

Ready or Not, Garlic Mustard Is Moving In: *Alliaria petiolata* as a Member of Eastern North American Forests

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Garlic mustard (Alliaria petiolata) is a nonnative, shade-tolerant forb that was introduced into North America in the mid-1800s. Currently, garlic mustard is spreading across the landscape at a rate of 6400 square kilometers per year. In this article, we synthesize the current state of knowledge on the mechanisms underlying garlic mustard's widespread success and the ecological impacts of its invasion. Although no single mechanism appears to explain the success of garlic mustard, a combination of plant traits—all slightly different from those of native plants—seems to confer garlic mustard with tremendous success in the new habitats it invades. The domination of this new species in eastern forests is clearly changing the ecology of these systems. The consequences of garlic mustard invasion include the loss of biological diversity, ripple effects through higher trophic levels, and changes in the function of soil microbial communities.

Keywords: *Alliaria petiolata*, garlic mustard, North American forests, invasive plant, glucosinolates

The impact of introduced, invasive species on communities and ecosystems is one of today's most pressing global environmental problems (Wilcove et al. 1998, Mack et al. 2000). Biological invasions are a leading cause of extinction and biodiversity loss (Wilcove et al. 1998), and invasive plants are permanently altering natural communities and their ecological characteristics (Mack et al. 2000). To date, generalizations about the mechanisms for invasive species' success and the susceptibility of communities to invasion have proven elusive. Consequently, it may make more sense to focus on individual species and their large-scale impacts than on general theories for all invasive species.

Garlic mustard, *Alliaria petiolata* (M. Bieb.) Cavara and Grande (formerly *Alliaria officinalis*), is one of the most problematic invasive plant species in eastern North American forests (Blossey et al. 2001, Stinson et al. 2006). Currently listed as a "noxious weed" in 6 of the 34 US states it has colonized (Nuzzo 2000), garlic mustard is spreading at an alarming rate (Nuzzo 1993a). Although garlic mustard possesses many of the characteristics of an "ideal weed" as defined by Baker (1974), this invasive, biennial forb is unique in that it is shade tolerant and capable of persisting, indeed thriving, in the forest understory. Also, unlike many other herbaceous invasive plants (D'Antonio et al. 1999), garlic mustard does not necessarily require a disturbance to become established or to proliferate (Meekins and McCarthy 2001).

In this article, we review the current understanding of garlic mustard as a highly successful invasive plant in eastern North America. We describe the introduction and early invasion of garlic mustard, and then discuss the mechanisms that appear to explain the widespread success of this nonnative plant species in eastern North American forests. Finally, we discuss the ecological impacts of garlic mustard invasion (figure 1).

The invasion

Garlic mustard is native to western Eurasia, where its home range extends from Italy in the south to Sweden in the north, and from England in the west to Russia in the east. It is also native to small portions of North Africa and Asia Minor (figure 2; Tutin et al. 1964, Cavers et al. 1979). In its native range, garlic mustard exists in relatively small populations (Blossey et al. 2001), most commonly in mesic, semishaded habitats at forest edges or adjacent to rivers (Grime et al.

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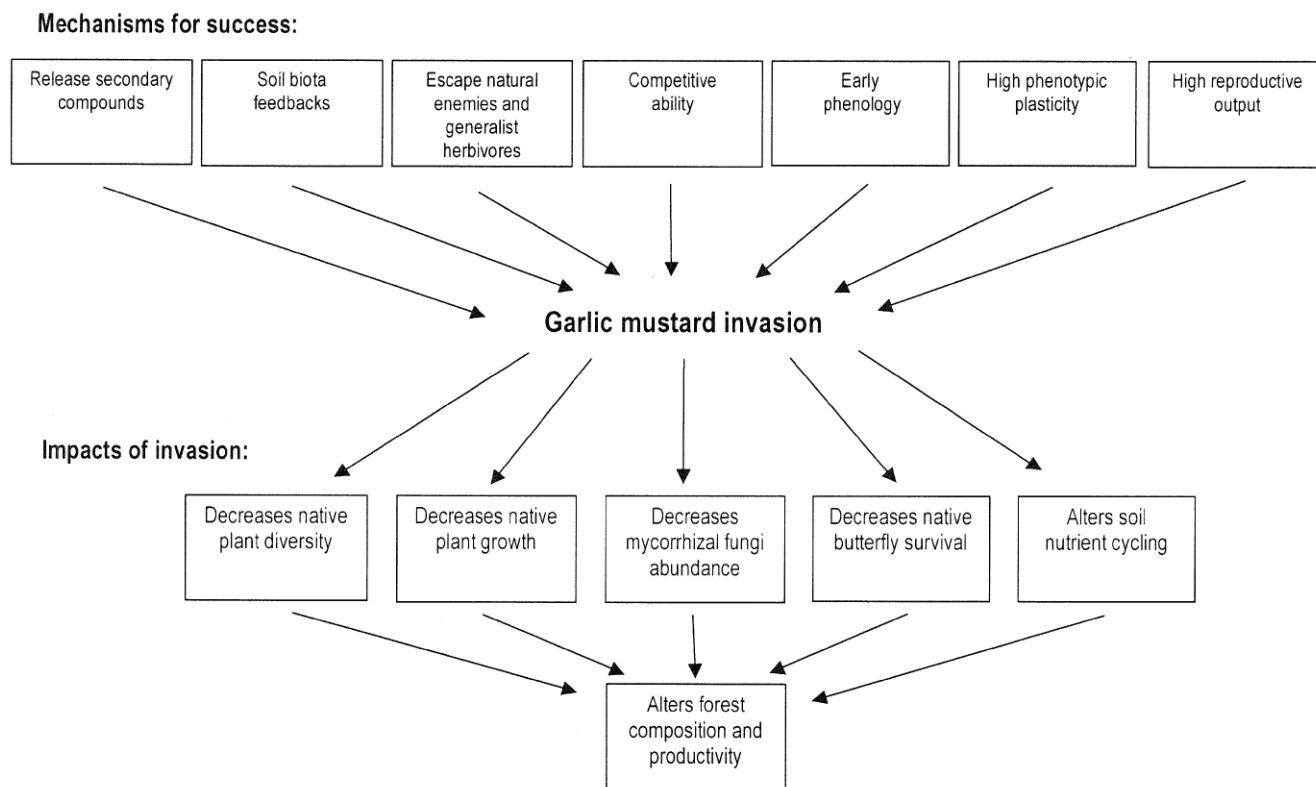


Figure 1. Conceptual diagram illustrating the mechanisms for the success of garlic mustard in its new range and the impacts of its invasion on eastern North American forests.

1988). Garlic mustard can be distinguished from other woodland mustards by its large, heart-shaped leaves, and by the characteristic garlic odor that emanates from all plant parts when crushed (Cavers et al. 1979).

Garlic mustard was introduced to North America by early colonists, who valued it both as a medicinal plant and as a garlic substitute (Grieve 1959). By 1868, garlic mustard was found growing in native communities in Long Island, New York (Nuzzo 1993a). Initially, garlic mustard was estimated to spread across the landscape at a rate of approximately 366 square kilometers (km²) per year (Nuzzo 1993a). Around 1930, the rate of expansion increased to approximately 1950 km² per year (Nuzzo 1993a). As of 1991, the rate of expansion—on the basis of presence or absence—was estimated at 6400 km² per year, faster than the expansion of purple loosestrife (*Lythrum salicaria*), a well-known and widely spread invasive plant (Nuzzo 1993a). Once garlic mustard is established, it becomes a permanent member of the plant community and proliferates rapidly into adjacent habitats (Nuzzo 1999).

Plant secondary compounds as a mechanism for success

Garlic mustard contains a variety of plant secondary compounds that lower its palatability to herbivores, including flavonoids, defense proteins, glycosides, and glucosinolates (Daxenbichler et al. 1991, Haribal and Renwick 2001, Cipollini

2002). Historically, these secondary compounds attracted the attention of ecologists because of their ability to deter herbivory (Freeland and Janzen 1974). However, recent studies suggest that these secondary compounds also affect seed germination and the growth of native plants, and alter the activity of soil biota, raising the possibility that secondary compounds in garlic mustard contribute to its overall success as an invader.

Of all the secondary compounds in garlic mustard, glucosinolates have received the most attention. Glucosinolates, a group of sulfur- and nitrogen (N)-containing compounds derived from amino acids, are responsible for the sharp taste of most mustard plants (Fahey et al. 2001). Although more than 120 different kinds of glucosinolates are known to exist (Fahey et al. 2001), the primary glucosinolate in garlic mustard is sinigrin (Larsen et al. 1983). The attached R group that distinguishes sinigrin from the rest of the glucosinolates is 2-propenyl (CH₂=CH-CH₂) (Fahey et al. 2001), and in garlic mustard seeds, this compound can account for as much as 3% by dry weight (Larsen et al. 1983).

Plants that contain glucosinolates also contain myrosinase (α -thioglucosidase glucohydrolase), a glycoprotein that is stored within the cytosol of myrosin and nonmyrosin cells, and hence is spatially separated from the glucosinolates (Fahey et al. 2001). Upon tissue damage or root exudation, myrosinase is released from storage, and this enzyme cleaves the glucose thioester of the glucosinolates to produce

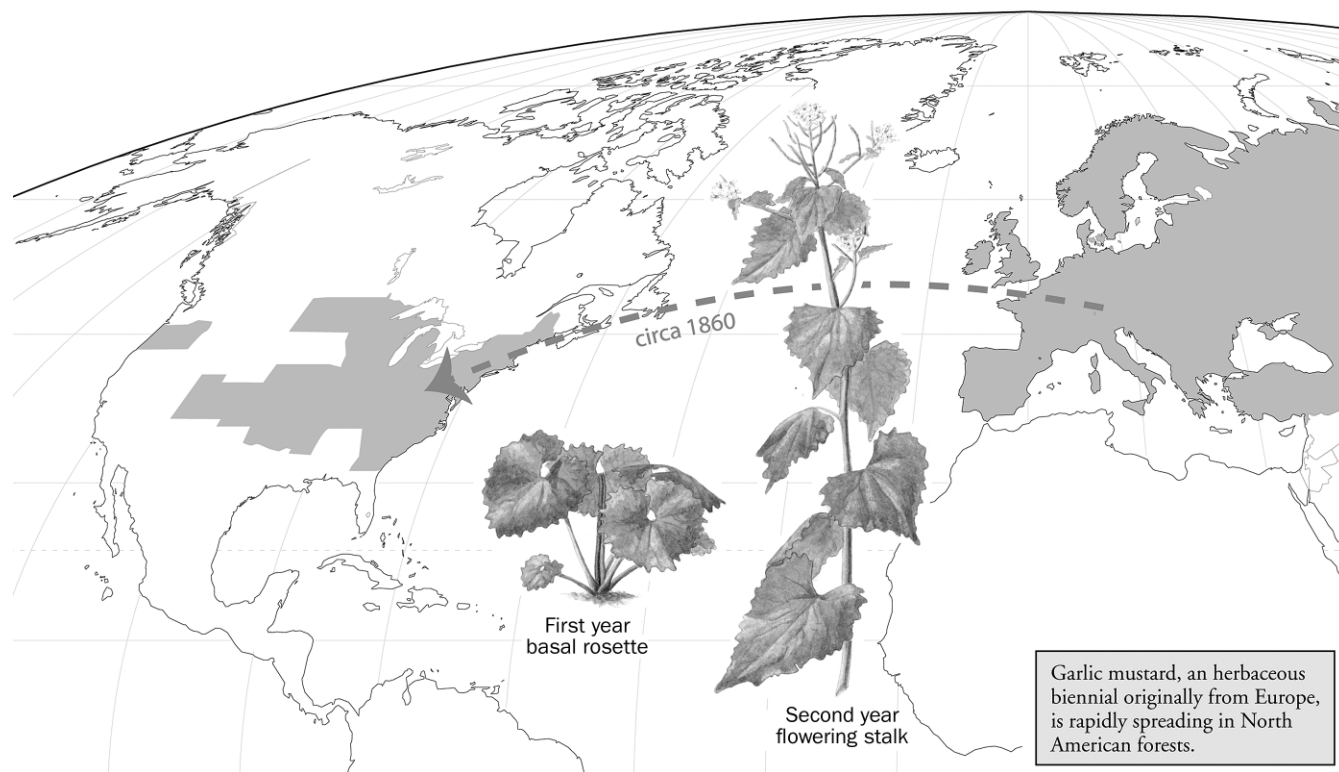


Figure 2. Image of first- and second-year garlic mustard plants and geographical introduction pattern. Illustration by Eliza K. Jewett; used courtesy of Kristin C. Lewis. © 2004 Eliza K. Jewett.

isothiocyanates (volatile mustard oils), nitriles, and thiocyanates (Fahey et al. 2001). In the mustard family, glucosinolates and their hydrolysis products act as a first line of defense against generalist insect herbivores (Fahey et al. 2001). These compounds are also involved in host-plant recognition by specialist predators (Fahey et al. 2001) and even act as attractants or stimulants for specialist butterfly species that lay their eggs on leaves containing glucosinolates (Chew 1988). The products of the hydrolysis of glucosinolates are cyanide compounds, well-known inhibitors of respiratory electron transport. These cyanide compounds are therefore toxic to a range of organisms, including fungi (Mayton et al. 1996), soil pests and pathogens (Brown and Morra 1997), insect herbivores (Chew 1988, Porter 1994), and other plants (Haromoto and Gallandt 2005).

Cipollini and Gruner (2007) recently found that garlic mustard also produces cyanide from an as yet unidentified cyanogenic compound. This potentially new pathway for cyanide production could provide a powerful weapon in the chemical arsenal of garlic mustard. They also found the concentration of cyanide in the tissues of garlic mustard to be as high as 100 parts per million fresh weight, a level 150 times that of native *Brassica* species, and a level considered toxic to most vertebrates. The highest concentrations of cyanide were found in young leaves of first-year plants (Cipollini and Gruner 2007).

Although it remains unclear exactly how these secondary compounds get into the soil, their presence appears to affect surrounding plants. Prati and Bossdorf (2004) found that the germination rate of a native woodland herb, rough avens (*Geum laciniatum*), was significantly reduced when grown in soils that were previously occupied by garlic mustard. To test for the specific effects of root exudates, they mixed experimental soil samples with activated carbon, a substrate that binds organic compounds in soil and thereby decreases their activity. They found that more seeds germinated in soils with activated carbon than in soils without activated carbon, implying that organic compounds released in the exudates of garlic mustard roots had a negative effect on the seed germination of native species.

Mustard plants have been used in agriculture to inhibit the activity of unwanted soil organisms (Brown and Morra 1997). They are widely recognized as break crops and soil biofumigators in agronomy. (The term “break crop” refers to the growth of mustard plants in rotation with a crop of interest.) By breaking the life cycle of many soilborne diseases and pests, the incorporation of mustard plant tissues into soil results in higher crop yields (Brown and Morra 1997). Mustard plants are also used as green manures. When tilled into the top layer of the soil, they biofumigate the soil by releasing volatile isothiocyanates. The consequence of this biofumigation is the inhibition of seedling emergence for many agricultural weeds (Haromoto and Gallandt 2005) and the

suppression of soilborne pests, pathogens, and disease organisms (Mayton et al. 1996, Brown and Morra 1997).

The ability of mustard plants to suppress soilborne pests and pathogens may facilitate the spread of garlic mustard in its new range. In a greenhouse experiment, Klironomos (2002) found that the growth of garlic mustard plants was not significantly affected by the presence of soil pathogens. In the “root training” portion of this experiment, Klironomos found that garlic mustard plants grew larger in soils previously occupied by garlic mustard plants than in those occupied by other plant species, and that the positive effect of garlic mustard on its own growth was larger than that of four other invasive species, Canada thistle (*Cirsium arvense*), leafy spurge (*Euphorbia esula*), purple loosestrife (*L. salicaria*), and Japanese knotweed (*Polygonum cuspidatum*). In contrast with the invasive species, the rare species Klironomos (2002) studied had a significant negative impact on their own growth. Klironomos concluded that plants differed in their ability to affect soil pest and pathogen loads. Given the diversity of secondary compounds in garlic mustard and the positive impact of garlic mustard on its own growth, the suppression of soilborne pests and pathogens through the release of secondary compounds may be an important component of this species’ success.

Natural enemies and competitive ability as mechanisms for success

One explanation for the success of invasive plants in general, and garlic mustard in particular, is the release from predation by native, specialist herbivores (i.e., the enemy release hypothesis; Keane and Crawley 2002). As many as 69 insect species are known to consume garlic mustard in Europe; none of these species are present in North America (Szentesi 1991). Field studies show that in North America, garlic mustard is relatively free from herbivory (Szentesi 1991, Nuzzo 2000, Blossey et al. 2001, Renwick et al. 2001), including browsing by the dominant generalist herbivore throughout much of eastern North America, white-tailed deer (*Odocoileus virginianus*; Williams and Ward 2006). Although no direct tests involving garlic mustard have been performed so far, it has been suggested that white-tailed deer may play an important role in the expansion of invasive plants by (a) creating soil disturbances that increase the available growing space for new seedlings and (b) preferentially browsing on native plants, thereby lowering the reproductive output of native species (Williams and Ward 2006). As deer typically choose not to consume garlic mustard plants (Nuzzo 2000), white-tailed deer may facilitate the establishment and the spread of garlic mustard by grazing on native vegetation.

Invasive plants are also often assumed to be better competitors than the native plants surrounding them (Baker 1974). Given that invasive plants usually lack natural enemies, optimal allocation theory would predict a decrease in the allocation of resources to produce defensive compounds in favor of allocation to promote growth, survivorship and

reproduction (Bazzaz et al. 1987). On the basis of this conceptual model, Blossey and Nötzold (1995) argued that selection should favor less defended but more competitive genotypes after a species enters its new range, a hypothesis they refer to as the evolution of increased competitive ability (EICA).

Although EICA provides an attractive explanation for the success of invasive species, more recent work on the growth rate of native and introduced populations of garlic mustard, and on the expression of inducible and constitutive defenses, does not support EICA, at least in garlic mustard (Bossdorf et al. 2004a, Cipollini et al. 2005, Lewis et al. 2006). In fact, Bossdorf and colleagues (2004b) proposed the evolution of reduced competitive ability (ERCA) as an alternative conceptual model for the successful invasion of garlic mustard into eastern North American forests. Noting that garlic mustard occurs in high densities, Bossdorf and colleagues (2004b) argued that if invasive species encountered greater intraspecific competition than interspecific competition in their new range, and if the traits controlling competitive ability incurred a fitness cost, then selection might act against highly competitive genotypes, thereby favoring genotypes with a reduced competitive ability in invasive populations.

Although there has been no direct test of this hypothesis, Meekins and McCarthy (1999) found that intraspecific competition was more intense than interspecific competition for several populations of garlic mustard in the United States, providing some evidence for ERCA. In addition, certain demographic properties of garlic mustard provide support for ERCA. First-year rosettes have been recorded at densities of up to 1800 seedlings per square meter (m^2) (Anderson et al. 1996), second-year plants occur in densities as high as 303 plants per m^2 , and the total dry-weight biomass of garlic mustard plants can reach 168 grams per m^2 . Moreover, self thinning in garlic mustard occurs only after the formation of dense, nearly monospecific stands (Meekins and McCarthy 2002). Thus, if ERCA holds true, a reduction in competitive ability may allow invasive populations of garlic mustard to shed attributes related to resource competition in favor of attributes, such as reproductive output, that are likely to confer greater success in its new range (Bossdorf et al. 2004a).

Phenology and reproduction as mechanisms for success

Most of the plant diversity in eastern North American forests is found in understory forbs (see the review in Whigham [2004]). These woodland herbs are predominantly deciduous perennials with limited seed production. The growth and reproduction of woodland herbs is primarily limited by understory light availability, and their spatial distribution is strongly influenced by the availability of resources within the understory (Whigham 2004).

The phenology and reproductive output of garlic mustard differ substantially from those of native species. Garlic mustard is an obligate biennial that produces a basal rosette of dark green leaves after germinating early in the spring (Cavers et

al. 1979, Baskin and Baskin 1992), before most native woodland herbs (Whigham 2004). The rosette plant overwinters green under the snow and then bolts (produces a flowering stem) in March and April of the following year, growing at a rate of 1.9 centimeters per day (Cavers et al. 1979, Anderson et al. 1996). It produces flowers from April through July and fruits from June through September (Anderson et al. 1996, Byers and Quinn 1998). Every viable second-year plant produces flowers, regardless of its size or site conditions (Susko and Lovett-Doust 1998), and plants can continue to produce flowers even after fruit production has started. As garlic mustard is a strict biennial, all second-year plants senesce and die soon after the fruits dehisce (Anderson et al. 1996).

In two hardwood forests in Illinois, garlic mustard plants reach their maximum photosynthetic rates during the early spring of their second growing season, a period when most native plants are still dormant (Myers and Anderson 2003). By growing in early spring, garlic mustard may acquire soil nutrients when other plants are inactive and take advantage of available light before the forest canopy develops. To date, the importance of the difference in phenology between garlic mustard and native plants has not been much studied, so it is unclear whether resource uptake in the spring contributes disproportionately to annual uptake. This is a critical area for future research.

Garlic mustard plants begin growing under high light conditions in early spring, which transition to low light conditions in the early summer. High levels of phenotypic plasticity contribute to persistence in heterogeneous environments and are a good predictor of invasive ability (Parker et al. 2003), a trait that also holds for garlic mustard. The sun and shade leaves of garlic mustard differ greatly in their maximum rate of photosynthesis, specific leaf mass, rubisco per unit leaf area, stomatal density, stomatal conductance, and chlorophyll concentration (Myers et al. 2005). Garlic mustard plants also show considerable adaptation to local light environments. Dhillion and Anderson (1999) found that the rate of photosynthesis in different populations of garlic mustard was maximized at the light level under which the populations initially grew (figure 3), indicating an optimal allocation of resources to photosynthesis (Bazzaz et al. 1987).

Garlic mustard reproduces only sexually (Cavers et al. 1979), and seeds are easily dispersed by a number of vectors, including wind, small mammals, water currents, and human transport (Cavers et al. 1979, Nuzzo 1993a, Blossey et al. 2001). Three aspects of garlic mustard's mating system appear to contribute to its success as an aggressive invader. First, flowers are adapted for generalist pollinators and have the ability to self-pollinate, thereby ensuring pollination and allowing one plant to initiate an entire population (Cruden et al. 1996). Typical pollinators are solitary bees (Andrenidae, Halictidae), honeybees (Apidae), and syrphid flies (Syrphidae). The individual flowers remain open for two to three days, with most flowers pollinated on the first day of opening (Cruden et al. 1996). If the flowers are not visited by pollinators within

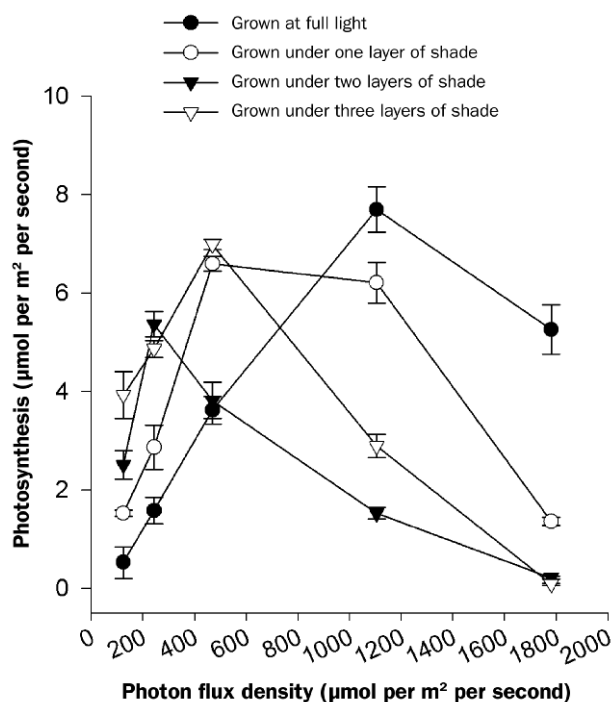


Figure 3. Photosynthetic rate of garlic mustard rosettes from high light (1140 micromoles per square meter per second) and three shaded environments (469, 243, and 125 micromoles per square meter per second, respectively). These data show that the rate of photosynthesis for different populations of garlic mustard was maximized at the light level under which the populations were initially grown. Adapted from Dhillion and Anderson (1999).

the first day, garlic mustard plants self-pollinate, typically on the second day that flowers are mature (Cruden et al. 1996).

Second, almost every pollinated garlic mustard ovule develops into a viable seed (Cruden et al. 1996), resulting in very high reproductive output. The fruits, 4- to 6-millimeter siliques, contain approximately 10 to 20 ovules each (Cavers et al. 1979). Seeds typically fall within a few meters of the mother plant and germinate after a period of at least 14 weeks of cold stratification at temperatures from 1 degree Celsius (°C) to 10°C, and 70% of seeds germinate in the first spring following production (Baskin and Baskin 1992). Seeds that do not germinate within the first year form seed banks that are viable in the soil for up to 10 years (Victoria Nuzzo, Natural Area Consultants, Richford, NY, and Bernd Blossey, Cornell University, Ithaca, NY, personal communications, 17 October 2007). One plant can produce more than 3500 seeds (Susko and Lovett-Doust 2000), with population seed production varying from around 9500 seeds per m² in northern Illinois (Nuzzo 1993b) to more than 107,000 seeds per m² in Ontario (Cavers et al. 1979).

The third aspect of garlic mustard's mating system that contributes to its success is that populations cross-pollinate at a high level, ensuring a large amount of genetic variability

(Cruden et al. 1996) and thereby avoiding the negative effects associated with inbreeding depression in founder populations. Populations of invasive species typically have low levels of genetic diversity both within and among populations, due to bottlenecks during the invasion process (Baker 1974), but this is not the case in garlic mustard. Genetic diversity in introduced populations of garlic mustard is similar to that of native garlic mustard populations (Meekins et al. 2000), implying little or no genetic bottleneck during introduction. Multiple introductions may have also contributed to the high genetic diversity of this plant (Meekins et al. 2000).

Impacts on the diversity and growth of native plants

There is great concern that invasion by garlic mustard will reduce the diversity of native plant communities (Anderson et al. 1996, McCarthy 1997), a concern borne out by field studies and removal experiments. Stinson and colleagues (2007) found a negative correlation between the abundance of garlic mustard in the forest understory and the diversity of native plant species in a western Massachusetts forest (figure 4a, 4b). In the same forest, the removal of 100% of the garlic mustard plants from invaded plots resulted in an increase in the diversity of native plant communities after just one year (figure 4c, 4d; Stinson et al. 2007), although partial eradication of garlic mustard had no effect on diversity in the short term (up to two years). McCarthy (1997) found that within the first year of garlic-mustard eradication in a floodplain forest in Maryland, the percentage of native annual plants, vines, and tree seedlings significantly increased. In addition, after two years of applying the herbicide glyphosate to patches of garlic mustard, Hochstedler and colleagues (2007) found a significantly greater cover of native spring perennials and graminoids; however, after five years of herbicide application, there was a marginally lower cover of annuals. Hochstedler and colleagues (2007) attribute the compositional differences in the forest-floor community to the competitive impacts of garlic mustard.

In contrast to the generally negative community-wide consequences of garlic mustard invasion, the response of individual species to the presence of garlic mustard is variable, with some species growing better and other species growing more poorly. Meekins and McCarthy (1999) found that the biomass of chestnut oak (*Quercus prinus*) seedlings growing in the presence of garlic mustard was 34.8% lower than when chestnut oak was grown in monoculture under a variety of densities and proportions of species combinations. By contrast, the biomass of box elder (*Acer negundo*) and jewelweed (*Impatiens capensis*) seedlings was 37.0% and 11.7% higher, respectively, in the presence of garlic mustard than it was when these species were grown in monoculture. Similarly,

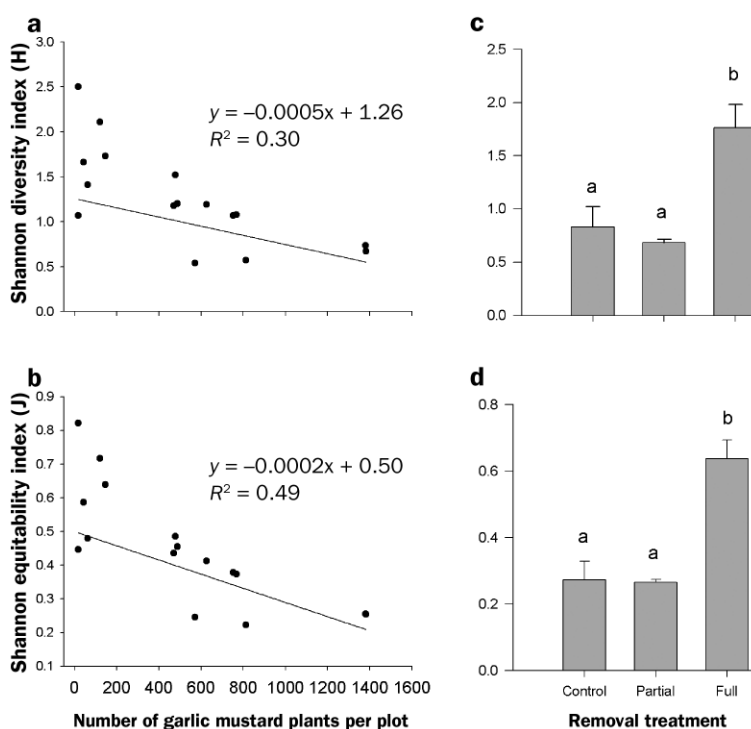


Figure 4. Shannon diversity index and Shannon equitability index as a function of garlic mustard abundance in a forest bordering Connecticut, Massachusetts, and New York (a, b), and in response to garlic mustard removal (c, d). Error bars represent ± 1 standard error of the mean (Stinson et al. 2007). Lowercase letters in (c) and (d) indicate significant differences ($p < 0.05$) among treatment means.

in a greenhouse experiment, we found that jack-in-the-pulpit (*Arisaema triphyllum*) grew significantly less rapidly in soils that had been previously occupied by garlic mustard than in soils previously occupied by jack-in-the-pulpit (figure 5a). By contrast, the growth of wheat was significantly higher in soils previously occupied by garlic mustard than those previously occupied by conspecifics (figure 5b). Collectively, these studies not only show that the invasion of garlic mustard has the potential to decrease the diversity of native plant communities but also suggest that garlic mustard invasion may alter the successional trajectory of forest communities by favoring the growth of some species over others.

The invasion of native communities by garlic mustard is also associated with a decline in the mycorrhizal status of native plants. In noninvaded soils, nearly 30% to 45% of the fine roots in sugar maple, white ash, and red maple seedlings were colonized by arbuscular mycorrhizal fungi, whereas this mutualistic relationship was almost completely eliminated in invaded soils (Stinson et al. 2006). Subsequent experiments with these same tree species showed that the growth rate and colonization of roots by arbuscular mycorrhizal fungi declined significantly in native soils conditioned by garlic mustard relative to uninvaded soils conditioned by other native plants (figure 6a, 6b). Since approximately 95% of all plant species (Smith and Read 1997), including every

woodland herb examined in temperate deciduous forests thus far (Whigham 2004), form symbiotic relationships with mycorrhizal fungi, disruption of this mutualism by the invasion of garlic mustard could have important community-level impacts. Indeed, garlic mustard invasion appears more likely to harm highly mycorrhizal-dependent species, such as tree seedlings and other woody plants, than those that are less dependent on mycorrhizal fungi (figure 6c). It also appears that garlic mustard invasions decrease the abundance of ectomycorrhizal colonization of fine roots (Benjamin E. Wolfe, Harvard University, Cambridge, MA, personal communication, 18 October 2007). The ability of garlic mustard to disrupt mycorrhizal associations and subsequently suppress native plant growth represents a novel mechanism by which an invasive plant can disrupt native communities (Stinson et al. 2006) and an important pathway by which garlic mustard may be altering forest regeneration.

Impacts on trophic interactions

The invasion of garlic mustard affects not only the diversity of native plant communities but the abundance of species at higher trophic levels. The rare West Virginia white butterfly (*Pieris virginiensis*) typically oviposits on toothwort (*Dentaria* spp.), a native member of the mustard family (Porter 1994). With the increasing abundance of garlic mustard, the West Virginia white butterfly is increasingly laying its eggs on the leaves of garlic mustard. Given that the percentage of eggs that hatch on garlic mustard leaves is significantly lower than on toothwort leaves (Porter 1994), there is growing evidence that the invasion of garlic mustard is decreasing the abundance of the West Virginia white butterfly.

There is also concern that invasion by garlic mustard is decreasing the abundance of the mustard white butterfly (*Pieris napi oleracea*), native to North America (Renwick et al. 2001). Field mustard (*Brassica rapa*) and wild radish (*Raphanus raphanistrum*) are the primary hosts for the mustard white butterfly. Garlic mustard can serve as an alternate host, but when mustard white butterflies oviposit on the leaves of garlic mustard, their larvae have lower survivorship than when they oviposit on native mustard plants (Renwick et al. 2001). In a modeling study, Keeler and colleagues (2006) found that when garlic mustard dominates the herbaceous plant community (i.e., > 50% cover), populations of the mustard white butterfly are predicted to become locally extinct within 50 years. The results of their modeling study

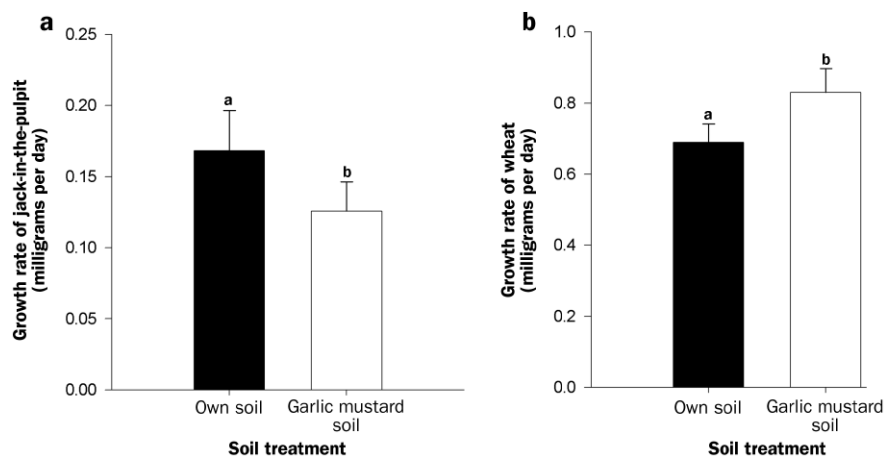


Figure 5. Growth rate (total dry weight in milligrams per day) of (a) jack-in-the-pulpit (*Arisaema triphyllum*) and (b) wheat (*Triticum aestivum*) plants grown in soils that previously contained either garlic mustard plants or plants of their own species. Before planting, uninvaded field soils were collected from two sites in northwestern Connecticut, and 250 grams of moist soil were weighed into each of 96 plastic pots (11.43 square centimeters each). The pots were split into three species treatments (three plants were grown from seed of either garlic mustard, jack-in-the-pulpit, or wheat), four greenhouse blocks, and eight replicates, and allowed to grow for a period of 12 weeks. Plants were grown in the Arnold Arboretum greenhouses in Jamaica Plain, Massachusetts, and received approximately 30 milliliters of water daily. Each plant was then completely removed, and the conditioned soils were planted with one newly germinated seedling of either a conspecific individual or garlic mustard and allowed to grow for 12 weeks. Final biomass was harvested and dried at 60 degrees Celsius for three days. Growth rate was calculated as above, and the belowground biomass was divided by number of days of growth. Error bars represent ± 1 standard error of the mean, and analysis of variance was used to infer statistical significance. The lowercase letters over the columns indicate significant differences ($p < 0.05$).

suggest that garlic mustard invasion is a primary factor driving the population decline of this native butterfly.

Impacts on soil nutrient cycling

The shift in plant species dominance that occurs during an invasion has the potential to substantially alter plant-soil interactions, especially nutrient cycling. These changes can have considerable and potentially long-lasting impacts because soil nutrient availability is an important factor in determining ecosystem stability and productivity (Hooper and Vitousek 1997). The effect of invasive species on ecosystem function is only now gaining broader recognition (reviewed in Ehrenfeld [2003]).

The quantity and chemistry of litter inputs to soils change with the presence of an invasive plant, and the change in litter inputs can alter litter decomposition, often increasing the rate of nutrient cycling in invaded areas (Ehrenfeld 2003). Ashton and colleagues (2005) found that the leaf litter of native and invasive species decomposed significantly faster in sites invaded by garlic mustard and Japanese honeysuckle (*Lonicera japonica*) than in sites dominated by native species. Ashton and colleagues also found that accel-

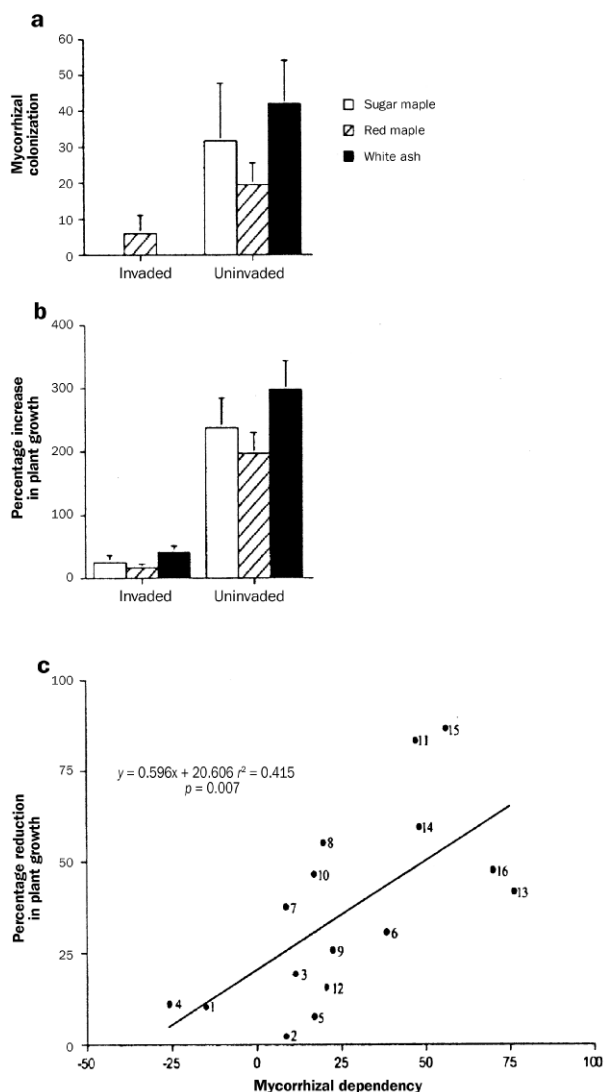


Figure 6. The effect of garlic mustard invasion on (a) mycorrhizal colonization and (b) growth of native tree seedlings (mean \pm 1 standard error). (c) Linear regression analysis showing the reduction in the rate of native plant growth, among species differing in mycorrhizal dependency, in soils influenced by garlic mustard. The reduction in growth was calculated as the difference between the growth rate of a species growing in soils previously colonized by garlic mustard and the growth rate of the same species growing in soils without garlic mustard. Mycorrhizal dependency was calculated as the difference in the rate of plant growth in the presence and absence of arbuscular mycorrhizal fungi. Study species ranked (from least to most dependent) as follows: 1, *Cichorium intybus*; 2, *Trifolium repens*; 3, *Plantago major*; 4, *Taraxacum officinale*; 5, *Solidago canadensis*; 6, *Chrysanthemum leucanthemum*; 7, *Daucus carota*; 8, *Asclepias syriaca*; 9, *Juniperus virginiana*; 10, *Populus deltoides*; 11, *Morus alba*; 12, *Prunus virginiana*; 13, *Fraxinus americana*; 14, *Acer saccharum*; 15, *Acer rubrum*; 16, *Prunus serotina* (Stinson et al. 2006).

erated rates of decomposition were associated with faster rates of N mineralization from decomposing litter. Consistent with Ashton and colleagues' results, inorganic N availability was significantly higher in invaded than in uninvaded soils in a series of Connecticut forest soils (figure 7a).

Few studies have focused on the effects of garlic mustard on phosphorus (P) cycling, although preliminary studies in Connecticut soils indicate significantly higher P availability in invaded soil compared with uninvaded soil (figure 7b). Unlike available N, which is largely derived from the decomposition of soil organic matter, P availability in soil is also derived from the weathering of soil minerals. In the related mustard plant rape (*Brassica napus*), a large efflux of hydrogen ions from roots correlated with a significant increase in P availability in the rhizosphere (Hedley et al. 1982), presumably because of faster rates of mineral weathering. If previously unavailable forms of P are solubilized in the rhizosphere of garlic mustard plants, increases in soil P availability in combination with higher soil N availability may confer a competitive advantage to garlic mustard, which is nonmycorrhizal, over native nonmustard plants whose mycorrhizal associations may have been disrupted.

Overall, it appears that soil nutrient availability is higher in soils invaded by garlic mustard, implying that garlic mustard alters belowground processes in the soils that it invades. The exact mechanism underlying greater nutrient availability is unknown, in part because few studies have related garlic mustard invasion to the composition and function of soil microbial communities. In general, however, faster rates of nutrient cycling in garlic mustard-invaded soils present something of a paradox for our understanding of this species' success. Nutrient availability is low relative to plant demand in temperate ecosystems, so we might expect native plants to respond positively to the increase in nutrient supply, yet the presence of garlic mustard is associated with declines in the growth rate of native plants and in the diversity of native plant communities. Thus, garlic mustard appears to have simultaneous positive effects (i.e., increased nutrient availability) and negative effects (i.e., decreased mycorrhizal colonization of fine roots) on belowground processes that, on balance, result in the loss of biological diversity in native communities.

Management options

The most effective method for the management of garlic mustard is to remove it before it sets seed; hence, control is most effective, and most economical, in late fall or early spring (Nuzzo 2000). After removal efforts, garlic mustard is likely to reestablish, either from the seed bank or through immigration, taking advantage of the newly created open space and resources (Baskin and Baskin 1992, Dhillon and Anderson 1999). Therefore, management efforts must be followed with continuous monitoring.

Herbicide application can reduce garlic mustard density and seedling frequency. The application of glyphosate can reduce garlic mustard cover by more than 91% (Nuzzo 1991),

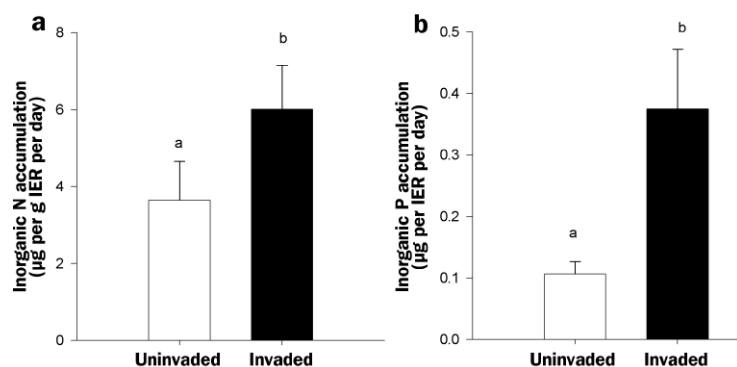


Figure 7. The accumulation of (a) inorganic nitrogen (N) and (b) inorganic phosphorus (P) on ion exchange resins (IERS) in six uninjured plots compared with six adjacent injured plots (1.2 × 1.2 meters) at each of three sites: Pine Plantation, Falls Village, Connecticut; Hammond Woods, Newton, Massachusetts; and Norfolk Land Trust, Norfolk, Connecticut. IER bags were created as described in Hart and Binkley (1984). One IER bag for N and one IER bag for P were placed into each plot during the growing season from mid May 2005 through early September 2005. After incubation, the resin bags measuring N flux were extracted in 2-molar KCl (potassium chloride). The resin bags measuring P flux were extracted in 0.5-molar NaHCO₃ (sodium bicarbonate). NH₄⁺-N (ammonium) was measured using the phenolate method, NO₃⁻-N (nitrate) was measured using cadmium column reduction, and PO₄³⁻-P (phosphate) was measured using the phosphate-P method on an autoanalyzer (Lachat Quickchem FIA +8000, Zellweger Analytics, Milwaukee, Wisconsin). The availability of N in the soil was assumed to correspond to the rate at which NH₄⁺ plus NO₃⁻ accumulated on the resins (micrograms [µg] N per gram dry resin per day). The availability of P was assumed to correspond to the accumulation rate of PO₄³⁻ on the resins (µg P per gram dry resin per day). Error bars represent ± 1 standard error of the mean, and analysis of variance was used to infer statistical significance. The lowercase letters over the columns indicate significant differences (for panel a, $p < 0.05$; for panel b, $p < 0.002$).

but spot application methods should be used to minimize collateral damage to the surrounding native plants. Garlic mustard seedlings that germinate after the application are not affected, because glyphosate is activated only when it contacts leaves (Nuzzo 2000). Removing garlic mustard plants by hand is an effective method of management as long as the upper half of the taproot is completely removed; otherwise, adventitious buds are left to send up new stalks. Pulling is labor-intensive and can result in substantial soil disturbance (Nuzzo 2000). For successful removal by cutting, plants must be cut at the ground level, because cutting at a height of even 10 centimeters above ground level can result in a 29% survival rate (Nuzzo 1991).

Prescribed burning provides inconsistent management results (Nuzzo 2000). Luken and Shea (2000) performed three years of dormant-season (March) burns and observed no change in the abundance of garlic mustard. On the other hand, Schwartz and Heim (1996) found that both dormant-

season and growing-season (May) burns decreased the presence of garlic mustard, and that after three years of burning, garlic mustard still had not recovered to pre-burn densities. Likewise, the density and richness of native herbs, shrubs, and saplings remained below pre-burn values three years after the growing-season burn. The current recommended burning technique for the destruction of garlic mustard in fire-adapted communities consists of mid-intensity, consecutive late spring fires to reduce the abundance of rosettes and seedlings (Nuzzo 1991).

Overall, traditional weed management approaches, such as chemical spraying, mechanical removal, and fire disturbance, have proven to be largely ineffective in the long-term control of garlic mustard in highly invaded areas (Blossey et al. 2001). Biological control—the introduction of host-specific natural enemies from the plant's native range—may prove useful in the control of garlic mustard. Simulated herbivory experiments with garlic mustard suggest that biocontrol agents will be able to significantly decrease garlic mustard survival and seed production (Rebek and O'Neil 2005). At least 69 phytophagous insects are associated with garlic mustard in Europe (Szentesi 1991). The most destructive of these are weevils (Curculionidae), leaf beetles (Chrysomelidae), and butterflies and moths (Lepidoptera) (Blossey et al. 2001). Recent tests have revealed that *Ceutorhynchus scrobicollis*, a root-feeding weevil, is the most promising biological control agent, and a petition to release the weevil into the wild is being prepared (Gerber et al. 2007).

Conclusions

Garlic mustard now occurs in 34 states within the coterminous United States and in four Canadian provinces (Nuzzo 2000). With increased human activity, garlic mustard is predicted to spread from Prince Edward Island, Canada (northeast), to Minnesota (northwest), Iowa (southwest), and western North Carolina (southeast) (Welk et al. 2002). Another large potential habitat for garlic mustard is the Pacific Northwest (Welk et al. 2002), and populations have also been reported in New Zealand (Webb et al. 1988).

No single plant attribute is likely to explain the success of garlic mustard as an invasive species. Rather, it appears that garlic mustard possesses a combination of traits, all slightly different from those of the surrounding native plants, which results in a highly successful species that is altering the composition and function of the native communities it invades. Garlic mustard exudes secondary compounds that interfere with native plant germination, growth, and ability to form symbiotic relationships (Prati and Bossdorf 2004, Stinson et al. 2006); it has escaped its natural enemies (Cavers et al. 1979) and incurs little tissue loss to generalist herbivores (Nuzzo 2000, Blossey et al. 2001); it competes successfully for resources (Meekins and McCarthy 1999); its phenology

is substantially different from that of other native species; it is highly plastic in response to environmental variability (Byers and Quinn 1998); and it has high reproductive output (Cavers et al. 1979). Moreover, if garlic mustard alters the soil environment in which it grows (e.g., by increasing nutrient supply or decreasing the abundance of mycorrhizal fungi in the soil), then the invasion by garlic mustard may have a positive feedback effect on its future success.

It appears that the invasion of garlic mustard into eastern North American forests is an inevitable change that will have profound effects on native communities and the function of forest ecosystems. Garlic mustard invasion results in a decrease in the abundance of native species and the diversity of the plant communities (McCarthy 1997, Stinson et al. 2007). By affecting the growth rate of tree seedlings, the invasion of garlic mustard into the forest understory is likely to alter forest regeneration, with potential impacts on forest composition well into the future (Meekins and McCarthy 1999, Stinson et al. 2006). Garlic mustard not only affects the plants in the communities that it invades but also changes the activity of soil microorganisms, nutrient cycling, and plant-insect interactions.

Additional research is needed to further our understanding of the complex interactions of this new member of eastern North American forests. The intricate nature of both the mechanisms for its success and the impacts of its invasion can serve as a model system for our understanding of other plant invasions. Although small-scale eradication of this species can be successful, management over large spatial scales is considerably more difficult, and as management strategies continue to develop, garlic mustard is rapidly invading new habitats. Ready or not, garlic mustard is moving into your neck of the woods.

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