

Nonconsumptive effects of a generalist ungulate herbivore drive decline of unpalatable forest herbs

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Abstract. High herbivore pressure is expected to benefit unpalatable species that co-occur with palatable browsed species. However, for five unpalatable understory species we found no evidence of benefit from deer browse. Detailed studies of one species in natural populations, *Arisaema triphyllum*, revealed surprising changes in its population structure and demography: deer browse level on a palatable species significantly correlates with reduced plant size and seed rain and male-biased sex ratios of co-occurring *Arisaema* populations. Analyses of individual size in five unpalatable forest plant species in long-term experimental paired deer enclosure/deer access plots corroborate the natural site results; all five species were smaller in deer access plots. Analyses of abiotic variables in natural and experimental sites suggest one potential mechanism for indirect effects of deer. Deer-mediated soil quality declines included increased soil penetration resistance and decreased leaf litter depth, which are known to hinder plant growth. Our results are likely applicable to other unpalatable forest species and have clear consequences for understory biodiversity. Unpalatable plant species in forests experiencing high deer numbers may be in decline along with their palatable neighbors. Our study implicates deer overabundance in the cascade of forest species decline and the urgency of this conservation issue in North America.

Key words: *Arisaema triphyllum*; biodiversity; generalist herbivores; indirect effects; indirect facilitation; *Odocoileus virginianus*; overbrowsing; palatable plants; Pennsylvania, USA; species interactions; *Trillium*; unbrowsed and unpalatable plants.

INTRODUCTION

Herbivores are key drivers of their individual prey plant's performance (reviewed in Gurevitch et al. 2000, Morris et al. 2007) and can profoundly affect the composition and function of plant populations and communities (reviewed in Huntly 1991, Strauss and Agrawal 1999). The effect of herbivores on co-occurring unpalatable plant species is less clear. Unpalatable or non-browsed species are predicted to benefit from herbivores if their consumption of palatable neighbors causes competitive release (Rooney and Waller 2003) or if high levels of herbivory favor increased abundances of unbrowsed species as palatable prey plants are lost from the community (Graff et al. 2007). Conversely, if the herbivores are large mammals, their nonconsumptive effects can create unfavorable conditions for both palatable and unpalatable plant growth. These include direct effects such as trampling (reviewed in Persson et al. 2000) or indirect influences via decreased soil fertility (Olofsson and Oksanen 2002, Bakker et al. 2004), degraded soil quality (Wardle et al. 2001), and poten-

tially increased exotic species abundance (Vavra et al. 2007). The extent to which unpalatable plants benefit from herbivores depends upon how the herbivores affect local abiotic and biotic contexts, which can vary over space and time (Wilson and Nisbet 1997, Graff et al. 2007, Alberti et al. 2008, Crain 2008).

White-tailed deer (*Odocoileus virginianus* Zimmerman; henceforth deer) are generalist herbivores that have clear detrimental effects on palatable plant populations (reviewed in Rooney and Waller 2003, Côté et al. 2004). In forests experiencing high deer densities, dramatic drops in both the abundance and population stability of browsed species are observed (e.g., Anderson and Loucks 1979, McGraw and Furedi 2005, Knight et al. 2009a), which can lead to greater proportions of unpalatable species within the community (Anderson and Loucks 1979, Horsley et al. 2003, Royo and Carson 2006). A recent large-scale study suggests that unpalatable and nonnative species are beneficiaries of long-term increases in deer activity (Wiegman and Waller 2006). Deer densities in eastern North America have increased dramatically over the past 50 years (McShea et al. 1997); however, at a local scale, deer use of forest habitats can vary substantially (DeCalesta and Stout 1997).

Here we test for nonconsumptive costs and benefits to unpalatable forest herbs in sites used by deer for forage.

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We define unpalatable species as those that are typically not browsed because they are either less preferred by deer or contain defensive chemicals. However, deer avoidance of unpalatable plants can vary in time and space, depending on the local availability of preferred forage species, and generally avoided species are sometimes consumed (e.g., Ruhren and Handel 2000). In this study, we use data from natural populations and replicated long-term deer exclusion experiments to quantify benefits or costs from deer browsing for unpalatable plant species. Specifically, to estimate effects on unpalatable plant demography, we quantify individual demographic traits of one focal unpalatable species, *Arisaema triphyllum* [L.] Schott (Araceae; hereafter *Arisaema*), in multiple natural beech–maple forest sites that differ in mean annual levels of deer browse on a co-occurring palatable species, *Trillium grandiflorum*. Second, to quantify the effects on unpalatable plants in general, we assess individual plant size of five unpalatable species, including *Arisaema*, growing within paired long-term deer exclusion/deer access plots. Both studies document deer avoidance yet show negative consequences of high deer presence for these unpalatable species. Finally, because large browsers are known to alter abiotic conditions important for plant growth, we test for this as a potential indirect effect on plant growth and performance.

MATERIALS AND METHODS

Natural sites.—In 2005, we established seven sites in Crawford County, Pennsylvania, USA (41°39'25" N, 80°25'23" W) that were separated by 2–42 km and where *Arisaema* and *Trillium* co-occur (Appendix A). In each site we established a 50 × 50 m study plot that we censused annually. Winter deer density estimates for the last decade in this area range from 4 to 18 deer/km² (Wallingford and Grund 2003) and historically have not exceeded 30 deer/km² (Redding 1995). Sale of Dibble Hill in 2006 resulted in only one year of data for that site.

Deer exclusion experiments.—Long-term paired 4-ha deer exclusion/deer access plots were erected in 1990 and subsequently maintained (McShea 2000) near Front Royal, Virginia, USA (38°55'05" N, 78°11'41" W) at the Smithsonian's Conservation and Research Center (CRC) and in the Shenandoah National Park (Matthews Arm [MA] and Keyser's Ridge [KR] sites). Treatment pairs are separated by 2–21 km. The deer exclusion plots are surrounded by 2.4 m high combination of woven and high tensile wire fencing, allowing all other animals to freely enter the plots. Mean deer density at the CRC in 2007 was 33 deer/km² (95% CL = 19–56 deer/km²) based on distance sampling methods (W. J. McShea, unpublished data) and match estimates for the past 18 years at the CRC (W. J. McShea, unpublished data) and the Shenandoah National Park (R. Gubler, personal communication).

Quantifying deer browse intensity in natural sites.—We used deer browse of *Trillium grandiflorum* [Michx.]

Salisb. (Liliaceae; hereafter *Trillium*), an established phyto-indicator of deer browse (Anderson 1994, Augustine and Jordan 1998, Augustine and DeCalesta 2003, Kirschbaum and Anacker 2005), as our index of deer browse intensity. Each year for three years (2005–2007), we sampled *Trillium* populations within three parallel 1 × 50 m transects that originated from a random location along one side of the 50 × 50 m study plots. In each transect we counted all stems of *Trillium* and recorded their stage (flowering or nonflowering) and browse status. Deer browse on *Trillium* results in a stem devoid of leaves with a cut parallel to the ground, which is distinct from lagomorph and rodent browse that results in cut stems at a 45° angle (Augustine and Jordan 1998). We calculated deer browse intensity at each site as the proportion of all *Trillium* stems that were browsed by deer across the three transects. The annual percentage of *Trillium* browsed in our study sites (2005–2007) ranged from 0 to 25% and were similar in magnitude to *Trillium* browse data collected previously at the same sites (Knight 2003). We calculated a six-year *Trillium* browse average for each natural site by averaging the three years of data (1999–2001) published in Knight (2003) with the 2005–2007 data from this study. Since large browsing ungulate herbivores' effects on plant community composition may be evidenced only after many years (e.g., Wiegman and Waller 2006), we used this long-term average in all subsequent analyses.

Focal species.—We chose *Arisaema* as the focal unpalatable species for detailed demographic study in the natural sites because it is a long-lived widespread understory perennial that expresses discrete gender stages (Bierzuchdek 1982). Individual *Arisaema* plants typically progress from vegetative to flowering and from male to female as their biomass increases. An individual's gender can switch across seasons as it grows (male to female) or shrinks (female to male) (Bierzuchdek 1982). *Arisaema*'s size-dependent gender switching allows us to quantify important changes in reproductive status that are less obvious in hermaphroditic species. In the deer exclusion paired plots (CRC, KR, MA) we measured size of *Arisaema* and additional unpalatable plants as available, including *Actaea racemosa* (Ranunculaceae, black bugbane), *Osmorhiza claytonii* (Apiaceae, Clayton's sweetroot), *Podophyllum peltatum* (Berberidaceae, mayapple), and *Botrychium virginianum* (Ophioglossaceae, rattlesnake fern). An ongoing, large-scale study in the CRC includes deer browse estimates for three of these species and supports their classification as plants that deer avoid (no. stems : percentage of stems browsed, *Arisaema*, 343:0.006%; *Actaea*, 120:0%; *Botrychium*, 35:0.008% [N. A. Bourg and W. J. McShea, unpublished data]).

Testing the effects of deer on *Arisaema*'s demographic traits in natural sites

To create an index of individual biomass we excavated, measured, and weighed plants from outside the

50 × 50 m plots. We found that stem diameter at ground level accurately predicts *Arisaema* biomass (Appendix B). In April 2005, all flowering *Arisaema* in the 50 × 50 m plots were permanently tagged ($N = 27\text{--}35$ flowering plants/site). We estimated biomass and gender of all tagged plants annually (2005–2007) and calculated sex ratio at each site as the proportion of male flowering plants. To estimate *Arisaema* density, in 2005 and 2006, we also counted and estimated biomass of all nonflowering plants in three 1 × 50 m transects (N total/site = 214–424). Finally, each year we tallied deer damage across all *Arisaema* individuals surveyed ($N = 9746$).

Female reproductive success.—For each female identified in our annual censuses, we counted the number of flowers, fruits, and the number of seeds/fruit in July 2005 and 2007. We calculated fruit set as number of fruits/number of flowers. We used these data to estimate *Arisaema*'s annual seed rain per square meter at each site as

$$\text{seed rain} = [(\text{no. females})(\text{mean no. fruits/female}) \\ \times (\text{mean no. seeds/fruit})] \div (\text{sample area})$$

and to calculate the two-year mean seed rain per site.

To examine the relationship between browse level in the natural sites and *Arisaema* demographic traits, we regressed mean flowering plant biomass, sex ratio, and seed rain per square meter on the mean annual *Trillium* browse level for the natural sites. We used site means for biomass and sex ratios because regression of these variables on browse levels did not differ in slopes among years (PROC GLM year × browse history, $P > 0.70$). We also tested for a relationship between *Trillium* or *Arisaema* density and browsing level at the seven natural sites. We compared fruit set among sites in 2005 and 2007 using ANOVA; 2005 data were square-root transformed to make the variances equal.

Testing the effects of deer on unpalatable plant species size in experimental plots

Due to the patchy distribution of the focal unpalatable species within the experimental plots, we first identified sampling areas within the three paired deer exclusion/deer access plots where the five focal unpalatable species occurred that were matched for aspect and slope of terrain, distance from the fence, and understory and canopy cover. One 1 × 50 m transect was marked in each sampling area. Every meter, we selected the individuals of the focal species closest to the meter mark and measured each for size. This process was repeated until 30–46 plants/transect were measured for each species in each plot. Not all focal species co-occurred at each site (Appendix C). To estimate size of the focal species, we measured stem diameter at the soil surface. For *Osmorhiza* and *Actaea*, we also measured plant height since height of those species is a good estimator of deer browse intensity (Webster and Parker 2000).

We determined the effect of deer exclusion on plant size by calculating the log response ratio, L (Hedges et al. 1999, Gurevitch and Hedges 2001), for each species at each site (CRC, KR, and MA) as $L = \ln(R) = \ln(\bar{X}_E) - \ln(\bar{X}_A)$ where \bar{X}_E is the mean species size in a deer exclusion plot and \bar{X}_A is the mean species size in a deer access plot. We used a mixed-model analysis to calculate the across-site mean effect sizes for each species, \bar{L}^* , under the assumption of random variation in effect size at different sites. Mixed-model analysis incorporates the within-species across-site pooled variances to produce a total variance in effect size for each species (Hedges et al. 1999). To determine whether deer exclusion had a general effect on unpalatable species sizes, we calculated the grand mean effect size across all species, \bar{L}^* .

Testing the effects of deer on abiotic site quality

Natural sites.—In 2005, we measured leaf litter depth at 10 locations along each of three transects in all 50 × 50 m plots ($N = 30$ locations/site). In 2006, we measured three abiotic variables (light, soil moisture, and soil penetration resistance) in six natural sites in the 50 × 50 m plots. To ensure uniformity of sampling conditions, all measurements were taken between 18 and 23 July when temperatures were seasonable with clear skies and no rain events. Between 11:00 and 13:00 on sampling dates, we quantified the amount of light reaching the soil surface (in micromoles per second per square meter) using a Li-Cor Quantum sensor and Li-1000 data logger (LI-COR, Lincoln, Nebraska, USA) at five points at 10-m intervals along three parallel transects evenly spaced within the plot ($N = 15$ points/plot). We determined soil moisture at five points at 10-m intervals along two parallel transects evenly spaced within the plot ($N = 10$ points/plot) using a soil moisture probe (Lincoln Soil Moisture Meter; Lincoln Irrigation, Lincoln, Nebraska, USA). Finally, we measured soil penetration resistance (in megapascals), a key metric of soil compaction, using a cone penetrometer (Field Scout SC-900, Spectrum Technologies, Plainfield, Illinois, USA). Because the corms and roots of *Arisaema* in our natural sites are found within the top 15 cm of soil, we measured soil penetration resistance to a depth of 15 cm, sampling 100 points at 5-m intervals on a grid across the entire plot.

We tested for differences in individual abiotic variables among sites (Appendix D), then created a multivariate descriptor of abiotic site quality using principal components analysis (PCA; Sokal and Rohlf 1995). Factors loaded were mean values of the variables light level, soil moisture, soil penetration resistance at 15 cm, and leaf litter depth for each site (Appendix D: Table D1). We regressed the site-specific PC1 and PC2 scores on mean browse level using bivariate regression. Next, to determine whether mean browse level, density of flowering *Trillium*, density of *Arisaema*, or soil quality (PC1) were significant predictors of *Arisaema* demographic variables, we used backward stepwise regression

(Sokal and Rohlf 1995). The model included all quadratic and interaction terms.

Experimental sites.—Between 4 and 6 June 2008 under uniformly dry and sunny conditions, we measured soil penetration resistance in each of the paired experimental plots (CRC, KR, MA) plus a fourth plot in Shenandoah National Park (Hilltop [HT]) to determine whether deer access plots had higher soil compaction relative to the 18-year deer exclusion plots. We used a maximum depth of 10 cm for all four paired plots because bedrock was often encountered at this depth. We sampled 25 points at 15-m intervals on a grid centered on the plant sampling transect in each plot. Data were analyzed using two-way MANOVA (PROC GLM) (Appendix D: Table D2).

All statistical analyses were performed using MATLAB (version R2006a; MathWorks, Natick, Massachusetts, USA) or SAS software, JMP IN 5.1 or SAS version 9.2 of the SAS System for Windows (SAS Institute, Cary, North Carolina, USA).

RESULTS

Effects of deer on unpalatable plant species

Across the three years of this study and seven natural sites, deer browse of *Arisaema* was a rare event and did not differ among sites. Only 0.6% of our 9746 censused *Arisaema* stems showed evidence of deer browse and only 0.3% showed any other sign of damage. These data validated *Arisaema*'s status as an unpalatable, unbrowsed species. In contrast, co-occurring *Trillium* in these sites were regularly browsed. Sites differed by an order of magnitude in their six-year average *Trillium* browse level (2.2–22.4%; Fig. 1A), with the DZ (lowest browse) and TW (highest browse) sites differing significantly (t test; $t = -2.9$, $df = 5$, $P = 0.04$; Fig. 1A). We found no correlation between mean *Trillium* browse level and density of *Trillium* or *Arisaema* (browse level \times *Trillium* density, $r = 0.12$, $P = 0.78$; browse level \times *Arisaema* density, $r = -0.37$, $P = 0.47$), indicating that deer were neither attracted to areas with higher *Trillium* density nor repelled by areas with high *Arisaema* density.

We found a significant negative relationship between the mean *Arisaema* flowering plant biomass and browse level on *Trillium* across the seven natural sites (Fig. 1B). We also found a significant positive relationship between browse level and male-biased sex ratios (Fig. 1C). In the three populations with highest browse levels, >80% of the flowering plants were male. Fruit set per flower differed among sites in 2005 (range = 13–44 fruits/flower; ANOVA, $F_{5,95} = 2.5$, $P = 0.04$) but not in 2007 (range = 14–32 fruits/flower; ANOVA, $F_{4,26} = 0.3$, $P = 0.89$). Fruit set differences in 2005 were not correlated with site differences in browse level, but were in 2007. While the two-year mean seed rain was low for all populations (range = 0–0.38 seeds/m²), it declined significantly as browse level on *Trillium* increased (Fig. 1D). Females were rare in highly browsed sites and in

one instance (TW 2005) totally absent. The number of flowering *Arisaema* stems did not differ across years within sites (ANOVA, $F_{5,16} = 1.9$, $P = 0.18$).

Of the three models run with backward stepwise regression, browse level was the only significant predictor of *Arisaema* demographic metrics in each analysis. In addition, flowering *Trillium* density was also a significant predictor of *Arisaema* flowering plant biomass (Appendix E).

All five unpalatable focal species were significantly larger in the deer exclusion plots relative to the deer access plots (Appendix C). The grand mean effect size of deer exclusion on plant size across all unpalatable focal species was significantly greater than zero ($\bar{L}^* = 0.41 \pm 0.11$ 95% CL; Appendix C).

Effects of deer on abiotic site quality

There were significant differences among sites for all abiotic variables; however no clear pattern related to mean herbivory levels emerged (Appendix D: Table D1). In the PCA, the first two eigenvectors combined to explain 87% of the variance among sites. Principal components axis 1 (eigenvalue = 2.4, 59% of total variance) was positively correlated with soil penetration resistance (eigenvector = 0.58) and litter depth (eigenvector = 0.60). Principal components axis 2 (eigenvalue = 1.1, 28% of total variance) was correlated positively with light level (eigenvector = 0.74) and negatively with soil moisture (eigenvector = -0.62). Principal components axis 1 decreased with increasing *Trillium* browse level ($P = 0.07$), signifying that high-browse sites have more compacted soils with less litter than low-browse sites (Fig. 1E). Principal components axis 2 and browse level were not correlated ($P > 0.90$).

In the paired experimental plots we found deer exclusion treatment, site, and their interaction all had significant effects on soil penetration resistance (Appendix D: Table D2). Soils exhibited significantly higher penetration resistance in the deer access plots relative to deer exclusion plots ($P > 0.05$; Appendix D). Soils in deer access plots required 4–145% more force to penetrate than those in the paired deer exclusion plots.

DISCUSSION

Our results clearly show that unpalatable plant species do not generally benefit from deer browsing on co-occurring palatable species. *Arisaema* demographic traits are correlated with increasing deer browse on *Trillium*. Where deer browse levels were highest, *Arisaema* had smaller individual plant size (Fig. 1B), male-biased sex ratios (Fig. 1C), and low seed rain (Fig. 1D). *Arisaema*'s demographic responses are not caused by herbivory by deer or any other herbivore. Deer browse of *Arisaema* was rare in both our natural (0.6%) and experimental (0.006%) study sites. Thus, the demographic trait declines observed here cannot be attributed to *Arisaema*'s associational susceptibility with *Trillium* (sensu White and Whitham 2000). Data from

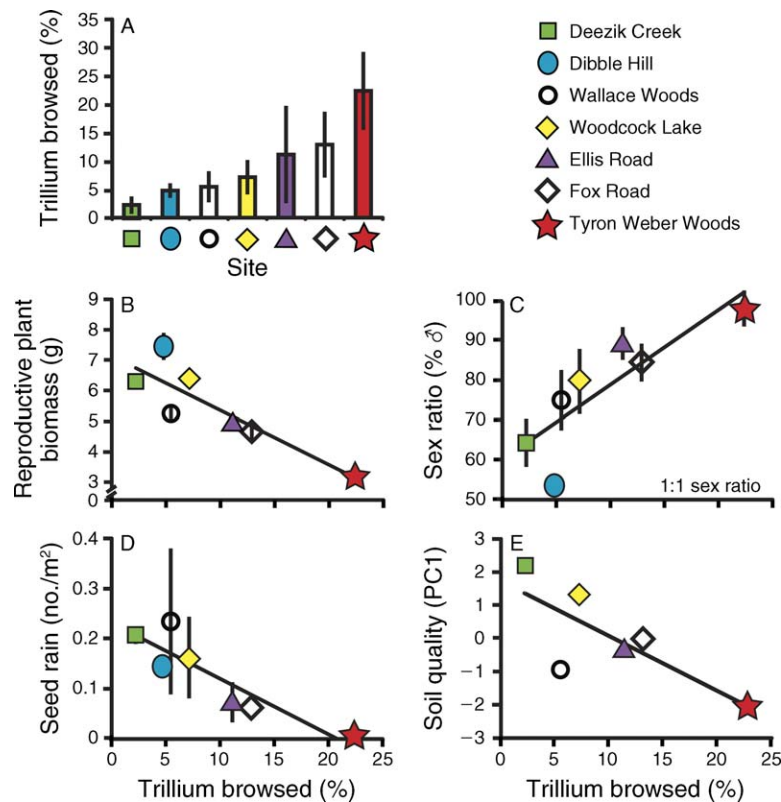


FIG. 1. Mean flowering plant size, population sex ratio, seed rain of *Arisaema triphyllum*, and soil quality are significantly related to mean percentage of deer browse of co-occurring *Trillium*. (A) Six-year site averages of percentage of *Trillium* browsed for seven Pennsylvania, USA, sites. (B–E) Relationships of *A. triphyllum* demographic metrics and soil quality with percentage of *Trillium* browse (mean \pm SE; error bars are obscured by some symbols): (B) mass of *A. triphyllum* flowering individuals ($y = -0.18x + 7.1$; $r^2 = 0.76$, $F_{1,6} = 16.0$, $P < 0.01$); (C) percentage of male *A. triphyllum* ($y = 1.90x + 60.2$; $r^2 = 0.72$, $F_{1,6} = 13.0$, $P < 0.02$; note that the x -axis represents 1:1 sex ratio); (D) seed rain ($y = -0.01x + 0.23$; $r^2 = 0.82$, $F_{1,6} = 22.4$, $P < 0.01$); and (E) soil quality (principal components axis 1; $y = -0.17x + 1.7$; $r^2 = 0.59$, $F_{1,5} = 5.84$, $P = 0.07$). Note that fresh mass and sex ratio means are based on three years of data and seed rain means are based on two years of data except for Dibble Hill, for which means are based on one year of data.

our deer exclusion experiments conclusively implicate deer as indirect causal agents of *Arisaema*'s declines and support the results from our natural sites. The significantly smaller plant size of all five unpalatable species in deer access plots relative to deer exclusion plots suggests this decline may be a widespread phenomenon wherever white-tailed deer or other ungulate overbrowsing occurs (e.g., Webster and Parker 2000).

The trends documented for our *Arisaema* populations are surprisingly similar in magnitude and direction to those reported for deer-browsed palatable species. High rates of ungulate herbivory on palatable forest perennial herbs invert the natural stage progression from vegetative to flowering because herbivory can halt or reverse their biomass accumulation (Augustine and DeCalesta 2003, Knight 2003). In *Trillium* spp., deer browsing results in smaller mean plant size, a reduced proportion of flowering plants, and declining populations (i.e., population growth rate $[\lambda] < 1$; Lubbers and Lechowicz 1989, Anderson 1994, Knight 2003). Across 12 *Trillium* populations, deer drove the significant negative rela-

tionship between λ and herbivory level (Knight et al. 2009a). Similarly, a viability analysis of 36 deer-browsed populations of American ginseng (*Panax quinquefolius* L.) revealed that 80% of these populations had >99% chance of extinction within 100 years (McGraw and Furedi 2005). For both studies, loss of population viability was driven by deer-mediated declines in individual plant stage and size. The fact that our focal species were significantly smaller in deer access relative to exclusion plots (Appendix C) suggests that these unpalatable species could also exhibit population decline if non-browsing deer effects are sustained.

Another aspect of decline is seen in *Arisaema* population sex ratios. The sex ratios of our populations are exceptionally male biased, overlapping the upper 14% of the sex ratio distribution from 74 *Arisaema* populations (Richardson and Clay 2001). Because the smallest flowering *Arisaema* plants within a population are male, declines in mean flowering plant size with increasing browse level at a site likely drive our observed highly skewed sex ratios. Size effects on gender

allocation can be expected for species that do not change genders, too. For example, in two *Trillium* species, the largest plants within each population had the highest proportional allocation to female function while the smallest plants allocated more to male function (Wright and Barrett 1999). Reductions in plant size and thus declines in female function (Fig. 1B, D) may be a cryptic but widespread outcome for plants in forests with persistent high ungulate browse levels. The low absolute number of *Ariseama* females in our study populations translates directly into low seed rain (Fig. 1D) and low recruitment potential. Although population growth rate is more sensitive to changes in adult survival than to changes in recruitment and early-stage-class survival (Pfister 1998), populations with no seedling recruitment are obviously non-sustaining and more vulnerable to stochastic extinction (Kery et al. 2000).

*Mechanisms driving negative effects
on unpalatable species*

In addition to deer browse levels, our natural sites undoubtedly differ in historical, biotic, and abiotic factors that could contribute to *Ariseama*'s performance declines. For example, local extreme storm or flooding events, anthropogenic disturbances due to logging, livestock grazing, agricultural, or recreational uses of forest sites, or the presence of exotic species could affect plants' vitality. We acknowledge that some of these factors could contribute to the size declines documented in our natural sites. However, these confounding effects are not an issue in our paired experimental deer access/deer exclusion plots. Results from those experiments provide clear evidence that deer are the causal agents behind the indirect negative effects on unpalatable species.

Currently, the exact mechanism of this indirect effect is unknown. However, our analyses of abiotic variables provide insight into one potential mechanism. The significantly higher levels of soil penetration resistance in deer access vs. deer exclusion experiments ($P = 0.014$; Appendix D: Table D2) show that when deer are present, soil compaction is higher. This interpretation is also consistent with PCA results (Fig. 1E) from the natural sites.

Trampling of forest and grassland habitat by domestic or wild ungulates is known to directly increase soil compaction (Cumming and Cumming 2003, Vavra et al. 2007) while their browsing causes loss of vegetation cover (Wardle et al. 2001) and reduces both leaf litter deposition and new fine-root growth of browsed species (Sharrow 2007). These losses can increase water runoff and soil erosion, indirectly increasing compaction and lowering water and nutrient availability (Cumming and Cumming 2003, Sharrow 2007). Soil compaction can directly reduce plant growth and seedling establishment (Bassett et al. 2005, Kyle et al. 2007).

Soil compaction caused by ungulates has the potential to modify the interaction between plant species and their soil mutualists. Arbuscular mycorrhizal fungi (AMF)

are vitally important for soil resource uptake of most forest perennial herbs and woody plants, including our focal species (Brundrett and Kendrick 1988, van der Heijden et al. 2008). Browsing by overabundant ungulates is linked to declines in abundance and function of soil mycorrhizae (Rossow et al. 1997) and decreases in the colonization rate of roots by beneficial AMF due to soil compaction (Waltert et al. 2002). Arbuscular mycorrhizal fungi hyphal growth is reduced in compacted soils where soil pore size ($<3 \mu\text{m}$) is smaller than most AMF hyphae's diameter ($5\text{--}20 \mu\text{m}$; Nadian et al. 1997). Finally, compaction can have long-term effects: soil compaction levels beyond the tolerances for plant growth or seedling establishment can persist for up to 30 years in forests retired from livestock grazing (Bassett et al. 2005, Sharrow 2007). The relationship between deer browse level and soil compaction observed in our study suggests that the diminished size of *Ariseama* and the other unpalatable species in the presence of deer may be attributable, at least in part, to these direct and indirect effects of deer on plant growth as mediated via the soil environment.

Our results contrast with other studies that suggest benefits to unpalatable species in heavily browsed forests (Anderson and Loucks 1979, Horsley et al. 2003, Wiegman and Waller 2006). We can think of several reasons for this difference. First, high levels of deer browse force an immediate and automatic increase in the relative abundance of unpalatable species as the abundance of browsed species declines. However, our data suggest that an initial positive response by unpalatable species can be reversed if high deer browse levels are sustained. Second, unlike our measures of individual plant performance, these studies used indirect metrics of species performance (i.e., percent cover or relative abundance). However, these indirect measures are poor predictors of population viability because the long life spans of perennial species create time delays (Colling and Matthies 2006) that obscure the detection of diminished performance with declines in habitat quality. Third, our data and that of Knight et al. (2009b) reveal that high levels of deer herbivory alter the soil environment, which can negate the positive effects of ungulate herbivores for unbrowsed species. Michalet et al. (2006) argue that positive interactions can be nullified when stress or disturbance reach extreme levels. Finally, the success of unpalatable species found in other studies could be evidence of the ghost of past benefits from deer. Recent studies document that the outcome of past transient negative interactions, such as interspecific competition (Miller et al. 2009) or granivory (Howe and Brown 2001), can significantly change the trajectory of community composition via the suppression of competitive subordinates or palatable species.

CONCLUSIONS

Ungulate herbivores are drivers of palatable plant community change worldwide (Côté et al. 2004, Royo and

Carson 2006, Vavra et al. 2007), but their interactions with unpalatable species are rarely addressed. This study suggests that populations of unpalatable species in forests can decline due to indirect negative effects of overabundant deer. Sustained high browsing pressure within a forest can result in a switch from an initially facilitative interaction with unpalatable species to direct and indirect negative interactions. The loss of biodiversity, in the form of native palatable and unpalatable species in the forest understory, is a likely outcome of overabundant deer.

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APPENDIX A

Locations of *Arisaema triphyllum* study populations (*Ecological Archives* E091-023-A1).

APPENDIX B

Methods and results for developing nondestructive biomass estimation from aboveground plant size for *Arisaema* (*Ecological Archives* E091-023-A2).

APPENDIX C

Effect size analysis of deer exclusion on unpalatable plant size for five focal species measured in paired deer access/deer exclusion plots (*Ecological Archives* E091-023-A3).

APPENDIX D

Statistical methods and results of analysis of independent abiotic variables, a table of mean abiotic values used in the principal components analysis, and MANOVA results for compaction data from experimental sites (*Ecological Archives* E091-023-A4).

APPENDIX E

Results of the stepwise backward regression (*Ecological Archives* E091-023-A5).