

The putative niche requirements and landscape dynamics of *Microstegium vimineum*: an invasive Asian grass

Robert J. Warren II · Justin P. Wright ·
Mark A. Bradford

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Abstract The theoretical foundations of population and community ecology stress the importance of identifying crucial niche requirements and life history stages of invasive species and, in doing so, give insight into research and management. We focus on *Microstegium vimineum*, an invasive grass which is causing marked changes in the structure and function of US forests. We describe *M. vimineum*'s life history and habitat characteristics, infer its niche requirements and synthesize this information in the context of population dynamics and management. Based on the results synthesized here, *M. vimineum*'s crucial niche requirements appear to be light (reproductive output), soil moisture (reproductive output, seedling recruitment) and aboveground coverage by leaf-litter and competing species (seedling recruitment and survival). These data suggest a source-sink dynamic might allow *M. vimineum* to disperse and thrive along sunny, and sometimes wet, edge habitats and, in turn, these populations might act as source populations for adjacent shady forest habitats. By evaluating

M. vimineum in the context of its stage-specific requirements, we highlight potential weaknesses in its life history that provide strategies for effective management.

Keywords *Microstegium vimineum* · Japanese stiltgrass · Nepalese browntop · Ecological theory · Invasive species · Niche · Management · Review

Introduction

Microstegium vimineum (Trin.) A. Camus is an exotic species that is becoming a problematic invader in eastern North America (Adams and Engelhardt 2009; Baiser et al. 2008; Civitello et al. 2008; DeMeester and Richter 2009; Flory 2010; Flory and Clay 2009a; Oswalt et al. 2007). It is commonly referred to as Japanese stiltgrass or Nepalese browntop and is an annual, C₄ grass (Poaceae) native to southeastern Asia. Its introduction to the US appears inadvertent as it was used as packing material in shipments from Asia (Barden 1987; Fairbrothers and Gray 1972). It was first noted in 1919, and it has rapidly spread throughout the eastern US (Horton and Neufeld 1998; Hunt and Zaremba 1992). It is increasingly an invasive species of concern (USDA 2008) due to its ability to invade forest understories and crowd out native vegetation (Flory and Clay 2009a; Marshall et al. 2009; Oswalt et al. 2007).

R. J. Warren II (✉) · M. A. Bradford
Yale School of Forestry and Environmental Studies,
New Haven, CT 06511, USA
e-mail: hexastylis@gmail.com

J. P. Wright
Department of Biology, Duke University, Durham,
NC 27708, USA

In the eastern US, *M. vimineum* germinates in early-to-mid spring (depending on latitude) but does not reach full growth potential until mid-summer when it can reach 2 m in length and eventually produce numerous seeds in autumn (Barden 1987; Hunt and Zaremba 1992; Redman 1995). Whereas shade-tolerant invasive species are uncommon (Martin et al. 2009; Von Holle et al. 2003), invasive grasses are certainly not. What makes *M. vimineum* unique is that it is both a C₄ grass and invasive species that can persist in the understory habitat of temperate forests (Cole and Weltzin 2005; Horton and Neufeld 1998; Oswalt et al. 2007). The C₄ photosynthetic pathway employed by *M. vimineum* is generally considered an adaptation for dry environments, and is associated with noxious invaders of open habitats (D'Antonio and Vitousek 1992; Horton and Neufeld 1998; Lambers et al. 1998). Presumably then, *M. vimineum* should have poor success as an understory forest invader and be better suited for arid, sunny habitats (Oswalt et al. 2007). However, it is commonly found in moist habitats, both in riparian zones under canopies and in open areas (Barden 1987; Fairbrothers and Gray 1972).

Whereas *M. vimineum*'s distribution in shady understories may be unusual, other aspects of its life history are not atypical for invasive species. Notably, *M. vimineum* has a high degree of phenotypic plasticity, self-fertilization, an annual life history with persistent seed bank and high seed production in recalcitrant stands (Claridge and Franklin 2002; Droste et al. 2010; Gibson et al. 2002; Horton and Neufeld 1998). A simple observation of a forest understory edge or flood-scoured bottomland forest covered in hectares of *M. vimineum* suggests the species is a prolific invader; however, it is not without its limits. *Microstegium vimineum* is not always a prolific seed producer or colonizer (Cheplick 2006, 2008), and it appears to be limited by stage-specific niche requirements such as light (reproductive output), soil moisture (reproductive output, seedling recruitment) and aboveground coverage by leaf-litter and competing species (seedling recruitment and survival) (e.g., Cheplick 2010; Christen and Matlack 2009; Cole and Weltzin 2004, 2005).

Here, we illustrate the potential for integration of general ecological knowledge with research on a specific invader, *M. vimineum*, to guide research and management of invasive species. Given that

M. vimineum is rapidly expanding its distribution and causing marked changes in the structure and function of US forests, our first objective is to describe *M. vimineum*'s life history and habitat characteristics to compile the available information on the species. Second, we synthesize information on *M. vimineum*'s potential niche requirements to ask what these requirements might mean for its population dynamics, permitting us to make research and management recommendations.

Environmental niche requirements

Investigation into a species' niche requires the pairing of specific abiotic drivers with performance in different life history stages (Pulliam 2000). The mere presence of *M. vimineum* in shady environments suggests shade tolerance, but niche assessment requires information about the success of crucial life history stages, across a range of light conditions. That is, although *M. vimineum* occurs in shady environments, it remains to be determined whether the per capita growth of shade populations supports continued persistence or requires seed input from proximate populations. That is, *M. vimineum* populations in shady habitat may not be self supporting (a "sink" in metapopulation terms) so that they would disappear without immigration from sunnier "source" populations. From this perspective, we examine the *M. vimineum* literature and evaluate whether putative niche requirements are inferred from habitat proxies or direct environmental measurements.

Light

Despite its notoriety as a shade-tolerant, invasive species, the growth and reproduction of *M. vimineum* are positively correlated with canopy openness, and the species occurs less frequently and grows poorly in shade (Barden 1996; Claridge and Franklin 2002; Cole and Weltzin 2004, 2005; Eschtruth and Battles 2009; Gibson et al. 2002; Glasgow and Matlack 2007; Marshall and Buckley 2008a). This suggests that shady habitats are tolerable but may not be optimal for *M. vimineum*. Nevertheless, *M. vimineum* exhibits a great deal of phenotypic and physiological plasticity in response to light microhabitats and adjusts well to moderately shady

conditions (Droste et al. 2010; Gibson et al. 2002; Horton and Neufeld 1998; Morrison et al. 2007). Indeed, Cole and Weltzin (2005) attribute its patchy distribution in forest understories to heterogeneous light environments.

As observed in most shade-tolerant plants, *M. vimineum* allocates greater biomass to above-ground tissue in relatively shady environments and produces larger, thinner leaves (Cheplick 2005; Claridge and Franklin 2002; Winter et al. 1982). These responses are expected to maximize sunlight interception per tissue mass in shade (Evans and Poorter 2001; Reich et al. 1997). In addition, *M. vimineum* plants increase tiller production and ground coverage in shady environments (Claridge and Franklin 2002), a strategy employed by individuals in poor microhabitats to forage for better patches (Cain 1994). Despite the fact *M. vimineum* employs the C₄-photosynthetic pathway, as opposed to the vast majority of shade-tolerant, understory herbs, which employ the C₃ pathway (Neufeld and Young 2003), its photosynthetic response curves closely resemble those observed for shade-adapted, understory plants (Barden 1996). Horton and Neufeld (1998) suggest that the C₄ pathway gives *M. vimineum* a light-harvesting advantage in the understory environment by allowing rapid photosynthetic induction for light harvest during rare, punctuated periods of high-intensity sunflecks. Efficient light harvest allows for relatively greater *M. vimineum* growth rates than co-occurring C₃ plants, whose photosynthetic induction is less rapid, which may give *M. vimineum* a competitive advantage in shade (Cole and Weltzin 2005). Specifically, *M. vimineum* individuals add biomass when exposed to as little as 5% ambient light (where ‘ambient’ is defined as an exposed site, no canopy); and maximum growth occurs where light levels are above 20–25% and below 50–75% of ambient (Claridge and Franklin 2002; Horton and Neufeld 1998; Winter et al. 1982). However, Flory (2010) found no leveling off in biomass acquisition with increasing light up to 65% and Droste et al. (2010) found that maximum plant growth occurred where light was highest in greenhouse experiments.

As an annual, *M. vimineum* depends on seed production and recruitment for population persistence, and its flowering is strongly correlated with increased plant biomass (Cheplick 2005; Gibson et al. 2002). The tight correlation means that growth and

reproduction respond similarly to light (Cheplick 2010; Claridge and Franklin 2002; Horton and Neufeld 1998; Winter et al. 1982). Increased seed production has been measured across sun vs. shade habitat (Huebner 2010a; Schramm and Ehrenfeld 2010), but canopy openness is a poor niche proxy as soil moisture, temperature and leaf litter also vary with canopy heterogeneity (Albrecht and McCarthy 2009; Warren 2010), making the direct measurement of multiple environmental variables along putative resource gradients or experimental manipulations necessary for conclusive associations. The correlation between *M. vimineum* growth and increased light (Claridge and Franklin 2002; Droste et al. 2010; Flory 2010; Horton and Neufeld 1998; Winter et al. 1982) suggests that reproduction increases with solar irradiation, and Cheplick (2010) demonstrated that seed production increased with direct sunlight and not soil moisture. Individual plants can produce 100–1,000 seeds, resulting in an estimated 0.1–4 million seeds per m² (Barden 1996; Cheplick 2008; Gibson et al. 2002; Judge et al. 2005). However, flowering and seed production vary considerably, and even fail, between years and across populations (Gibson et al. 2002). *Microstegium vimineum* produces both cleistogamous (closed, self-fertilizing) and chasmogamous (open, outcrossing) flowers, and the proportion of cleistogamous seeds appear to increase with light (Cheplick 2007). Self-fertilization is a low-energy alternative to outcrossing that may give colonizers an advantage in establishing small satellite populations where resources and pollinators are limited (Campbell et al. 1983; Cheplick 2008; Price and Jain 1981). For *M. vimineum*, the option to self-fertilize could be advantageous in establishing founding populations in understory habitats where resources are patchy.

Soil properties

The impact of soil moisture on *M. vimineum* life history has received less attention, and far less empirical measurement, than the impact of light. Often, invasive grasses are colonizers of early successional habitat and exhibit associated traits, such as drought tolerance (D’Antonio and Chambers 2006), but *M. vimineum* appears somewhat dependent on relatively higher levels of soil moisture within occupied distribution ranges (Cheplick 2010; Droste

et al. 2010; Flory and Clay 2009a; Gibson et al. 2002). Indeed, *M. vimineum* occurs more often in mesic habitats (Cole and Weltzin 2004; Gibson et al. 2002; Glasgow and Matlack 2007), but, as with light, few data exist with direct measurements of soil moisture across *M. vimineum* distributions. Its abundance and flowering decrease with seasonal and annual drought (Barden 1987; Cole and Weltzin 2004; Gibson et al. 2002), and dramatically rebound with drought cessation (Barden 1987; Yurkonis and Meiners 2006). Drought treatments reduce growth in greenhouse plants (Droste et al. 2010). Predictably, *M. vimineum* does best where the levels of both light and soil moisture are highest (Cole and Weltzin 2004; Flory 2010). Furthermore, *M. vimineum* appears to be a robust invader of wetland habitats, where moisture, light and nutrients are high, and litter-layer thickness often is low (DeMeester and Richter 2009; Hogan and Walbridge 2009). In fact, Touchette and Romanello (2010) suggest *M. vimineum* has physiological adaptations—shallow roots and steady leaf water potential—that make it tolerant of flooded soils.

The increased abundance of *M. vimineum* in moist habitats may reflect increased recruitment success (Glasgow and Matlack 2007). Successful seedling recruitment depends on the ability of an individual propagule to reach a given microsite and, subsequently, survive the environmental conditions contained therein (Casper and Castelli 2007; Donovan et al. 1993; Padilla et al. 2007; Purdy et al. 2002; Schupp 1995). *Microstegium vimineum* seedling survival decreases with summer drought (Cheplick 2010) and seedlings positioned higher in leaf litter (presumably in a drier environment) experience higher mortality than those in contact with soil (Schramm and Ehrenfeld 2010). Greenhouse studies indicate that the overall germination success for *M. vimineum* can be high (80–90%) (Cheplick 2005; Cole and Weltzin 2005). Further, as an annual plant, *M. vimineum* relies on recruitment from a soil seed bank for persistence, and *M. vimineum* seeds appear to remain viable for at least three years (Barden 1987; Gibson et al. 2002; Judge 2008). The persistence of a viable seed bank gives *M. vimineum* the ability to rebound from repeated stressors such as drought or herbicide treatment that induce mortality or reproductive failure (Gibson et al. 2002; Judge 2008; Judge et al. 2005; Webster et al. 2008). While *M. vimineum* seeds can remain dormant and, in doing

so, may minimize the need for annual reproduction, successful dormancy depends on seed viability. Seed viability depends on the environmental conditions (e.g., carbon gain and physiological stress) experienced by the maternal plant (Gallagher and Fuerst 2006).

An impressive body of literature addresses the impact of *M. vimineum* on soil chemistry and nutrient cycling (see Niche Construction below); however, investigation into *M. vimineum* soil requirements is somewhat limited. The plants generally are found in acidic soils (pH 4.4–6.5) (Cole and Weltzin 2004; Gibson et al. 2002), but these soils are less acidic than where it is absent (Kourtev et al. 1998). The plants occur more often in moist, well-drained soils, but abundance declines with increased sand content (Barden 1996; Cole and Weltzin 2004; Gibson et al. 2002; Kourtev et al. 1998; Redman 1995). These factors appear secondary to soil nitrogen, however, which appears to be a critical component (along with light and soil moisture) in the *M. vimineum* life cycle (Claridge and Franklin 2002; DeMeester 2009; Kourtev et al. 1998; Redman 1995). Moreover, nutrient availability can augment reproductive output where light levels are low (Claridge and Franklin 2002). However, correlations between nitrogen availability and *M. vimineum* presence may reflect its ability to stimulate nitrification, or its inability to colonize where leaf litter is thick and recalcitrant, rather than niche requirements per se (see below).

Temperature

Very little is known about the temperature requirements for *M. vimineum*. Barden (1987) noted that a late spring frost killed up to 50% of *M. vimineum* seedlings, but Redman (1995) reported that the seed bank can withstand winter temperatures that drop to -21 to -23°C .

Dispersal

Whereas *M. vimineum* is considered an aggressive forest colonizer, little data has been collected on its dispersal mode and range, and what evidence exists is somewhat anecdotal. In fact, the most cited reference on *M. vimineum* dispersal is based entirely on speculative personal observations (Mehrhoff 2000).

This is an unreliable assessment of dispersal. For example, it is oft-speculated that *M. vimineum* seeds are dispersed in floodwaters (Eschtruth and Battles 2009; Mehrhoff 2000). However, floodwaters also scour away leaf litter and vegetation (Barden 1987), and correspond with moist environments, making the supposition that seedlings on floodplains indicate flood dispersal a potentially spurious correlation if they arrived via other means and floodplains simply represent favorable microsites. A second speculation is that *M. vimineum* seeds travel via animal fur or human clothing (Baiser et al. 2008; Mehrhoff 2000) despite the fact that trampling and selective deer browsing (Baiser et al. 2008) potentially create suitable regeneration points for the plant whether or not the disturbers carry the seeds (Cole and Weltzin 2005). As such, the mode (or modes) for *M. vimineum* seed dispersal is at this point unknown.

Contrary to the expectations for an aggressive invader, the existing empirical data for *M. vimineum* suggests it is a poor local disperser with estimated annual dispersal distances typically between 0.03 and 2 m, with a reported maximum of 10 m (Barden 1987; Christen and Matlack 2009; Gibson et al. 2002; Huebner 2010b; Oswalt and Oswalt 2007; Rauschert et al. 2010). These local rates do not explain *M. vimineum*'s rate of spread at the regional scale (Barden 1987; Cole and Weltzin 2004; Huebner 2010b). The discrepancy between the regional spread of *M. vimineum* and recorded dispersal rates suggests an anthropogenic mode of spread (Huebner 2010b; Rauschert et al. 2010). Direct data are scarce, but the transport of feed and garden hay and topsoil is a possible culprit (see Howard 2005; NPS 1999), as is road management (Huebner 2010b; Rauschert et al. 2010). Clearly, *M. vimineum* dispersal is a ripe area for research as well as a potentially effective weak point for targeted management.

Niche construction

Soil microbes drive litter nutrient mineralization, and the chemical composition of root exudation and senesced plant tissue can influence the composition of microbial communities (Carreiro et al. 2000; Kourtev et al. 2002b). The invasion of *M. vimineum* causes changes both in soil microbial communities and nitrogen mineralization rates relative to native

species and uninvaded locations (Ehrenfeld et al. 2001; Kourtev et al. 2002a; Kourtev et al. 1998, 2002b; McGrath and Binkley 2009), and this field evidence has been verified using controlled greenhouse experiments (Kourtev et al. 2003). Given that *M. vimineum* vigorously utilizes soil nitrogen, invasion is believed to create a positive feedback loop by increasing nitrification rates and available nitrate that significantly alters forest soil dynamics (Ehrenfeld et al. 2001; Kourtev et al. 2003). Increases in soil pH coincide with the higher nitrification rates in *M. vimineum* patches (Ehrenfeld et al. 2001; Kourtev et al. 1998; McGrath and Binkley 2009), an expected correlation as nitrification is presumed to be limited in low pH soils (Paul and Clark 1996). Little data exist concerning the impact of *M. vimineum* on soil carbon cycling, although Strickland et al. (2010) report that the plant's presence is associated with accelerated belowground carbon cycling and reductions in soil organic carbon stocks. Notably, exotic earthworms were not found to be associated with *M. vimineum* presence in the southeastern US forest where Strickland et al. (2009) worked. However, they have been found to be associated with *M. vimineum* in northeastern forests (Belote and Jones 2009; Nuzzo et al. 2009). This association may itself explain impacts on nitrogen cycling and also facilitate *M. vimineum* recruitment by reductions in litter depth, given known effects of exotic earthworms on both of these process variables (Bohlen et al. 2004a, b).

Microstegium vimineum's apparent role in accelerating nitrogen and carbon cycling should correspond with decreased litter accumulation and soil organic matter in its vicinity, and it does (Cole and Weltzin 2004; Kourtev et al. 2002a; Kourtev et al. 1998), but see (DeMeester 2009; Ehrenfeld et al. 2001). Notably, Ehrenfeld et al. (2001) found that *M. vimineum* presence had no effect on the recalcitrant, lignin-rich litter of *Quercus* sp., suggesting that some forest systems may resist the invasive plant's influence. Moreover, taken as a whole, the interactions between *M. vimineum* and forest litter are potentially iterative, where a decrease in litter layer mass may facilitate *M. vimineum* establishment, which then in turn accelerates litter decay rates reinforcing or maintaining reduced litter layers. This iterative process necessitates that conclusions based on spatial comparisons between invaded and uninvaded plots must be

confirmed temporally (i.e. baseline data is required prior to invasion of a site) and/or experimentally (e.g., Civitello et al. 2008) to decouple cause and effect. Further, as *M. vimineum* thatch accumulates after senescence, the effect the plant's litter has on its own persistence needs exploration.

By altering soil nutrient cycling and pH, *M. vimineum* may change the structure and function of the soil biota as well as make habitats unsuitable or less competitively advantageous for native plant species (Ehrenfeld et al. 2001; Vitousek 1990). Indeed, *M. vimineum* recruitment fares better where leaf litter is thin or absent, and accelerated litter decomposition would benefit its own seed recruitment. Thus, once established, *M. vimineum* populations theoretically could prompt a positive-feedback structure that benefits their own persistence and spread (Ehrenfeld et al. 2001). The potential construction of niche 'space' by an invasive species such as *M. vimineum* may occur spatially by establishing a core population that modifies adjacent habitat or temporally by establishing during favorable years and stabilizing habitat to buffer unfavorable years (Crooks 2002; Wright and Jones 2006).

Biotic niche

Competition

The propensity for *M. vimineum* populations to form dense monocultures in understory forest environments is consistent with patterns found in native understory species worldwide (Royo and Carson 2006). However, the scale and speed exhibited by *M. vimineum* in forming these monocultures outmatches that exhibited by native species and poses a threat to species diversity in North American, temperate forest systems (Baiser et al. 2008; Barden 1987; DeMeester and Richter 2009; Flory 2010; Flory and Clay 2009a, b; Marshall et al. 2009; Morrison et al. 2007; Oswalt et al. 2007). *Microstegium vimineum* invasions and subsequent spread have been linked observationally and experimentally with declines in native herbaceous and woody understory diversity and biomass (Barden 1987; Flory 2010; Flory and Clay 2009a; Hunt and Zaremba 1992; Marshall et al. 2009; Oswalt et al. 2007; Redman 1995).

The decrease in native vegetation corresponding with *M. vimineum* invasion may be attributable to reduced light levels beneath the grass canopy as seen in other graminoid invaders (D'Antonio et al. 1998; Dyer and Rice 1999), but the evidence is scant. The ability for *M. vimineum* to outcompete *Lonicera japonica*, an invasive vine, appeared to be facilitated by its ability to overtop the vine and appropriate incoming light (Belote and Weltzin 2006). However, Leicht et al. (2005) found that *M. vimineum*'s competitive advantage over two grass species was independent of the light environment. The light environment beneath temperate forest canopies is highly spatially heterogeneous, but varies predictably with canopy senescence. Theoretically, herbaceous plants potentially may gain more advantage by segregating temporal more than spatial variation in light (Neufeld and Young 2003). In doing so, the understory vegetation can be sorted into light guilds based on the time of year they are best suited for carbon acquisition: spring ephemerals, summergreens, wintergreens and evergreens. If the key mechanism underlying *M. vimineum*'s competitive effects is light interception, summergreens should come in most conflict with *M. vimineum* (given that summer is when it is growing) while spring ephemerals and wintergreens should be unaffected. While Adams and Engelhardt (2009) did not assess *M. vimineum*-native species diversity in terms of light guilds, they did find that *M. vimineum* had a temporal impact, and it was greatest in late summer. We suggest that future research into *M. vimineum* impacts on native vegetation target plants with specific requirements, such as light guilds, rather than overall diversity. This approach would provide insight into the mechanisms behind *M. vimineum* success. For example, research into dense fern stands, structurally similar to those formed by *M. vimineum*, found that overall tree seedling diversity declined beneath the fern canopy, but the effects were species specific, and some species were unaffected (George and Bazzaz 1999a, b). Similarly, Marshall et al. (2009) found detrimental species-specific impacts of *M. vimineum* on tree seedling growth and survival. This suggests that *M. vimineum* stands could influence the structure and succession of forest patches.

Microstegium vimineum is clearly not an unbounded colonizer, given ample evidence suggesting it has

numerous and significant niche limitations, particularly relatively high litter thickness and lower soil moisture and light (see earlier sections). Nonetheless, it is an aggressive colonizer within its suitable habitat—relatively high understory light and soil moisture for reproduction and thin or absent leaf litter for recruitment. The inability for *M. vimineum* to invade fields and other open areas that are already vegetated suggests it is only a good competitor in shady environments (Barden 1987; Cole and Weltzin 2004; Flory et al. 2007). For example, Flory et al. (2007) found that *M. vimineum* out-competed an exotic *Dichanthelium* grass beneath shade treatments, but the *Dichanthelium* sp. dominated *M. vimineum* in full sun. As Leicht et al. (2005) found no difference in *M. vimineum*'s competitive advantage over two grasses between light and shade treatments, however, additional correlates of shady habitats may mediate *M. vimineum* competitive interactions.

Biotic interactions

There is very little data concerning *M. vimineum* biotic interactions beyond competition. Barden (1996) observed a wilting disease in a group of potted plants, and Bradford et al. (2010) have observed native herbivores deriving their carbon exclusively from *M. vimineum*, albeit herbivory may be a recent occurrence in an established invasion. Kleczewski and Flory (2010) have identified a fungal disease that infects some *M. vimineum* populations and causes leaf spots, wilting and some mortality. In greenhouse experiments, the disease reduced seed production by more than 40% (Kleczewski and Flory 2010); however, the impacts in natural settings have not yet been explored. Whereas biotic interactions can limit species from habitats that would otherwise be suitable, they can also facilitate spread or persistence in habitats that would otherwise be unsuitable (Bruno et al. 2003). Native white-tailed deer and exotic earthworms, both of which are associated with increasingly extensive changes in forest understory communities, engineer conditions conducive for *M. vimineum* establishment and spread (Baiser et al. 2008; Eschtruth and Battles 2009; Nuzzo et al. 2009). The likely mechanism for this association is a dramatic reduction in forest floor litter by exotic earthworms (Bohlen et al. 2004a, b;

Nuzzo et al. 2009) and leaf litter disturbance and selective browsing of *M. vimineum* competitors by deer (Baiser et al. 2008; Knight et al. 2009). For example, selective herbivory by white-tailed deer—which generally avoid eating *M. vimineum* (Barden 1987)—during drought years prevented native woody seedlings from displacing *M. vimineum* (Webster et al. 2008).

Litter-layer

Species invasions have long been associated with forest disturbance (Elton 1958; Gilliam and Turrill 1993; Lockwood et al. 2007), and this legacy may have spurred a focus on canopy disturbance and understory light in explaining *M. vimineum* distributions. This focus has left a key habitat variable overlooked: ground leaf litter (Marshall and Buckley 2008b; Oswalt and Oswalt 2007). The *M. vimineum* literature is replete with anecdotal and/or indirect connections between plant presence and bare soil, disturbed ground-layer vegetation or thin leaf litter (Barden 1987; Christen and Matlack 2009; Gibson et al. 2002; Glasgow and Matlack 2007; Knight et al. 2009; Redman 1995). *Microstegium vimineum* variation in response to canopy openness may also reflect leaf litter accumulation (Cole and Weltzin 2004, 2005; see Oswalt and Oswalt 2007). In experiments conducted by Oswalt and Oswalt (2007), litter removal led to vigorous spread of *M. vimineum* seedlings, although this effect was less strong in recruitment experiments conducted by Marshall and Buckley (2008b) and Schramm and Ehrenfeld (2010). However, Schramm and Ehrenfeld (2010) did find that seeds trapped relatively higher in the leaf litter had higher mortality.

The mechanism by which litter cover might inhibit *M. vimineum* is unknown. Cues for seed germination include light and soil moisture, the environmental drivers recognized as controls on *M. vimineum* distributions (Boyd and Van Acker 2004; Xiong and Nilsson 1999). Ground-layer litter may filter or block sunlight and/or prevent the seeds from contacting mineral soil which reduces the ability to imbibe moisture (Malik and Vandenberg 1987; Schramm and Ehrenfeld 2010; Wuest et al. 1999; Xiong and Nilsson 1999). Bare soil exposure caused by perturbations such as flood scouring (Barden 1987), drought (Yurkonis and Meiners 2006) and fire

(Glasgow and Matlack 2007) breaks down these environmental barriers and *M. vimineum* recruitment responds vigorously. This response is not unique to *M. vimineum*. Litter disturbance appears an important factor not only in the recruitment of native and invasive grasses (Belote and Jones 2009; Cheplick 1998), but plants as a whole (Xiong and Nilsson 1999). Further, the same factors associated with increased *M. vimineum* abundance—e.g., fire, flooding and animal trampling—promote plant communities as a whole (Carson and Peterson 1990; Foster and Gross 1998).

Synthesis: population dynamics and management implications

Microstegium vimineum populations can be found across a variety of habitats within a geographic region and, as illustrated in this paper, there is not reason to assume that birth and death rates are the same in all habitats. Key *M. vimineum* life stages, particularly recruitment and reproduction, are limited by abiotic and biotic interactions. These niche requirements prevent the plant from persisting everywhere in a landscape, meaning that *M. vimineum* colonization and persistence in a geographic region is not purely stochastic. Instead, as we anticipate from the assumptions underlying niche theory, it is likely that suitable habitat exists within a matrix of unsuitable habitat at the regional scale. This means that aspects of *M. vimineum*'s life history, such as dispersal ability, recruitment success and reproductive output, determine whether it establishes and persists in a landscape. It seems unlikely that each life stage responds equally in all habitats, and *M. vimineum* may become established in locations where within-habitat reproduction is insufficient to maintain the population (i.e. "sink" habitat). Nevertheless, the population may persist with sufficient propagule emigration from proximate populations where within-habitat reproduction exceeds the requirements for persistence (i.e. "source" habitat). Metapopulation dynamics are important for clarifying *M. vimineum* niche requirements and may inform its management, but the impacts of *M. vimineum* sink populations on native ecosystems may be just as detrimental as source populations.

Based on the research synthesized here, *M. vimineum*'s crucial niche requirements appear to be light (reproductive output), soil moisture (reproductive output, seedling recruitment) and above-ground coverage by leaf-litter and competing species (seedling recruitment and survival). Touchette and Romanello (2010) noted that few investigations have attempted to address the ecological requirements of *M. vimineum*, and most of these were conducted as landscape-level surveys. This approach treats habitat and landscape position as niche, which is misleading as differences in landscape position encompass differences in multiple environmental variables, any of which might drive the demographic responses of species (Guisan and Zimmermann 2000; Warren 2010). Whereas some researchers (e.g., Grinnell 1917; Whittaker 1956) use species' location as a niche proxy, all modern use of the niche, as defined by Hutchinson (1957), considers niche a species' requirements for persistence and not its location in the landscape (Chase and Leibold 2003; Hutchinson 1957, 1959; Kearney 2006; Pulliam 2000). Indeed, the use of landscape position as a niche proxy has been roundly criticized as inaccurate (Austin 2002; Guisan and Zimmermann 2000; Warren 2010). By using habitat (e.g., canopy openness) rather than niche requirements (e.g., diffuse light), there is no insight into mechanism, and poor ability for prediction (Austin 2002; Guisan and Zimmermann 2000; Warren 2010).

A second important component in elucidating a species' niche is stage-specific (e.g., germination, growth, reproduction) investigation rather than mere correlation between presence and/or abundance and environmental conditions. In this regard, the *M. vimineum* literature is replete with stage-specific research (Cheplick 2008, 2010; Gibson et al. 2002; Huebner 2010a; Schramm and Ehrenfeld 2010; Touchette and Romanello 2010) which can be used to infer population-level *M. vimineum* dynamics. For example, a source-sink dynamic may occur temporally as well as spatially if *M. vimineum* plants become established in suitable habitats during favorable years, but these populations fail without continued seed input from populations in stable habitats. *Microstegium vimineum*'s persistent seed bank may buffer against bad years in poor habitats; however, seed quality and dormancy longevity are determined by the paternal environment (Gallagher and Fuerst

2006), suggesting that plants in low light may not only produce fewer seeds, but those produced may be less fit and able to sustain dormancy.

Gibson et al. (2002) found great variance in between-population productivity between years and speculated that populations in high-light, trailside habitats may act as propagule sources for those in shadier or drier habitats. Cheplick (2008) found that plants from low-light, forest-interior habitats produced significantly less seed mass than those from high-light populations at the edges. This dynamic might allow *M. vimineum* to disperse and thrive along sunny, and sometimes wet, roadside habitats and ditches (Huebner 2010a; Mortensen et al. 2009). In turn, these populations might act as source populations for adjacent forest habitats (Christen and Matlack 2009; Cole and Weltzin 2004; Huebner 2010b). Nonetheless, sufficient dispersal of propagules from source to sink habitats is crucial to maintain this dynamic, and measured *M. vimineum* dispersal distances of 1–2 m (Huebner 2010b; Rauschert et al. 2010) seem insufficient, making additional research necessary for testing this hypothesis.

Management implications

By reviewing *M. vimineum* research in the context of stage-specific requirements, we highlight potential weaknesses in its life history and opportunities for effective management. The increase in reproduction (seed production) in higher sunlight, and decrease in germination where leaf litter is thick, indicates that forest understory populations may be sinks fed by input from source populations in higher light, litter disturbed habitats, such as those found along roadsides and streams (Cheplick 2010; Christen and Matlack 2009; Cole and Weltzin 2004; Huebner 2010a, b; Mortensen et al. 2009). If so, eradication of the source populations should eradicate the forest sinks (Pulliam 1988), which has been suggested for invasive species (Hulme 2003) including *M. vimineum* (Huebner 2010b). A second implication of our review is that *M. vimineum* may be dispersal-limited, with long-distance dispersal potentially occurring by anthropogenic transport (Evans et al. 2006; NPS 1999). Robust evidence for this possibility is needed and might highlight an opportunity for effective management of the species spread.

Whereas much of invasion biology is focused on understanding the causes and consequences of invasion under current conditions, anthropogenic changes to climate, nitrogen cycling and land use are likely to significantly impact the success of invasive species (Bradford et al. 2007; D'Antonio and Vitousek 1992; Dukes and Mooney 1999). For example, our review suggests that increased nitrogen deposition might lead to increased growth and greater displacement of native species in areas where *M. vimineum* is already present but will have relatively small effects on rates of spread. Alternatively, increased drought is likely to impact all life stages and significantly reduce the distribution of *M. vimineum* throughout the landscape. Overall we demonstrate how identification of niche limitations and controls over key demographic stages (recruitment, survival, growth, reproduction, dispersal) can be used to help identify potential strategies for managing invasive species. We use *M. vimineum* as an in-depth case study, but suggest that this approach should be universally applicable given its reliance on ecological theory to inform invasive species research, understanding and management.

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