Commentary

A novel mechanism to explain success of invasive herbaceous species at the expense of natives in eastern hardwood forests

Among the more intriguing topics in general ecology courses are the symbiotic relationships (the '-isms' as I sometimes present them – mutualism, commensalism, and parasitism). Of these, mutualism is typically the most appealing to students. The scenario that different species can not only co-exist, but can also provide essential resources/services for one another, resonates well with all but the least interested in the course. Ultimately, however, there is also the palpable degree of dismay when they discover that these relationships arise from mutual exploitation, rather than from some benign force of nature. A flip-side of this, in many ways a type of dark side of nature, is something most ecology students have experienced directly – the degrading effects of invasive plant species on plant communities. Whether it is a verdant blanket of kudzu (*Pueraria lobata*) on Carolina pines, Japanese knotweed (*Microstegium vimineum*) extending beyond paths of the Appalachian Trail, or garlic mustard (*Alliaria petiolata*) creating a monospecific carpet on the forest floor of a temperate hardwood forest, most students have witnessed this phenomenon, with the more curious asking: why? Why is it that invasive species attain, and then maintain, the edge over their native counterparts? Building on earlier work published out of the same laboratory (Cantor *et al.*, 2011; Brouwer *et al.*, 2015), Hale *et al.*, in this issue of *New Phytologist* (pp. 542–549) address this very important question, and do so in a creative way, ultimately elucidating a novel explanation that answers this question – at least in part – for eastern hardwood forests, and they do so by invoking one of the more well-known mutualistic relationships: mycorrhizas.

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First, let us consider the ubiquitous nature of mycorrhizal associations, which arise from infection of roots of vascular plants by certain non-pathogenic fungi. The fungus exploits the plant root as a source of labile carbon (C), whereas the plant benefits from both enhanced access to soil resources, such as essential nutrients and H_2O, and increased defense against infection by pathogenic fungi (Martin *et al.*, 2007). Mycorrhizal fungi are a heterogeneous group comprising numerous species of the Phylum Glomeromycota, among other fungal phyla, and colonize roots of *c.* 240 000 plant species in essentially all terrestrial ecosystems (Öpik *et al.*, 2008). Depending on one's estimate of global vascular plant richness, this suggests that nearly 90% of vascular plants form mutualistic associations with mycorrhizal fungi. Thus, it is the non-mycorrhizal plants that are the exception to the rule, rather than the other way around.

Next, we should consider the unfortunately ubiquitous nature of species invasions, especially those of eastern deciduous forests of North America. As Luken (2014) pointed out, however, species invasions are not really that prevalent under non-disturbed conditions in such forests. The number of non-indigenous plant species, which can be quite high following stand-initiating events after canopy removal, decreases profoundly with successional age; this suggests a general competitive advantage of native over non-native plants (Luken, 2014). In fact, B. W. Wells, known for his early work in successional old-fields of the North Carolina Piedmont, described those early successional communities as a 'melting pot where foreigners and natives mingle' (Peet *et al.*, 2014). Thus, implicit in this scenario is that increased dominance of invasive species is usually associated with chronic anthropogenic disturbance; indeed, evidence strongly supports this contention – most successful invasions are facilitated to a great degree by such disturbances (Meekins & McCarthy, 2001; Reinhart & Callaway, 2006; Ehrenfeld, 2010).

One of the more aggressive invaders of the herbaceous layer of eastern deciduous forests of North America is garlic mustard (Luken, 2014). Like many of its invasive counterparts, garlic mustard did not mysteriously, insidiously creep into the North American flora. Rather, it was brought to the region from its native Europe by early colonists who used it for medicinal purposes and food (note: the genus *Alliaria* is derived from the genus *Allium* – garlic and relatives). Initial documentation for the species was in 1868 in the state of New York (Meekins & McCarthy, 2001). It owes much of its invasive success to a breadth of environmental tolerances and life history strategies. As a member of the Brassicaceae, it grows quickly and equally well under high-light and low-light conditions. An obligate biennial with first-year rosettes (Fig. 1a) followed in the second year by flowers (Fig. 1b), it is also self-compatible and produces numerous small seeds. Accordingly, a disturbance-initiated introduction of only a few individuals can quickly result in the monoculture dominance depicted in Fig. 1(b). Unlike strictly
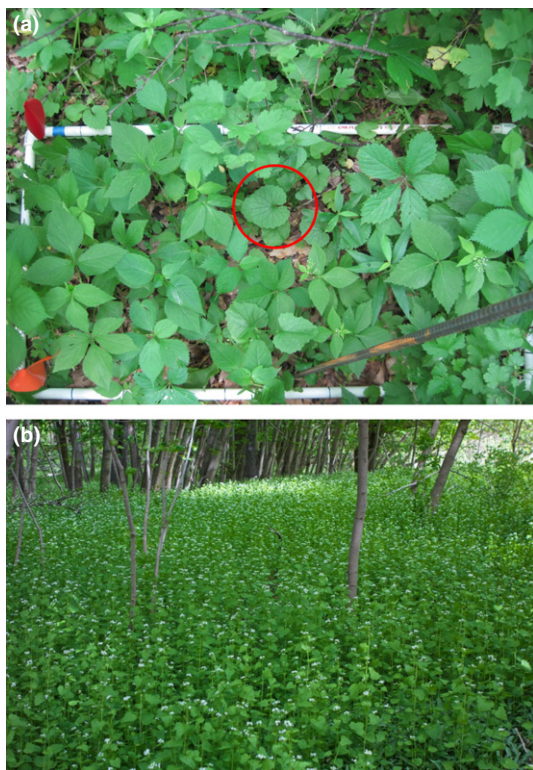
Fig. 1 (a) Garlic mustard co-existing among native species of the herbaceous layer of a deciduous forest of east-central Minnesota (Davis *et al.*, 2015). Note encircled cordate basal leaf in center, typical of vegetative first year of this obligate biennial (photograph credit: Mark Davis). (b) Garlic mustard as it dominates the herbaceous layer of a narrow strip of valley floor of a highly disturbed municipal woodland in Toronto, Canada (photograph credit: Roy Murray).

ruderal species with narrow habitat requirements and limited competitive capabilities, garlic mustard has demonstrated competitive superiority under a wide variety of conditions (Meekins & McCarthy, 2001).

However, direct interspecific competition is not the only mechanism to explain garlic mustard's propensity to aggressively dominate the forest herbaceous layer of impacted eastern hardwood forests (Fig. 1b). Considerable work has demonstrated conclusively that garlic mustard produces secondary compounds with allelopathic properties, particularly glucosinolate-derived compounds that are both highly bioactive and effective antifungal agents. An example would be allyl isothiocyanate, which is derived from sinigrin, a glucosinolate found in several species of the Brassicaceae, such as Brussels sprouts and broccoli (Cantor *et al.*, 2011).

Hale *et al.* initially address this mechanism by developing a conceptual model that takes allelopathic effects a step further – tying it into plant C balance and the cost/benefit associated with vascular plant roots hosting mycorrhizal fungi (which the authors refer to as root fungal symbionts (RFS)) (see Fig. 1 in Hale *et al.*). In an uninvaded forest, with the mycorrhizal hyphal network intact, the plant gives up a moderate amount of C as photosynthetic products to the fungus, which provides a considerable benefit to the plant via enhanced availability of

resources (i.e. H_2O and nutrients). However, in an invaded forest, with a well-established invasive plant cover, the fungicidal effects of invasive plant allelochemicals inhibit the soil hyphal network, but allow the internal root symbionts to remain intact. Under this scenario, there is actually greater C cost to the plant to maintain the symbionts, while gaining but a modicum of benefit because of the minimal hyphal network (Fig. 1 in Hale *et al.*).

To test their model, Hale *et al.* carried out a five-month field study wherein they added various materials to growth pots of feathery false lily of the valley (*Maianthemum racemosum*), a native forest herb which supports mycorrhizas and which is an important component in herbaceous layer communities throughout eastern deciduous forests (Gilliam, 2014). Materials included (1) green leaves of garlic mustard, (2) a non-systemic fungicide, and (3) green leaves of dames rocket (*Hesperis matronalis*), another member of the Brassicaceae. Because it lacks allelopathic properties, this served as the control in the experiment. In addition to monitoring the soil hyphal network, they measured several variables associated with ecophysiology (via direct measurement of net photosynthesis, transpiration, leaf conductance on intact plants) and C allocation (via harvesting and including C storage, root biomass, and asexual reproduction).

Notably, the effects of additions of fresh foliar material of garlic mustard and fungicide were essentially identical. Not only were there the expected reductions in mycorrhizal network biomass (Cantor *et al.*, 2011; Brouwer *et al.*, 2015), but there were also reductions in all ecophysiological and C allocation measurements in treated pots relative to controls receiving fresh, non-allelopathic foliar material (Hale *et al.*).

Hale *et al.* provide evidence that quite clearly supports their general mechanistic hypothesis (their fig. 1) for local extinction of native species in forests invaded by species with allelopathic properties. Inhibition of the mycorrhizal hyphal network by allelochemicals produced by the invasive garlic mustard creates C stress for native species resulting in both decreased plant vigor and, ultimately, abundance.

The work of Hale *et al.* is important and timely. The effects of successful plant invaders include a sharp drop in species richness of the herbaceous layer, the stratum with up to 90% of species richness in many forests (Gilliam, 2014). To be sure, there are other mechanisms that explain the success of invasive plants in novel terrestrial habitats, none of which is mutually exclusive to the others. In addition to the more 'textbook' explanations related to niche release via absence of native competitors and herbivores, these include invader-mediated changes in soil microbial communities (Reinhart & Callaway, 2006; Coats & Rumpho, 2014), changes in ecosystem-level function (e.g. nutrient cycling and energy flow; Ehrenfeld, 2010), and interference in reproductive patterns in native plant species (Jolls & Whigham, 2014). Gilliam (2006) suggested that excess nitrogen (N) can contribute simultaneously to increasing likelihood of invasion and invasion-driven changes in soil N dynamics. Clearly, the work of Hale *et al.* provides an intriguing addition to our understanding of how invasive plants function in impacted forest ecosystems.

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