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Diversity declines in Microstegium vimineum (Japanese stiltgrass) patches

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ABSTRACT

The spread of invasive plant species and their impacts on plant communities have received international attention as global trade and global environmental change enhance the colonization and establishment of introduced species and threaten the integrity of native ecosystems. Because introduced species vary in their impact, studying the relationship between invasion and native communities is necessary to guide allocation of finite management resources. By studying adjacent pairs of invaded and uninvaded plots across an eastern United States forested landscape, we demonstrate Microstegium vimineum was associated with local declines in species richness and cover of native species. Negative impacts of M. vimineum on species richness did not emerge until August when M. vimineum cover and height were greatest, highlighting the value of following study subjects through the growing season. In contrast, native species cover was already lower in invaded plots early in the growing season. M. vimineum invasion was not the only important driver of species richness and community composition within the study region; abiotic environmental gradients, such as soil nitrate concentration and pH, across the six study sites were also important in affecting species richness and cover, but lessened in explanatory power through the growing season. We conclude that M. vimineum has effects on community structure that may have long-term consequences for biodiversity. Studies which track sites through time and consider multiple scales are required as invaders impact multiple biotic and abiotic factors operating at different spatial and temporal scales.

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1. Introduction

Invasive plants are considered a global threat to ecosystems. They have been charged with homogenizing regional biotas (McKinney, 2004) and causing local declines of native species (Lodge et al., 2000; Mack et al., 2000). However, studies that seek to assess the impact of invasive plants on native ecosystems are usually conducted at fine spatial scales and not designed to separate the local effects of an invasive species from the effects of regional variation in environmental factors on plant communities (e.g., Dickens et al., 2005; Yurkonis et al., 2005; Gerber et al., 2008). This is despite evidence that plant biodiversity patterns reflect abiotic gradients, such as nutrient availability, even in highly invaded systems (Corney et al., 2004; Erskine Ogden and Rejmanek, 2005).

Making management decisions regarding invasive species involves predicting the outcome of taking no action, and weighing that against various control options. As such, research that elucidates the impacts of taking no action is crucial. One way to gauge the impact of an invasive species is to test if it is impacting the biodiversity of recipient plant communities, as is generally assumed but not necessarily always the case. For example, if an invading species uses resources in different ways than resident species, then the invading species may have little impact on the native vegetation (Levine and D'Antonio, 1999). In contrast, if an invader changes the disturbance regime or resource supply rates, large and sometimes cascading impacts may be expected (D'Antonio and Vitousek, 1992; Jäger et al., 2007).

Despite growing concern about the impact of invasive species, biogeography and environmental heterogeneity can swamp the effects of local interspecific interactions between an invading species and the resident community (Huston, 1999). Thus, multiple spatial scales need to be studied to reliably discern the relative importance of invasion on diversity (Pauchard and Shea, 2006). Likewise, the factors that make a community susceptible to invasion, and the factors that make a species invasive can both vary over time (Davis et al., 2000). Accordingly, it is possible that the impact of invasion varies not just spatially, but also temporally (Clarke et al., 2005; Bjerknes et al., 2007). Thus, the impact of an invading species needs to be studied across sites and through time, otherwise it is possible to miss the patterns entirely.

Just as methodology must reflect the fact that many herbaceous species have a brief window of maximum production, it must also take into account the constraints inherent in studying invasive species. While experimental methods are necessary to definitively





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determine patterns and mechanisms, an experimental approach using invasive species has limitations. Greenhouse studies are often criticized for being too artificial, however adding an invasive species to an uninvaded area raises ethical issues. Removal studies rely on an untested assumption that removing a plant will delete its impact, but we know that many invaders have legacies such as altered soil nutrient cycling (Valtonen et al., 2006). Oldfield studies that monitor vegetation over many decades spanning the invasion of multiple species have been used to shed light on the impact of invasion (e.g., Meiners et al., 2001, 2004). However, long-term studies are uncommon (Puth and Post, 2005), and the immediacy of invasion sometimes necessitates shorter-term studies to provide guidelines to management.

Carefully designed observational studies can make an important contribution to our understanding of the impact of invasion and the mechanisms underlying successful invasions. Here we describe a study of invaded sites across a fragmented forested landscape, with paired invaded and uninvaded plots immediately adjacent to one another at each study site. Uninvaded areas are frequently used as control plots (Kotanen, 1997; Alvarez and Cushman, 2002; Ortega and Pearson, 2005); however, paired plots that are immediately adjacent to each other located at multiple sites separated by several kilometers is an uncommon but advantageous design (Chabrerie et al., 2008). With such a design both local and regional scales can be observed. An invasive species with a patchy distribution is ideal as it allows for observation of uninvaded plots located very close to invaded plots, minimizing covarying environmental variables that could confound the study.

We studied the impact of Microstegium vimineum (Japanese stiltgrass) on native vegetation in the Chesapeake and Ohio Canal National Historical Park, located adjacent to the Potomac River in Maryland, USA. M. vimineum is a grass native to Asia that was introduced into Tennessee by 1919 (Fairbrothers and Gray, 1972). Since that time it has spread through the eastern United States. It is a shade tolerant forest herb that thrives in disturbed locations (Winter et al., 1982; Barden, 1987; Horton and Neufeld, 1998). M. vimineum appears to elevate soil nitrification rates and pH levels and is associated with different soil microbiota than adjacent natives (Ehrenfeld et al., 2001; Kourtev et al., 2002). Overland flow, deer, and humans spread the species easily, though it apparently is unpalatable to deer (Barden, 1987; Mehrhoff, 2000). It exhibits phenotypic plasticity (Claridge and Franklin, 2003; Cole and Weltzin, 2004), apparently able to compensate for suboptimal levels of one resource when there was a sufficient supply of some other resource. *M. vimineum* does not appear to exhibit allelopathy (Barden, 1987; Cole and Weltzin, 2005). It uses the C4 photosynthetic pathway, and though it germinates in April, it reaches peak productivity in August and does not set seed until September (Barden, 1987). Despite high levels of management concern over M. vimineum, the extent to which it is associated with declines in native species is unknown.

We predicted that invaded plots would support a different plant community than uninvaded plots at a local scale and that species richness would be lower in invaded plots. We further predicted a positive correlation between native and exotic species richness at a landscape scale in keeping with existing research (e.g., Stohlgren et al., 2003). *M. vimineum* grows most rapidly in July and August, and is still small in June. We therefore predicted that a negative association between *M. vimineum* and other species at local scales would be greater in August than in June. We predicted that soil nutrients and light levels would be lower in invaded plots than uninvaded plots, reflecting the species' abilities to alter resource levels. We hypothesized that direct interactions, such as facilitation and competition, as opposed to indirect interactions such as those impacting dispersal, would explain the impact of *M. vimine*- *um* on other species, and as such predicted that the seed bank in invaded and uninvaded plots would not differ.

2. Methods

To test our predictions, we conducted a botanical survey along the Chesapeake and Ohio Canal National Historical Park (C&O), USA, in 2005. This survey allowed selection of six sites in May 2006 that supported *M. vimineum*. At each site we delineated two adjacent plots, one invaded with *M. vimineum* and one uninvaded, that appeared to be similar in environmental conditions. Aboveground vegetation was surveyed three times during the growing season. Samples from the soil seedbank were germinated in the greenhouse, and abiotic environmental variables were measured in the field in the summer of 2006.

2.1. Study sites

The six study sites are situated in C&O where it transects the Ridge and Valley physiographic province, spanning the area between Hagerstown and Cumberland in Allegany and Washington counties of Maryland, USA. The park was once a location of high levels of disturbance with the construction and operation of the canal in the 1800s. The canal ceased operations in 1924, and has been owned by the National Park Service since 1938. Most of the park is forested and recent human disturbance to the study sites is minimal. White-tailed deer were frequently noted at study sites. The climate is temperate and mesic deciduous forest is the dominant cover type. Sites are named for the nearest C&O milemarker (110, 128, 156, 162, 166, 170). C&O is a linear park, which approximately follows the north bank of the Potomac River for 297 km. Hence, as the milemarker names would indicate, sites were at least 6.4 km (4 miles) apart, and the whole study area encompassed an approximately linear stretch of 96.5 km (60 miles).

2.2. Site selection

Potential sites were identified using information from a botanical survey conducted in the summer of 2005. When potential locations were revisited in May 2006, the first site encountered that met a list of a priori criteria was selected to minimize bias in site selection. Site selection continued until six sites were identified. More than six sites would not have been logistically feasible to sample. The criteria used for selecting study sites included identifying a 6 m \times 4 m plot with at least 50% cover of *M. vimineum* ("invaded" treatment) immediately adjacent to a plot of the same size with less than 15% cover of M. vimineum ("uninvaded" treatment), as determined by visual estimation. Sites had to be free of any obvious environmental gradients that would mask or confound the relationship between M. vimineum and other species, such as fence lines or abrupt changes in forest cover. Sites had to be out of view of any trail or road, though owing to the linear nature of C&O, all sites were within 500 m of a trail. All sites were located in deciduous forest, none were placed immediately adjacent to the canal, river or other water, and all plots were on flat ground and located on substrate of alluvial origin (Southworth et al., 2001). At four sites the overstory was dominated by Acer negundo, one site was dominated by Liriodendron tulipifera (site 128), and one by Platanus occidentalis (site 162).

2.3. Field methods

At each of the six study sites, a 2 m buffer strip separated the 4×6 m invaded and uninvaded plots. Each plot was divided into a grid of 24–1 m² subplots. Two subplots within the plot were

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