

# A *Panax*-centric view of invasive species

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**Abstract** Plant-centric sampling provides a novel approach to quantifying the potential impact of invasive species on native plant species. The aim of this study was to determine the level of exposure of individuals and populations of *Panax quinquefolius* to invasive plant species using this approach in thirty natural ginseng populations. A high level of invasion was found with 63–70% of ginseng populations containing at least one invasive species. Approximately one-third of all individuals were found in close proximity to invasive plants. The most prevalent invasive species were *Rosa multiflora* and *Berberis thunbergii*. The exposure to invasives of plants in different size classes varied among populations. Invasive species presence increased with greater ginseng population sizes and presence of harvest. The abundance of invasives plants within forest interiors near this valuable medicinal herb suggests that the economic and ecological costs of competitive interactions with native species could be high.

**Keywords** Invasive species · *Panax quinquefolius* · American ginseng

## Introduction

Invasive species are economically and biologically damaging to the ecosystems in which they have been introduced (Pimentel et al. 2005; Wilcove et al. 1998). Escape from natural predators and pathogens (Callaway and Aschehoug 2000; Mitchell and Power 2003; Wolfe 2002), novel “weapons” (Bais et al. 2003; Callaway and Ridenour 2004), photosynthetic efficiency (Nagel and Griffin 2004), fast growth and prolific reproduction are some of the attributes of successful invasive plants (Kolar and Lodge 2001). Invasive plants can even change ecosystem properties such as soil chemistry (Ehrenfeld and Scott 2001) or ecosystem development (Vitousek et al. 1987). Most invasive plant species compete with natives for limited resources and some exude allelochemicals from their roots or through foliar leaching (Dorning and Cipollini 2005; Heisey 1990, 1996; Rose et al. 1983). Removal of established, invasive plants has been shown to cause an increase in native recruitment and diversity, thus suggesting they do suppress native species (McCarthy 1997; Thomson 2005). Those findings have considerable implications for forest regeneration following an invasion.

While literature on the effects of non-native invasive species on native species is extensive, no studies have examined the importance of invasives for economically valuable, native medicinal plant species. One widespread medicinal plant is American ginseng (*Panax quinquefolius*). Ginseng is an herbaceous perennial found within eastern deciduous forest

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interiors of North America. Ginseng is a flagship species that is not only important in an economic sense but also the harvest has great social and cultural significance, particularly in Appalachia (Bailey 1999). Currently, ginseng is uncommon, rare or endangered in most of its range (USDA 2007). Due to high levels of harvest and declining populations, ginseng harvest is listed on Appendix II of CITES (Convention on the International Trade in Endangered Species of Wild Fauna and Flora) (Robbins 2000; USFWS 2005). Despite this listing, there is still a great need for more information on the population and conservation status of ginseng (Robbins 2000), especially since invasive species pose some of the greatest threats to rare and endangered species (Wilcove et al. 1998).

Ginseng is a long-lived, slow-growing herb (Charron and Gagnon 1991) with populations that are threatened by poor harvest practices (Van der Voort and McGraw 2006), deer browsing (McGraw and Furedi 2005) and inbreeding along with reduced genetic diversity (Cruse-Sanders and Hamrick 2004; Mooney and McGraw 2007). Similar to other understory forest species, *P. quinquefolius* forms vesicular-arbuscular mycorrhizal (VAM) associations (Seo and Anderson 1990) which allow *P. quinquefolius* to survive in a range of soil conditions, particularly those that are phosphorus limited (Anderson et al. 1993). Allelopathic invasive plants produce chemical constituents that have been found to inhibit mycorrhizal colonization and growth (Roberts and Anderson 2001; Rose et al. 1983; Stinson et al. 2006), and would be expected, in turn, to negatively affect species dependent on those associations.

As a widespread, long-lived and slow-growing species of forest interiors, ginseng's exposure and susceptibility to invasive species is unknown. On one hand, many invasives occupy disturbed habitats (Hobbs and Huenneke 1992; Marvier et al. 2004; Stoltgren et al. 1999), which are uncharacteristic for forest herbs such as ginseng (Anderson et al. 1993). However, the diversity of habitats ginseng occupies (McGraw et al. 2003), the fact some invasive plants do penetrate undisturbed forests (Ehrenfeld 1997; Knapp and Canham 2000; Nuzzo 1999; Weber and Gibson 2007), and the long lifetimes of ginseng plants, suggest that the effects of invasives could be important. Furthermore, given ginseng's widespread occurrence in eastern deciduous forests (Charron and Gagnon 1991), ginseng may be exposed to invasives at

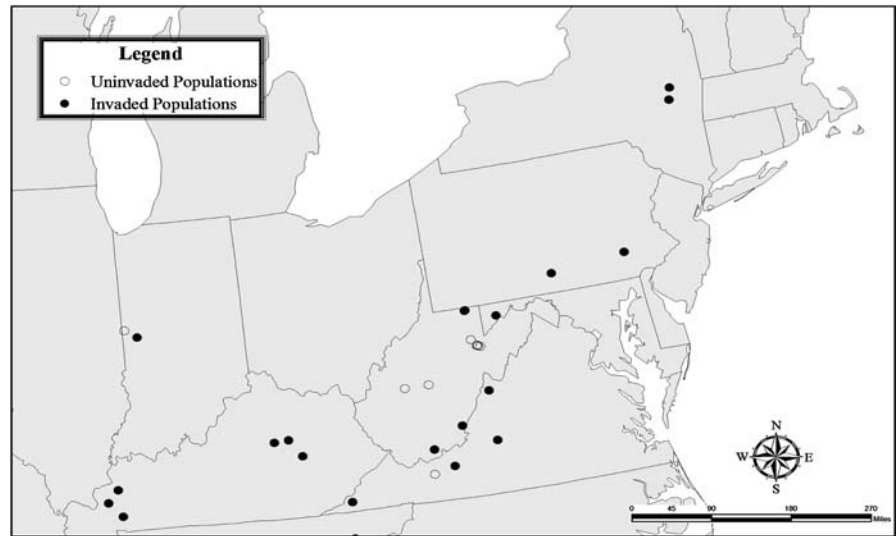
rates similar to other understory herbs. A study by Anderson et al. (1993) in Illinois found some of the most common herbs within ginseng populations included *Smilacina racemosa*, *Arisaema triphyllum*, *Sanicula marilandica*, *Phryma leptostachya*, *Podophyllum peltatum*, *Circaea quadrisulcata*, *Sanguinaria canadensis*, *Galium circaezans*, *Geranium maculatum* and *Osmorhiza claytonia*. With their similar niches, such understory species may be exposed to comparable levels of invasive species.

Given the importance of ginseng and the current threat of invasive plant species, the purpose of this study was to address the following questions: (1) What is the level of exposure of ginseng populations and individuals to invasive plant species? (2) What species of invasive plants are most abundant within ginseng populations? (3) Are all size classes of ginseng equally exposed to invasive plants or are certain stages more exposed than others? (4) Is presence of invasive species predicted by population size, elevation, latitude, and/or previous harvest?

## Methods

To assay invasive species, presence/absence data were recorded in 30 natural ginseng populations over the course of 2 years (2006 and 2007). Two years of censusing were necessary to ensure detection of invasive species that may have been missed inadvertently due to rarity or crypticity. These widely distributed populations were located in seven states (IN, KY, MD, NY, PA, VA, and WV), covering much of the breadth of ginseng's natural range (Fig. 1). The surveys were performed in mid to late May when the individual ginseng plants had fully emerged from dormancy and were least likely to have been deer browsed. Dormant plants were not surveyed; however plants that had emerged but had evidence of deer browse were included. Most populations were located within mixed mesophytic forests with tree species such as sugar maple (*Acer saccharum*) and tulip poplar (*Liriodendron tulipifera*) dominating the overstory (Table 1). Populations were located in a range of elevations and latitudes representative of the wide variety of habitats that ginseng occupies (Table 1). Furthermore, a few populations were located within marginal or atypical habitat for ginseng and some have been previously harvested.

**Fig. 1** Distribution of invaded and uninvaded study populations spread over 7 states in 2007



The invasive species survey was done while censusing ginseng for a long-term demographic study. Within each population, plants were located each year using a series of digital photographs, distances and directions to individuals that were cryptically tagged with engraved aluminum nails. New seedlings and new plants were given new nails and identification numbers as they were found, and the leaf number of each plant was recorded to delineate size classes. A total of 4,540 ginseng were surveyed in 2006 and 4,279 in 2007.

Traditionally, presence-absence surveys utilize randomly placed transects or quadrats to sample species occurrence (McIntyre et al. 1995; Weber and Gibson 2007). However, the aim of this paper was to examine the level of exposure of only ginseng plants. Therefore, invasive species' presence data were collected on a plant-by-plant basis to determine the total proportion of individuals exposed to invasive plants as well as the frequency of invasive plants at each site. Invasive, herbaceous plants were recorded as present if they fell within a 2 m radius of a ginseng plant, while shrubs were recorded as present if within 5 m, and trees if within 10 m. These distances were conservatively chosen to represent the outer limits of distances at which the invasive plants may competitively or chemically affect ginseng. For example, allelopathic trees such as tree-of-heaven not only emit allelochemicals from roots but also from leaf litter (Heisey 1990; Heisey 1996) which would make 10 m a reasonable distance for possible effects. These distances may

overestimate the number of plants that presently affect ginseng but conservatively estimate the number that are 'poised' to potentially impact ginseng in the near future. For instance, garlic mustard has been found to spread 5.4 m/year (Nuzzo 1999). Without knowing the competitive reach of each invasive species, this first approximation of competitive range was made as a compromise between these two factors.

Data on invasive species' presence were used to calculate the proportion of ginseng populations with invasive species present as well as the proportion of ginseng individuals with an invasive plant within a potentially competitive range. Absence of invasive species in a population does not imply that they are not present at the site; only that there were none within competitive range of ginseng. Relative abundance of the invasive species was compared using the *Panax*-centric presence data as well. For those populations that had invasives, the proportion of each ginseng size class that had invasives within competitive range was calculated. Size categories were based on the leaf number (1, 2, and 3 or more), roughly corresponding to seedlings, juveniles and adults (Charron and Gagnon 1991; McGraw and Furedi 2005). Data were then analyzed using a log-likelihood test to determine if there were differences among populations and size classes ('main effects' in the model) in proportion of individual ginseng plants with invasive species in competitive range. The interaction term was included to determine whether size class differences varied among populations.

**Table 1** Attributes of study populations

State	Population	Known harvest history	Overstory	Elevation (m)	Latitude <sup>a</sup>
WV	1	Y	MM	775	37.4
WV	2	N	AH	764	39.1
KY	3	N	MM	314	37.5
WV	4	N	AH	758	39.0
MD	5	Y	MM	577	39.5
WV	6	Y	MM	370	38.5
WV	7	N	AH	630	39.0
KY	8	Y	MM	148	37.3
PA	9	Y	MM	146	40.2
KY	10	N	MM	276	37.6
KY	11	Y	MM	217	37.8
WV	12	N	MM	618	37.8
NY	13	N	AH	466	42.5
VA	14	Y	MM	743	36.9
PA	15	N	MM	230	40.0
WV	16	Y	MM	258	38.5
KY	17	N	MM	106	37.1
VA	18	N	AH	1073	38.2
VA	19	Y	OH	595	37.4
WV	20	Y	MM	538	39.7
WV	21	Y	MM	526	39.7
VA	22	Y	MM	591	37.1
WV	23	N	MM	333	39.6
KY	24	N	MM	167	36.9
NY	25	Y	AH	204	42.7
IN	26	Y	MM	194	39.9
IN	27	N	MM	171	40.0
WV	28	N	AH	761	39.1
WV	29	N	MM	783	39.1
VA	30	N	OH	591	37.0
7 States	30 Populations	46% Harvested	67% MM 27% AH 6% OH		

<sup>a</sup> Measured in decimal degrees and rounded for this table to protect location of populations

Harvest history (during census period): N = none, Y = yes; Overstory: MM = mixed mesophytic, AH = Allegheny hardwoods, OH = oak-hickory

Presence of invasive species was related to ginseng population size, elevation, and latitude using logistic regression to test the hypothesis that these environmental variables would predict presence of invasives. *A priori*, we expected that small populations and those from high elevations and latitudes would have a lower probability of invasive species presence. For populations with invasive species, we used linear regression to examine the number of ginseng plants with an invasive in range as a function of population size as well as the proportion of

ginseng plants with invasives in range as a function of population size. Finally, a log-likelihood test was used to determine if the presence of harvest would predict presence of invasive species.

## Results

Invasive plant species were found in 19 out of 30 ginseng populations (63%) in 2006 and 21 out of 30 ginseng populations (70%) in 2007 (Table 2, Fig. 1).

**Table 2** Proportion of ginseng individuals with invasive plant within competitive range in each population in 2006 and 2007

Population	2006 Invaded/N	2007 Invaded/N	Invasive species present
1	57/63	44/44	BT <sup>a</sup> , RM
2	0/34	0/22	N/A
3	0/433	3/344	RM <sup>b</sup>
4	26/86	29/87	BT
5	104/175	91/184	AP
6	0/60	0/71	N/A
7	0/11	0/10	N/A
8	0/48	19/38	LO <sup>b</sup>
9	93/100	90/102	AC <sup>a</sup> , AP, BT, EU <sup>a</sup> , LS, LO, RM
10	34/91	44/93	LJ, RM
11	104/281	114/155	LO, MV <sup>a</sup> , RM
12	14/151	27/138	BT, EA <sup>b</sup> , LO, RM
13	7/320	3/342	BT
14	44/213	44/153	MV <sup>a</sup> , RM
15	347/387	421/485	AA, BT, EU <sup>a</sup> , MV <sup>a</sup> , RM, RP
16	5/97	0/94	RM
17	10/99	53/65	AA <sup>b</sup> , LO, LJ
18	9/55	20/45	AP, LO <sup>b</sup> , RM <sup>b</sup>
19	251/311	239/241	AP, LO, RM
20	48/126	51/124	RM
21	32/407	39/407	AA <sup>b</sup> , BT, RM
22	114/130	68/112	BT, LO, LJ <sup>b</sup> , RM
23	0/162	0/104	N/A
24	0/63	126/126	AA <sup>b</sup>
25	22/76	33/102	BT, LO <sup>b</sup>
26	8/131	26/126	AP <sup>b</sup> , LO <sup>b</sup> , RM
27	0/160	0/168	N/A
28	0/100	0/103	N/A
29	0/136	0/159	N/A
30	0/33	0/35	N/A
Total	1,329/4,540	1,584/4,279	

<sup>a</sup> 2006 only; <sup>b</sup> 2007 only

AA = *Ailanthus altissima*,  
 AC = *Acer platanoides*,  
 AP = *Alliaria petiolata*,  
 BT = *Berberis thunbergii*  
 EU = *Eleagnus umbellata*,  
 EA = *Euonymus alatus*,  
 LS = *Ligustrum spp.*,  
 LJ = *Lonicera japonica*  
 LO = *Lonicera spp.*,  
 MS = *Microstegium*  
*vimineum*, RM = *Rosa*  
*multiflora*, RP = *Rubus*  
*phoenicolasius*

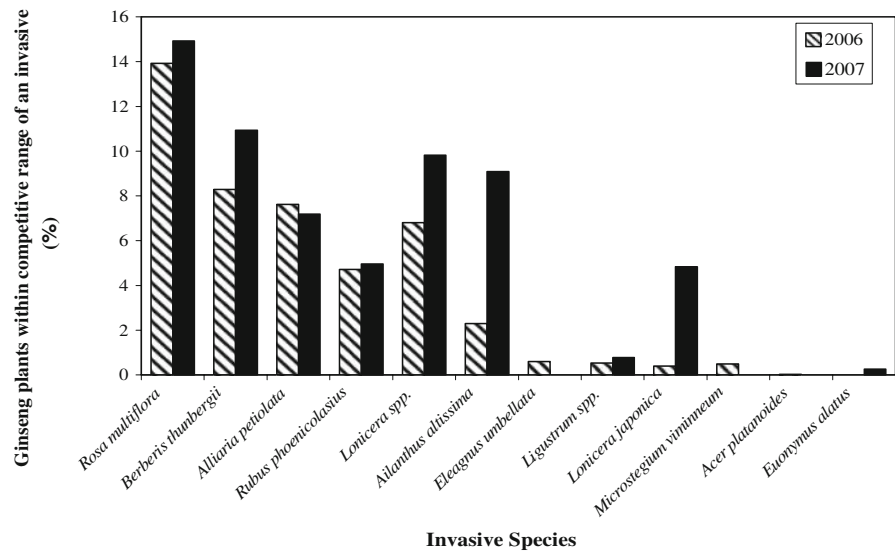
Furthermore, 10 populations in 2006 had more than one invasive species while 13 populations had multiple invasive species in 2007 (Table 2). In 2006, one site, population 9, contained 7 different invasive species (Table 2).

As with populations, exposure of ginseng individuals within was high. A total of 1,329 out of 4,540 (29.3%) ginseng individuals had an invasive plant within competitive range in 2006 and 1,584 out of 4279 (37.0%) ginseng were exposed to invasive plants in 2007.

Twelve invasive species were found within the study populations. Overall, two herbaceous invasive

species (*Alliaria petiolata* and *Microstegium vimineum*), eight shrub species (*Lonicera japonica*, *Lonicera sp.*, *Rosa multiflora*, *Berberis thunbergii*, *Rubus phoenicolasius*, *Elaeagnus umbellata*, *Euonymus alatus*, *Ligustrum spp.*), and two tree species (*Acer platanoides* and *Ailanthus altissima*) were found within ginseng populations. Due to the timing of the survey and the lack of reproductive structures, the bush honeysuckles and privet were not identified to the species level. Therefore, the bush honeysuckle category may have included up to four species (*Lonicera tatarica*, *L. morrowii*, *L. x bella* and *L. maackii*) and the privet category could have

**Fig. 2** Percentage of individual ginseng plants having a particular invasive within competitive range for 2006 ( $N = 4,540$ ) and 2007 ( $N = 4,279$ )



included either *Ligustrum obtusifolium* or *Ligustrum vulgare*. The most abundant invasive species at the individual and population levels for both years were multiflora rose (*Rosa multiflora*) and Japanese barberry (*Berberis thunbergii*) (Table 2, Fig. 2).

Different size classes of ginseng were not equally exposed to invasive species, however the specific pattern varied among populations (population  $\times$  size class of ginseng interaction; 2006,  $L - R = 103.049$ ,  $P < 0.0001$ ; 2007,  $L - R = 83.2903$ ,  $P < 0.0001$ ). In 2006 and 2007, sites such as 1, 9 and 15 all had greater than 80% invasion in all classes (Fig. 3a, b). In contrast, sites such as 4 and 18 had higher proportions of seedlings with invasives in range while population 11, 12 and 20 had more adults exposed in 2006 (Fig. 3a). In 2007, populations 19 and 24 also had greater than 80% invasion (Fig. 3b). Also in 2007, population 4 had mostly seedlings exposed while population 18 had mostly juveniles and populations 11 and 20 had more adults (Fig. 3b).

In 2006, there was no clear propensity for larger populations to contain invasive species ( $\chi^2 = 2.191$ ,  $P = 0.1388$ ), however in 2007, there was a significant positive relationship between population size and presence of invasives ( $\chi^2 = 4.726$ ,  $P = 0.0297$ ). For populations with invasive plants, the number of ginseng individuals with invasives in range was positively related to population size in 2006 (slope = 0.429468,  $P = 0.0199$ ) and 2007 (slope = 0.389218,  $P = 0.0156$ ). However, in invaded populations, the proportion of individuals with invasives in range was not

related to population size in either year (slope = 0.0005,  $P = 0.9469$ ; slope =  $-0.0005$ ,  $P = 0.3903$ ).

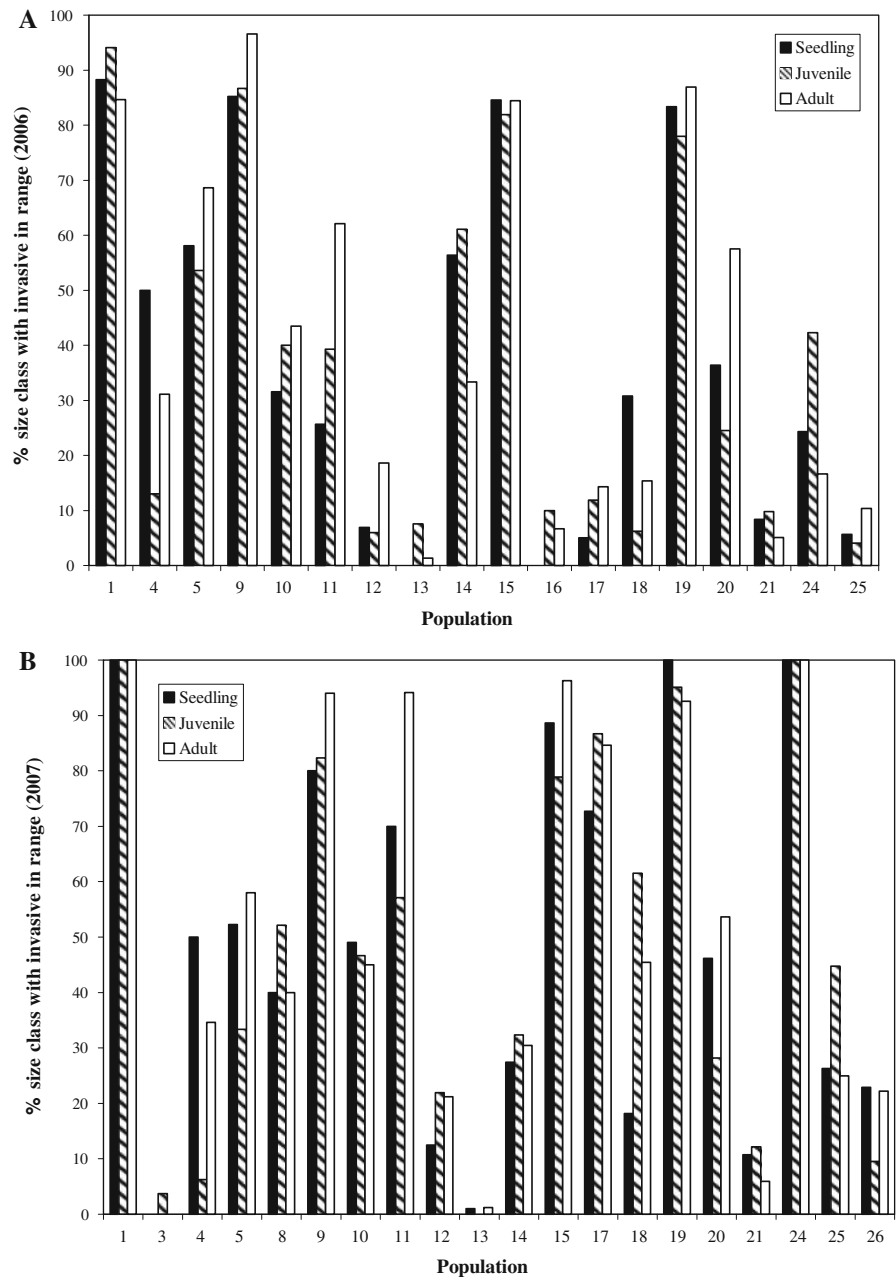
Elevation did not significantly affect the presence of invasive species in 2006 or 2007 ( $\chi^2 = 0.012207$ ,  $P = 0.9120$ ;  $\chi^2 = 1.2622$ ,  $P = 0.2612$ ), nor did latitude ( $\chi^2 = 0.609945$ ,  $P = .4348$ ;  $\chi^2 = 1.2622$ ,  $P = 0.2612$ ). In 2006 and 2007, previously harvested populations were more likely to contain invasive species ( $L - R = 6.016$ ,  $P = 0.0142$ ;  $L - R = 5.6599$ ,  $P = 0.0174$ ).

## Discussion

Documenting the presence of an invasive plant species in a community is of limited value with respect to estimating potential impact. Using individual plants of a native species as a phytometer (Antonovics and Primack 1982), however, comes closer to quantifying potential impact. This study is the first attempt to document the level of exposure of a particular understory herb to invasive plant species on a plant-centric basis across much of its range.

Past land use history may explain the presence of invasive plant species (Lundgren et al. 2004), particularly at sites containing multiple invasive species and high numbers of invasion. Population 9 had the highest diversity of invasive species and was located in a small tract of land fragmented by housing development which may explain the presence of ornamental species such as *Ligustrum* spp. Another

**Fig. 3** Percentage of individuals within ginseng size classes having invasives in competitive range in (a) 2006, and (b) 2007



population, 1, which contained a high level of *Rosa multiflora*, was previously disturbed by municipal activity and is also bordered by agricultural fields. In the case of population 15, it had nearby agricultural fields. While these populations of ginseng were within marginal habitats for the species, in such environments invasive species may have a negative consequence for continued persistence. With increased suburban sprawl and forest fragmentation,

an increasing fraction of ginseng populations may be found in these environments.

Site-specific factors may explain the differences in invaded size classes of ginseng by population. Populations 1, 9 and 15 were located within marginal habitat, which could explain the high levels of invasion among all size classes. The high level of invasion among the seedling class at population 18 may have been due to greater recruitment near the

edge of the forest, closest to light gaps where many of the invasives reside. In 2006, a higher proportion of seedlings at population 11 had invasives in range, while a recent harvest in 2007 removed half of the adults from the population in a portion of the site that was least invaded.

The increased likelihood that larger populations of ginseng were invaded and contained multiple invasive species was most likely due to the fact that larger populations covered more area, thus increasing the probability of encountering invasive species. If this were not the case, then the proportion of individuals with invasives in range would have also been a function of population size, and this was not found.

Harvested populations also tended to have invasive species. Removal of ginseng for harvest disturbs the litter layer and may facilitate colonization by invasives or other species, depending on availability of propagules. How species react to disturbance depends not only on characteristics of the disturbance (size, intensity, and timing) but also the attributes of surrounding species (Hobbs and Huenneke 1992). Several of the harvested populations were in atypical and marginal habitat, close to edges in which humans could easily access, harvest and disturb the landscape to allow invasive colonization. Species such as *A. petiolata* are not facilitated by litter disturbance (Meekins and McCarthy 2001), yet others such as *M. vimineum* have been found to positively respond (Oswalt and Oswalt 2007). Humans may further function as vectors for invasive plants by accidentally importing seeds on their shoes, clothing and equipment.

Invasives such as *Rosa multiflora* (affecting 13.9–14.9% of ginseng plants) and *Berberis thunbergii* (affecting 8.3–10.9% of ginseng plants) were the most ubiquitous invaders among ginseng individuals and populations. *R. multiflora* has been found to be one of the most frequent invasive plants in an old growth forest in Indiana (Weber and Gibson 2007), and within forest fragments (Brothers and Spingam 1992). Another study found both invasive species to be dominant across their sites (Lundgren et al. 2004). *R. multiflora* has been found to create dense thickets which may competitively exclude native species, while *Berberis thunbergii* may alter the microbial community structure within soils in as little as 3 months (Kourtev et al. 2002; Kourtev et al. 2003).

Dispersal patterns of the invasives found on ginseng sites may explain their presence in forest interiors. Birds and mammals have been found to disperse many of the invasive honeysuckles, *R. multiflora* and *B. thunbergii* (Vellend 2002; Myers et al. 2004; Ehrenfeld 1997). Indeed, some invasive plants were originally planted for wildlife forage (Dyess et al. 1994; Ehrenfeld 1997; Handley 1945; Steavenson 1946). *L. tatarica* was even found to be preferentially selected by frugivores (Drummond 2005). Long distance dispersal and ability to invade canopy gaps by species such as *A. altissima* may also explain presence in forest interiors (Knapp and Canham 2000; Landenberger et al. 2007).

The abundance of particular invasive species changed between 2006 and 2007. Although there were exceptions, most differences between years were not interpreted as reflecting spread or decline of the invasive species. In the case of bush honeysuckle (*Lonicera* sp.), more was found in 2007, but this is likely due to increased detection of this species group by surveyors after unexpectedly encountering them in the first year. However, the greater presence of *Ailanthus altissima* in 2007 than in 2006 was due to new colonization by seedlings in four previously uninvaded populations. *Lonicera japonica*, known to produce dense mats of vegetation which excludes native seedlings (Hardt 1986; Myster and Pickett 1992), had increased presence around ginseng individuals between 2006 and 2007. The absence of *Microstegium vimineum*, *Acer platanoides*, and *Euonymus alatus* in 2007 was due to the dormancy or death of ginseng individuals near them, though the invasives were still present. The same occurrence happened in population 16, in which no invasives were recorded in competitive range of ginseng in 2007. Between 2006 and 2007, a late frost also caused many ginseng individuals to go dormant or die, which caused a decline in total ginseng population numbers and potentially an increase in the percentage of invasives. Several populations were further harvested between the 2 years which could also account for changes in invasive presence/absence.

Several invasive plants found in ginseng populations have allelopathic properties. *L. maackii* extracts from leaves and roots on seed germination revealed significant decreases in germination of 3 herb species (Dorning and Cipollini 2005). *A. altissima* also has



been found to reduce growth of seedlings from several crop species (De Feo et al. 2003; Heisey 1990; 1996). Garlic mustard is another allelopathic species whose extracts were found to reduce germination and colonization of mycorrhizae of several crop species (Prati and Bossdorf 2004; Roberts and Anderson 2001) as well as reduced the growth of arbuscular-mycorrhizal fungi (AMF) dependent tree species (Stinson et al. 2006). Changes in arbuscular-mycorrhizal fungi can have not only individual effects on host plants but also population and community level impacts (Smith and Read 1997).

Overall, a high level of invasion was found within ginseng populations and within competitive ranges of ginseng. Given ginseng's widespread distribution within eastern deciduous forests, it is probable that other similar understory plants experience a comparable level of exposure. The presence of multiple invasive species within ginseng populations also presents the possibility of inter-invasive facilitation through factors such as soil modification (Jordan et al. 2007). Alteration of soils by allelopathy (Heisey 1990; 1996; Prati and Bossdorf 2004; Roberts and Anderson 2001; Stinson et al. 2006) or through litter inputs (Wolfe and Klironomos 2005) may change nutrients in soil which could impact vegetative and reproductive success in ginseng (Shahi 2007). Interactions between invasive species and ginseng may have undesirable effects on demography of ginseng, especially in addition to the current pressures of harvest and deer browse.

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## References

- Anderson RC, Fralish JS, Armstrong JE (1993) The ecology and biology of *Panax quinquefolium* L. (Araliaceae) in Illinois. *Am Midl Nat* 129:357–372. doi:10.2307/2426517
- Antonovics J, Primack RB (1982) Experimental ecological genetics in *Plantago*. VI. The demography of seedling transplants of *P. lanceolata*. *J Ecol* 70:55–75. doi:10.2307/2259864
- Bailey B (1999) Social and economic impacts of wild harvested products. Ph.D. Dissertation, West Virginia University, Morgantown, WV
- Bais HP, Vepachedu R, Gilroy S, Callaway RM, Vivanco JM (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* 301(5):1377–1380. doi:10.1126/science.1083245
- Brothers TS, Spingam A (1992) Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conserv Biol* 6(1):91–100. doi:10.1046/j.1523-1739.1992.610091.x
- Callaway RM, Aschehoug ET (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290:521–523. doi:10.1126/science.290.5491.521
- Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Front Ecol* 2(8):436–443
- Charron D, Gagnon D (1991) The demography of northern populations of *Panax quinquefolium* (American ginseng). *J Ecol* 79(2):431–445. doi:10.2307/2260724
- Cruse-Sanders JM, Hamrick JL (2004) Spatial and genetic structure within populations of wild American ginseng (*Panax quinquefolium* L. Araliaceae). *J Hered* 95(4):309–321. doi:10.1093/jhered/esh046
- De Feo V, De Martino L, Quaranta E, Pizza C (2003) Isolation of phytotoxic compounds from tree-of-heaven (*Ailanthus altissima* Swingle). *J Agric Food Chem* 51(5):1177–1180. doi:10.1021/jf020686+
- Dorning M, Cipollini D (2005) Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecol* 184(2):287–296. doi:10.1007/s11258-005-9073-4
- Drummond BA (2005) The selection of native and invasive plants by frugivorous birds in Maine. *Northeast Nat* 12(1):33–44. doi:10.1656/1092-6194(2005)012[0033:TSONAIJ]2.0.CO;2
- Dyess JG, Causey MK, Striblin HL, Lockaby BG (1994) Effects of fertilization on production and quality of Japanese honeysuckle. *Southern J Appl Forestry* 18:68–71
- Ehrenfeld JG (1997) Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC). *J Torrey Bot Soc* 124(2):210–215. doi:10.2307/2996586
- Ehrenfeld JG, Scott NS (2001) Invasive species and the soil: effects on organisms and ecosystem processes. *Ecol Appl* 11(5):1259–1260. doi:10.1890/1051-0761(2001)011[1259:ISATSEJ]2.0.CO;2
- Handley CO (1945) Japanese honeysuckle in wildlife. *J Wildl Manage* 9:261–264. doi:10.2307/3796367
- Hardt RA (1986) Japanese honeysuckle: from “one of the best” to ruthless pest. *Arnoldia* 25(3):27–34
- Heisey RM (1990) Allelopathic and herbicidal effects of extracts from Tree of Heaven (*Ailanthus altissima*). *Am J Bot* 77(5):662–670. doi:10.2307/2444812
- Heisey RM (1996) Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characterization of its herbicidal activity. *Am J Bot* 83(2):192–200. doi:10.2307/2445938
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv Biol* 6(3):324–337. doi:10.1046/j.1523-1739.1992.06030324.x
- Jordan NR, Larson DL, Huerd SC (2007) Soil modification by invasive plants: effects on native and invasive species of mixed-grass prairies. *Biol Invasions* 10(2):177–190
- Knapp LB, Canham CD (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth

- and recruitment in canopy gaps. *J Torrey Bot Soc* 127:307–315. doi:[10.2307/3088649](https://doi.org/10.2307/3088649)
- Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends Ecol Evol* 16(4):199–204. doi:[10.1016/S0169-5347\(01\)02101-2](https://doi.org/10.1016/S0169-5347(01)02101-2)
- Kourtev PS, Ehrenfeld JG, Haggblom M (2002) Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83(11):3152–3166
- Kourtev PS, Ehrenfeld JG, Haggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biol Biochem* 35:895–905. doi:[10.1016/S0038-0717\(03\)00120-2](https://doi.org/10.1016/S0038-0717(03)00120-2)
- Landenberger RE, Kota NL, McGraw JB (2007) Seed dispersal of the non-native invasive tree *Ailanthus altissima* into contrasting environments. *Plant Ecol* 192(1):55–70. doi:[10.1007/s11258-006-9226-0](https://doi.org/10.1007/s11258-006-9226-0)
- Lundgren MR, Small CJ, Dreyer GD (2004) Influence of land use and site characteristics on invasive plant abundance in the Quinebaug highlands of southern New England. *Northeast Nat* 11(3):313–332. doi:[10.1656/1092-6194\(2004\)011\[0313:IOLUAS\]2.0.CO;2](https://doi.org/10.1656/1092-6194(2004)011[0313:IOLUAS]2.0.CO;2)
- Marvier M, Karieva P, Neubert MG (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Anal* 24(4):869–878. doi:[10.1111/j.0272-4332.2004.00485.x](https://doi.org/10.1111/j.0272-4332.2004.00485.x)
- McCarthy B (1997) Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae). In: Luken JO, Thieret JW (eds) *Assessment and management of plant invasions*. Springer-Verlag, New York, pp 117–130
- McGraw JB, Furedi MA (2005) Deer browsing and population viability of a forest understory plant. *Science* 307:920–922. doi:[10.1126/science.1107036](https://doi.org/10.1126/science.1107036)
- McGraw JB, Sers SM, Van der Voort ME (2003) Distribution and abundance of *Hydrastis canadensis* L. (Ranunculaceae) and *Panax quinquefolius* L. (Araliaceae) in the central Appalachian region. *J Torrey Bot Soc* 130(2): 62–69. doi:[10.2307/3557530](https://doi.org/10.2307/3557530)
- McIntyre S, Lavorel S, Tremont RM (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J Ecol* 83(1):31–44. doi:[10.2307/2261148](https://doi.org/10.2307/2261148)
- Meekins JF, McCarthy BC (2001) Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecol Appl* 11(5):1336–1348. doi:[10.1890/1051-0761\(2001\)011\[1336:EOEVOT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1336:EOEVOT]2.0.CO;2)
- Mitchell CG, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421:625–627. doi:[10.1038/nature01317](https://doi.org/10.1038/nature01317)
- Mooney EH, McGraw JB (2007) Alteration of selection regime resulting from harvest of American ginseng, *Panax quinquefolius*. *Conserv Genet* 8:57–67. doi:[10.1007/s10592-006-9148-3](https://doi.org/10.1007/s10592-006-9148-3)
- Myers JA, Vellend M, Gardescu S, Marks PL (2004) Seed dispersal by white-tailed deer: implications for long-distance dispersal, invasion, and migration of plants in eastern North America. *Oecologia* 139(1):1432–1939
- Myster RW, Pickett STA (1992) Dynamics of associations between plants in ten old fields during 31 years of succession. *J Ecol* 80:291–302. doi:[10.2307/2261012](https://doi.org/10.2307/2261012)
- Nagel JM, Griffin KL (2004) Can gas-exchange characteristics help explain the invasive success of *Lythrum salicaria*?. *Biol Invasions* 6:101–111. doi:[10.1023/B:BINV.0000010125.93370.32](https://doi.org/10.1023/B:BINV.0000010125.93370.32)
- Nuzzo V (1999) Invasion pattern of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. *Biol Invasions* 1:169–179. doi:[10.1023/A:1010009514048](https://doi.org/10.1023/A:1010009514048)
- Oswalt CM, Oswalt SN (2007) Winter litter disturbance facilitates the spread of the nonnative invasive grass *Microstegium vimineum* (Trin.) A. Camus. *For Ecol Manage* 249(3):199–203
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* 52:273–288. doi:[10.1016/j.ecolecon.2004.07.013](https://doi.org/10.1016/j.ecolecon.2004.07.013)
- Prati D, Bossdorf O (2004) Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *Am J Bot* 91(2):285–288. doi:[10.3732/ajb.91.2.285](https://doi.org/10.3732/ajb.91.2.285)
- Robbins CS (2000) Comparative analysis of management regimes and medicinal plant trade monitoring mechanisms for American ginseng and goldenseal. *Conserv Biol* 14:1422–1434. doi:[10.1046/j.1523-1739.2000.99100.x](https://doi.org/10.1046/j.1523-1739.2000.99100.x)
- Roberts KJ, Anderson RC (2001) Effect of garlic mustard [*Alliaria petiolata*] (Beib. Cavara & Grande)] extracts on plants and arbuscular mycorrhizal (AM) fungi. *Am Midl Nat* 146:146–152. doi:[10.1674/0003-0031\(2001\)146\[0146:EOGMAP\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2001)146[0146:EOGMAP]2.0.CO;2)
- Rose SL, Perry DA, Pilz D, Schoeneberger MM (1983) Allelopathic effects of litter on the growth and colonization of mycorrhizal fungi. *J Chem Ecol* 9(8):1153–1162. doi:[10.1007/BF00982218](https://doi.org/10.1007/BF00982218)
- Seo H, Anderson RC (1990) Effect of soil microbial and mycorrhizal associations on the productivity and photosynthetic rates of *Panax quinquefolium* L. *Myc Soc Am Newsl* 41:4
- Shahi DP (2007) Effects of density on reproduction and demographic structures of American ginseng (*Panax quinquefolius*) populations in Ohio. PhD dissertation. Bowling Green State University; Bowling Green, OH
- Smith SE, Read DJ (1997) *Mycorrhizal symbiosis*. Academic Press, San Diego
- Stevenson HA (1946) Multiflora rose for farm hedges. *J Wildl Manage* 10(3):227–234. doi:[10.2307/3795837](https://doi.org/10.2307/3795837)
- Stinson KA, Campbell SA, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biol* 4(5):0727–0731
- Stolgren TJ, Schell LD, Heuvel BV (1999) How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecol Appl* 9:45–64. doi:[10.1890/1051-0761\(1999\)009\[0045:HGASQA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[0045:HGASQA]2.0.CO;2)
- Thomson D (2005) Measuring the effects of invasive species on the demography of a rare endemic plant. *Biol Invasions* 7:615–624. doi:[10.1007/s10530-004-5853-3](https://doi.org/10.1007/s10530-004-5853-3)
- United States Department of Agriculture, Natural Resources Conservation Service (2007) The PLANTS Database

- (<http://plants.usda.gov>, 11 December 2007). National Plant Data Center, Baton Rouge, LA 70874-4490 USA
- United States Fish and Wildlife Service (2005) Convention permit applications for wild American ginseng harvested in 2005. Washington, DC, USA
- Van der Voort ME, McGraw JB (2006) Effects of harvester behavior on populations growth rate affects sustainability of ginseng trade. *Biol Conserv* 130:505–516. doi: [10.1016/j.biocon.2006.01.010](https://doi.org/10.1016/j.biocon.2006.01.010)
- Vellend M (2002) A pest and an invader: white-tailed deer (*Odocoileus virginianus* Zimm.) as a seed dispersal agent for honeysuckle shrubs (*Lonicera* L.). *Nat Areas J* 22(3):230–234
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Watson PA (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238(4828):802–804. doi: [10.1126/science.238.4828.802](https://doi.org/10.1126/science.238.4828.802)
- Weber JS, Gibson KD (2007) Exotic plant species in old-growth forest in Indiana. *Weed Sci* 55:299–304. doi: [10.1614/WS-06-164.1](https://doi.org/10.1614/WS-06-164.1)
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *Bioscience* 48(8):607–615. doi: [10.2307/1313420](https://doi.org/10.2307/1313420)
- Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *Am Nat* 160(6):705–711. doi: [10.1086/343872](https://doi.org/10.1086/343872)
- Wolfe BE, Klironomos JN (2005) Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55(6):477–488. doi: [10.1641/0006-3568\(2005\)055\[0477:BNGSCA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[0477:BNGSCA]2.0.CO;2)