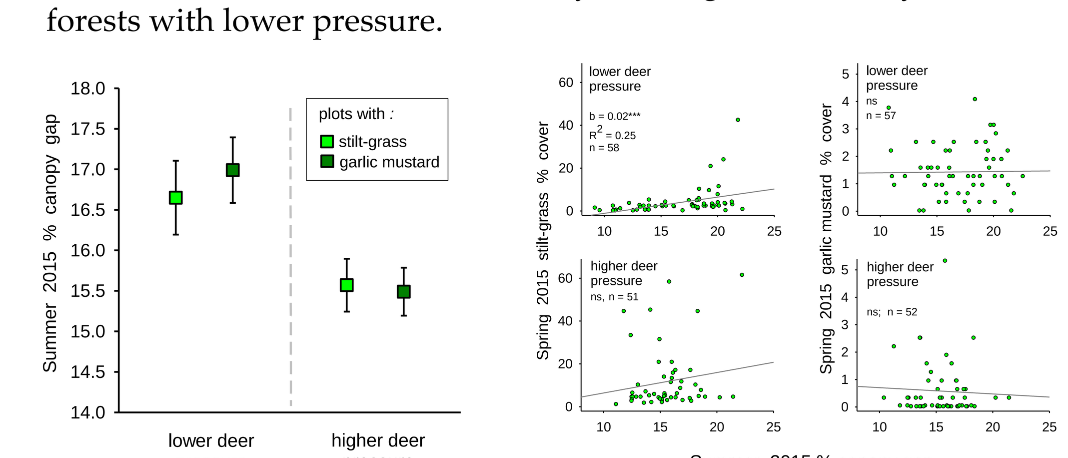


3 Environmental factors: soil water potential & canopy light

A. Soil water potential (swp) was lower in the forests with higher deer pressure, especially in the set of plots with stilt-grass addition (ANOVA, $F_{1,109}$ = 6.59, P = 0.01) and the set with garlic mustard addition (ANOVA, $F_{1,108}$ = 4.25, P = 0.04; means ± se, number of plots from left to right: 29, 59, 58, 27, 52, 53). In the forests with overall lower swp (and higher deer pressure), stilt-grass establishment increased with swp. Garlic mustard was less strongly affected by swp in those forests.



B. Canopy gap fraction was lower in the forests with higher deer pressure, in both the set of plots with stilt-grass (ANOVA, $F_{1,110}$ = 3.54, P = 0.06) and the set with garlic mustard (ANOVA, $F_{1,109}$ = 8.82, P = 0.004; means ± se, number of plots from left to right: 59, 57, 53, 54). However, canopy gap had only a weak influence on establishment, only of stilt-grass, and only in the forests with lower pressure.



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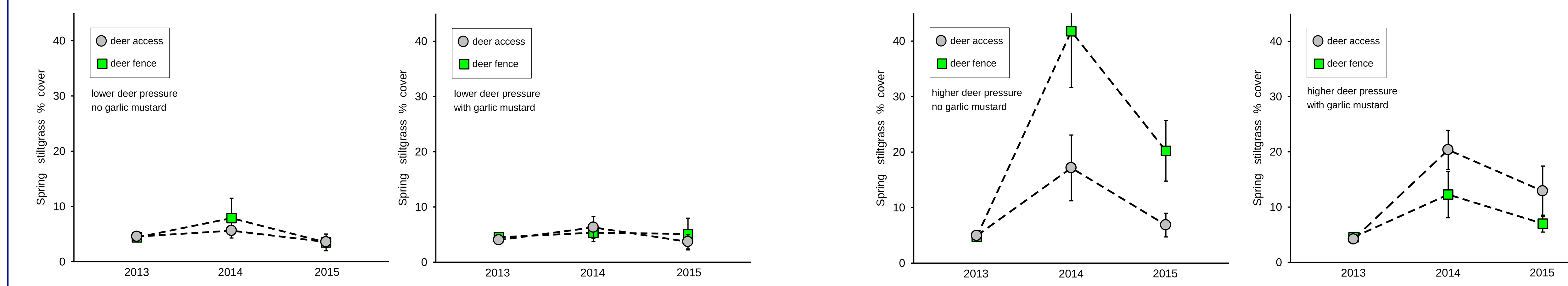
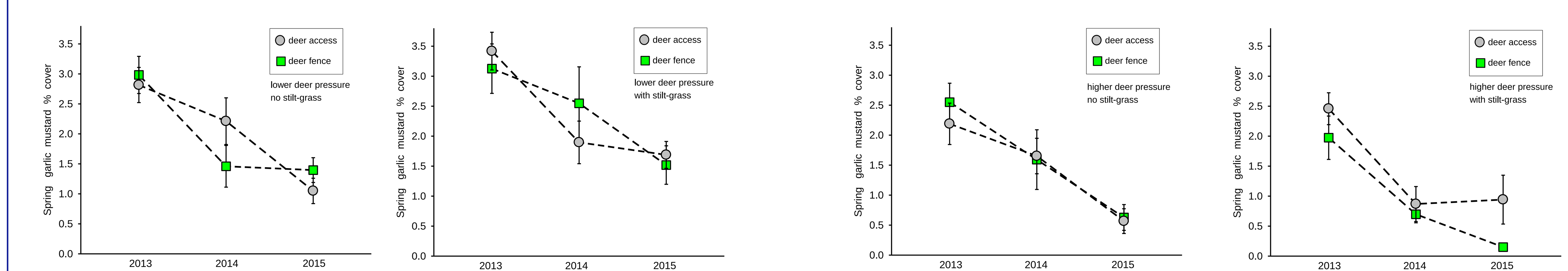
4 Deer pressure, deer exclusion, and co-invaders

The factorial treatments of deer access/exclusion and co-invader presence/absence, in the context of lower and higher ambient deer pressure, presented a complex scenario for stilt-grass and garlic mustard establishment over three years.

Stilt-grass establishment was influenced by the interaction of all three factors. In the forests with higher deer pressure only, stilt-grass established more when protected from deer when growing without garlic mustard, but in the plots where garlic mustard also was added, stilt-grass established less when protected from deer.
(2015 ANOVA, deer pressure x fencing x garlic mustard addition: $F_{1,104}$ = 5.85, P = 0.02; means ± se, n = 27 to 29)



Garlic mustard establishment was influenced consistently by deer pressure; it established especially poorly in the forests with higher deer pressure. Also, its establishment was influenced by the interaction of fencing and stilt-grass addition; fencing increased its establishment somewhat in the absence of stilt-grass, but in the presence of stilt-grass, fenced garlic mustard established less. (2015 ANOVA, deer pressure $F_{1,105}$ = 36.79, P < 0.0001, fencing x addition $F_{1,105}$ = 4.38, P = 0.04; means ± se, n = 27 to 29)



Discussion

Ecological interactions between overabundant deer and multiple invasive plants species could be the key factors structuring plant communities in '21st century' forests – those in the urbanizing landscape. A manipulative, experimental approach with well-replicated, novel, staged invasions offers a powerful way to investigate the interacting roles of deer and invasive plants without the constraint of invasion history, and in the context of different ambient deer pressures.

Our experiment has, so far, indicated a strong asymmetry between the two invasive species we are studying. Japanese stilt-grass established at a much greater rate in our suburban forests than did garlic mustard, even though both are vigorous, known invaders of the herb layer in fragmented, deciduous woodlands. It does not appear that their interactions will lead to any sort of invasional meltdown. Rather, stilt-grass is likely to be the sole dominant species in the herb layer, leaving the plant community relatively free of direct competition from the garlic mustard – stilt-grass duo in early spring.

Deer pressure is providing an ecosystem change that appeared to promote stilt-grass, supporting the 'passenger model' of invasion. The greater success of stilt-grass in forests with higher deer pressure is likely due to more available niche space caused by overbrowsing of the native plant community. In contrast, garlic mustard was about twice as successful in the forests with lower deer pressure, but the invasion was so low in all the forests that it is unlikely to have any ecological importance, if the trend continues.

Curiously, the stilt-grass plots in the forests with higher deer pressure also had lower soil water potential (swp) and less canopy gap openings than in the forests with lower deer pressure, which should make them less hospitable for stilt-grass. Although it may be that stilt-grass invasion has *caused* the lower swp, the fact that stilt-grass is more successful under higher deer pressure in spite of lower swp and light suggests a very strong role for deer.

It should follow that when the plant community is protected from deer (inside the fences), in the forests with higher deer pressure, stilt-grass would fare less well as the plant community recovers and niche space is filled. Indeed, we observed lower average stilt-grass cover inside fences – but only in the set of plots that also had garlic mustard added. In the stilt-grass-only plots, it actually fared *better* when fenced. This interactive effect can not be due to any competitive effect from garlic mustard, since its lowest cover was in the fenced plots within the higher-deer-pressure forests. These intriguing results require further study.