



# Indirect Effects of Pandemic Deer Overabundance Inferred from Caterpillar-Host Relations

LAURA WHEATALL,\* TIM NUTTLE,\* † ‡ AND ELLEN YERGER\*

\*Department of Biology, Indiana University of Pennsylvania, 114 Weyandt Hall, Indiana, PA 15705, U.S.A.

†Ecological Services Division, Civil & Environmental Consultants Inc., 333 Baldwin Road, Pittsburgh, PA 15205, U.S.A.

**Abstract:** Externally feeding phytophagous insect larvae (i.e., caterpillars, here, larval Lepidoptera and sawflies, Hymenoptera: Symphyta) are important canopy herbivores and prey resources in temperate deciduous forests. However, composition of forest trees has changed dramatically in the eastern United States since 1900. In particular, browsing by high densities of white-tailed deer (*Odocoileus virginianus*) has resulted in forests dominated by browse-tolerant species, such as black cherry (*Prunus serotina*), and greatly reduced relative abundance of other tree species, notably pin cherry (*Prunus pensylvanica*) and birches (*Betula* spp.). To quantify effects of these changes on caterpillars, we sampled caterpillars from 960 branch tips of the 8 tree species that comprise 95% of trees in Allegheny hardwood forests: red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), sugar maple (*Acer saccharum*), sweet birch (*Betula lenta*), yellow birch (*Betula allegheniensis*), American beech (*Fagus grandifolia*), black cherry, and pin cherry. We collected 547 caterpillar specimens that belonged to 66 Lepidoptera and 10 Hymenoptera species. Caterpillar density, species richness, and community composition differed significantly among tree species sampled. Pin cherry, nearly eliminated at high deer density, had the highest density and diversity of caterpillars. Pin cherry shared a common caterpillar community with black cherry, which was distinct from those of other tree hosts. As high deer density continues to replace diverse forests of cherries, maples, birches, and beech with monodominant stands of black cherry, up to 66% of caterpillar species may be eliminated. Hence, deer-induced changes in forest vegetation are likely to ricochet back up forest food webs and therefore negatively affect species that depend on caterpillars and moths for food and pollination.

**Keywords:** Allegheny hardwoods, herbivory, Lepidoptera, northern hardwoods, Pennsylvania, sawflies

Efectos Indirectos de la Sobreabundancia de Venados Pandémicos Inferida de Relaciones Orugas-Huéspedes

**Resumen:** Las larvas de insectos fitófagos (i.e., orugas, aquí, larvas de Lepidoptera y moscas sierra, Hymenoptera: Symphyta) son importantes herbívoros y presas del dosel en bosques deciduos templados. Sin embargo, la composición de árboles forestales ha cambiado dramáticamente en el este de Estados Unidos desde 1900. En particular, el ramoneo de altas densidades de venado cola blanca (*Odocoileus virginianus*) ha resultado en bosques dominados por especies tolerantes al ramoneo, como *Prunus serotina*, y la gran disminución de la abundancia relativa de otras especies de árboles, notablemente *Prunus pensylvanica* y abedules (*Betula* spp.). Para cuantificar los efectos de estos cambios sobre las orugas, muestreamos orugas de 960 extremos de ramas de las 8 especies de árboles que comprenden 95% de los árboles en los bosques de maderas duras de Allegheny: *Acer rubrum*, *A. pensylvanicum*, *A. saccharum*, *Betula lenta*, *B. allegheniensis*, *Fagus grandifolia*, *Prunus serotina* y *P. pensylvanica*. Recolectamos 547 especímenes de oruga pertenecientes a 66 especies de Lepidoptera y 10 de Hymenoptera. La densidad, riqueza de especies y composición de la comunidad de orugas difirió significativamente entre las especies de árboles muestreadas. *Prunus pensylvanica*, casi eliminada en alta densidad de venados, tuvo la mayor densidad y diversidad de orugas. *P. pensylvanica* compartió la comunidad de orugas con *P. serotina*, que fue diferente en los otros árboles huéspedes. A medida que la alta densidad de venados continúa reemplazando los bosques diversos de cerezos, maples, abedules y bayas con bosques monodominantes de *Prunus serotina*, se podría eliminar hasta el 66% de las especies de orugas. Por lo tanto, es probable que los cambios en la vegetación forestal inducidos por venados reboten en

‡email nuttle@cecinc.com

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*las redes alimenticias de los bosques y consecuentemente afectan negativamente a especies que dependen de orugas y polillas para su alimentación y polinización.*

**Palabras Clave:** herbivoría, Lepidoptera, maderas duras de Allegheny, maderas duras del norte, moscas sierra, Pennsylvania

## Introduction

It is now firmly established that high densities of ungulate browsers caused by extirpation of carnivores and population management by humans can dramatically alter forest vegetation (e.g., Russell et al. 2001; Rooney & Waller 2003; Côté et al. 2004). For example, in their landmark study investigating effects of white-tailed deer (*Odocoileus virginianus*) in large enclosures ranging in deer density from 3.9 to 31.2 deer per km<sup>2</sup>, Tilghman (1989) and Horsley et al. (2003) established that densities over approximately 8 deer per km<sup>2</sup>—common across wide areas of eastern North America—cause dramatic shifts in vegetation during the stand-initiation stage (1979–1990). Specifically, because deer preferentially browse certain species, at high densities they cause delayed and depauperate regeneration of most tree species. As a result, forest vegetation at high deer densities becomes dominated by unpalatable species such that regenerating trees are up to 90% black cherry (*Prunus serotina*) and understory cover is up to 90% ferns (particularly hay-scented fern [*Dennstaedtia punctilobula*]) (Horsley et al. 2003; T.N., unpublished data). Besides black cherry, other tree species that are more abundant at high deer densities, due to deer avoidance, are striped maple (*Acer pensylvanicum*) and American beech (*Fagus grandifolia*). Species that are less abundant when deer density is high, due to preferential browsing, include pin cherry (*Prunus pennsylvanica*), sugar maple (*Acer saccharum*), and birch (*Betula allegheniensis* and *Betula lenta*) (Tilghman 1989; Horsley et al. 2003; Nuttle et al. 2013). Although magnitude of effects and species identities may differ, these results appear typical of what occurs throughout eastern North America and in other parts of the world where deer densities are high (e.g., Russell et al. 2001; Côté et al. 2004; Royo & Carson 2006).

It is likely that changes in forest vegetation induced by deer browsing will have additional indirect negative effects on forest ecosystems (Rooney & Waller 2003). Results of studies of effects of deer browsing on insects and their predators are variable, and so far no one has addressed effects of deer-induced changes in vegetation composition, as opposed to structure, on other ecosystem components (Côté et al. 2004). Almost certainly, reduced species diversity of forest vegetation is likely to reduce diversity of phytophagous insects and insect pollinators (Tilghman 1989; Rooney 2001) and result in increased instability of insect populations (Vehviläinen et al. 2007). Furthermore, deer-induced changes in composition of forest regeneration potentially produce long-

term legacies of these direct and indirect effects that persist as long as altered tree communities persist in the forest canopy (Nuttle et al. 2011).

Of all insect functional groups, caterpillars (here, externally feeding phytophagous larvae of butterflies, moths, and sawflies [Lepidoptera and Hymenoptera: Symphyta]) are particularly important as canopy herbivores in temperate forests (Futuyma & Gould 1979) and as an essential resource for insectivorous birds. Most species of forest caterpillars develop into moths and therefore are also important prey for bats. Although less well known than for diurnal butterflies, many species of moths (e.g., Geometridae, Noctuidae, Saturniidae, and Sphingidae) are pollinators. Therefore, because tree species differ in quality as food for caterpillars (Singer et al. 2012), different tree species host different assemblages of caterpillar species (e.g., Butler & Strazanac 2000), caterpillar species may differ in palatability to predators (Bernays & Cornelius 1989), and only some moths are pollinators, deer-induced changes in forest vegetation are likely to ricochet (Nuttle et al. 2011) back up forest food webs to affect birds, bats, and plants that rely on caterpillars and moths for food and pollination.

Nuttle et al. (2011) provide evidence linking deer-induced changes in vegetation of Allegheny hardwood forests to density of caterpillars and insectivorous birds in the context of the long-term, large-scale research begun by Tilghman (1989). Here, we report on a more detailed study of relations between trees of Allegheny hardwood forests and their caterpillar faunas with the aim of providing a more mechanistic account of the long-term, indirect effects of overabundant deer populations on forest communities.

## Methods

### Caterpillar Sampling

We sampled caterpillars from trees adjacent to or within the 4 study sites of Tilghman (1989), deCalesta (1994), Horsley et al. (2003), and Nuttle et al. (2011). Sites were in the Allegheny National Forest and state and private lands in Warren, McKean, Elk, and Forest Counties, Pennsylvania (U.S.A.). All sites consisted of a mosaic of uncut stands, shelterwood cuts, and clearcuts of varying ages. Tree species we sampled for caterpillars were those that collectively comprised >95% of tree basal area in these forests: American beech, black cherry, pin cherry, sweet birch, yellow birch, red maple (*Acer rubrum*), sugar maple, and striped maple. All species were present at

each site in stands that were part of Tilghman's (1989) original research and stands in the surrounding forest. Although composition of experimental stands differed depending on deer-density treatment—from nearly pure black cherry stands in the highest deer-density treatment (31.2 deer per km<sup>2</sup>) to mixed stands with no one species over 50% basal area at the lower deer densities (3.9–7.8 deer per km<sup>2</sup>)—all conditions and treatments were equally present at all study sites. Stands of surrounding forests at all sites consisted of predominately medium- to high-diversity Allegheny hardwoods ranging in age from recent clearcuts and shelterwood cuts to mature forests. Thus, each study site was a close replicate in terms of age distribution and tree species composition.

Each week between 10 May and 16 July 2010 (coinciding with breeding activity of insectivorous birds), we sampled branches on 24 trees (3 trees of each species) at each site (960 samples total). On each selected tree, we used a tree pruner and pole-mounted collection bag to collect a branch tip approximately 0.5-m long from 4–5 m above the ground (Johnson 2000). We selected trees and branches without regard to sun exposure, although trees and branches were usually along edges of clearcuts, fields, and access roads mostly in matrix stands (i.e., generally not within experimental stands); hence, sampled branches did not relate directly to experimental effects of deer density. Rather, caterpillars from sampled branches represented caterpillar communities on different tree species where the effects of deer browsing on these tree species are known from the experiment (Tilghman 1989; Horsley et al. 2003; Nuttle et al. 2011).

We sealed collection bags and took them to the laboratory, where all caterpillars were collected, counted, and photographed with a calibrated digital camera mounted on a dissecting microscope. Later, we used the photographs to aid in identification of specimens to species. Leaves from each sampled branch were removed, dried to constant mass, and weighed for calculation of caterpillar density per unit leaf mass.

### Caterpillar Identification

Because many Lepidoptera are undifferentiated in early instars, rearing caterpillars to later instars or to adults is often necessary for identification. We placed each caterpillar in an individual clear plastic 250-mL container with a small shoot (1–3 leaves) from their host tree species and assigned the container a unique lot number. We tentatively assigned a morphospecies to each caterpillar. We provided fresh leaves every other day or as necessary. We maintained the collected caterpillars in the laboratory until they died or emerged as adults. Although there are no comprehensive keys for caterpillar identification, it was usually possible to identify caterpillars in later instars with Wagner et al. (2001) and Wagner (2005) and emerged adults with Covell (2005). Some larval identifications (from jpg files) were made by D. Wagner. Specimens

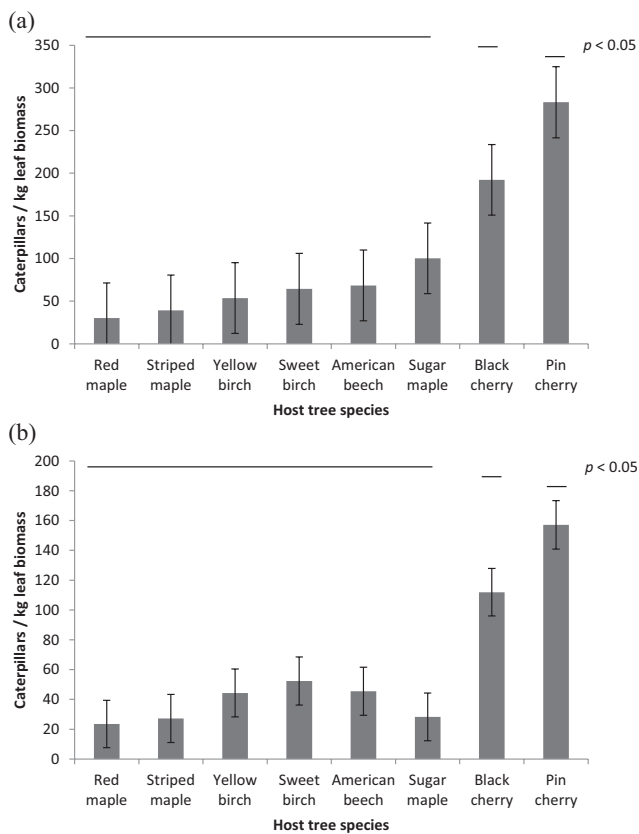
that could not be identified morphologically (usually because they died in early instars) were preserved in 95% ethanol and retained for identification by DNA barcoding.

Analysis of morphologically unidentifiable specimens was completed by Canadian Centre for DNA Barcoding (CCDB) at University of Guelph. We used different methods to sample caterpillar tissue for DNA extraction. For smaller specimens, we sampled the anterior half of the caterpillar (head capsule and prolegs) because these portions generally contain sufficient DNA for identification (according to instructions provided by CCDB). Because many samples were large and because too much tissue inhibits DNA amplification, we sampled only the head capsule of larger specimens. For some reared adult specimens, we sampled legs or antennae. We dissected pupae and sampled tissues or hemolymph. In some failed pupae, (pharate) moths were close to emergence such that it was possible to sample legs or antennae. The CCDB provided sequences of the mitochondrial COI gene, which we matched with sequences on record with the Barcode of Life Database to obtain identifications ([www.boldsystems.org](http://www.boldsystems.org)). We submitted 156 caterpillar specimens to CCDB and used positive identifications to resolve identities of larval specimens previously determined as belonging to the same morphospecies. For some molecular identifications, the sample's DNA sequence matched 2 taxa in the CCDB database with equal similarity. Because it was not possible to distinguish between them, we listed both taxa.

### Data Analyses

Success rate for identification and rearing of caterpillars <6 mm in length was low; therefore, these individuals were excluded from analyses. We quantified caterpillar density per sample as number of caterpillars per kilogram leaf dry weight per branch tip. We analyzed mean caterpillar density among tree species with analysis of variance in PROC MIXED (SAS version 9.3) (SAS Institute, Cary, North Carolina). Tree species was the fixed effect and site was the random effect. Following a significant *F* test, we performed multiple comparisons with LSMEANS.

Because the density of caterpillars per branch tip was low (average <1 per branch tip), we pooled branch tips across samples to derive meaningful estimates of species richness on different hosts. Hence, all samples from a given tree species at a given study site were pooled, a process that yielded a sample size of 4 replicates (sites) for each of the 8 tree species. This level of pooling also sums across phenological variation among caterpillar species on the different hosts. All host tree species were sampled with the same number ( $n = 120$ ) of approximately equally sized tree branches, obviating the need for rarefaction to equalize sample size in comparing species richness. Although pooling individual branches in this manner reduces replication and thus statistical power, it may provide enough power to detect large differences



**Figure 1.** Mean density of (a) all caterpillars ( $p < 0.0001$ ,  $df = 7, 951$ ) and (b) caterpillars excluding forest and eastern tent caterpillars ( $p < 0.0001$ ,  $df = 7, 951$ ) on the dominant tree species in Allegheny hardwood forests of northwestern Pennsylvania during May to July 2010. Error bars are 1 SE. Within each panel, tree species under a common horizontal line do not differ ( $p > 0.05$ ).

among tree species. Therefore, because of the low level of replication, we considered  $p \leq 0.10$  significant in the analyses of species richness and community composition (although we report actual  $p$  values).

We tested differences in caterpillar species richness among tree species with PROC GLM in SAS (version 9.3). Following a significant  $F$  test, we performed multiple comparisons with LSMEANS. As a measure of caterpillar community differences among tree species, we computed  $\beta$  diversity, or the turnover of caterpillar communities from one host to another relative to the total caterpillar community (McCune & Grace 2002). One metric of  $\beta$  diversity is the  $\gamma$  diversity (species richness of the entire sample, or all caterpillars on all host species) divided by the mean  $\alpha$  diversity among the tree species (where  $\alpha$  diversity is the total number of species encountered on a given tree species). Significance of differences in caterpillar community composition among tree species was determined with blocked multiresponse permuta-

tion procedure (MRBP) in PC-ORD (version 5.0). The MRBP is a nonparametric test for the hypothesis of no difference between 2 or more groups (here, tree species) on the basis of a comparison of within-group to between-group similarity (McCune & Grace 2002). Sites were the blocking variable. We calculated differences in community composition with the Euclidean distance metric on relative abundances (McCune & Grace 2002).

## Results

### Caterpillar Density

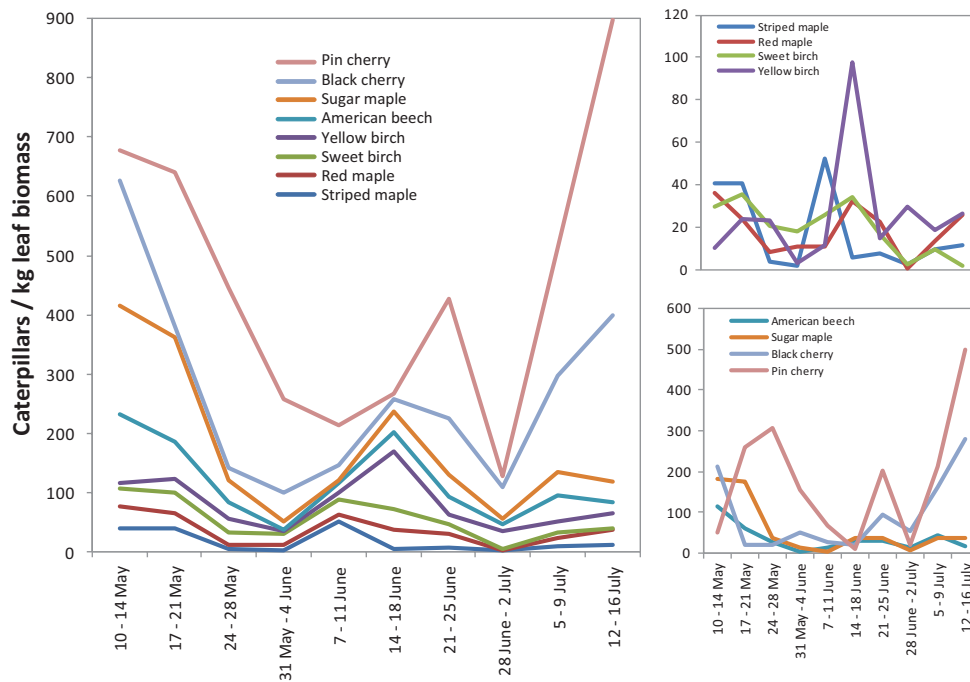
Caterpillar density per unit leaf mass differed among tree species ( $p < 0.0001$ ,  $df = 7,951$ ; Fig. 1a). There were significantly more caterpillars per unit leaf mass on pin cherry than on any other tree species; black cherry had significantly more caterpillars per unit leaf mass than every other species except pin cherry (Fig. 1a). Striped maple and red maple had the lowest densities of caterpillars per unit leaf mass, although densities differed significantly only from those on pin and black cherry. However, 2010 was an outbreak year for forest tent caterpillar (*Malacosoma disstria*) at one site (in McKean County) and for eastern tent caterpillar (*Malacosoma americanum*) at another site (in Elk County). To see how much these outbreaks dominated caterpillar-density patterns on the different hosts, we removed both species of tent caterpillars from the analyses. The differences and relative rankings in caterpillar density among tree species remained significant ( $p < 0.0001$ ,  $df = 7,951$ ) (Fig. 1b), but sugar maple dropped from third highest to third lowest in caterpillars per leaf mass because forest tent caterpillar was most abundant on it. Temporally, caterpillar density showed 2 peaks, early and late in the sampling period (Fig. 2).

### Caterpillar Identification

We collected 547 caterpillar specimens (>6-mm long) throughout the 10-week spring-summer collection period (Table 1). Of these, 87.57% were identified to family and 85.92% were identified to species. A total of eighteen Lepidoptera and 4 Hymenoptera:Symphyta (sawfly) families were identified. Within Lepidoptera, 66 species were represented. There were 10 sawfly species represented. Lepidoptera were more abundant (94.78% of identified individuals) than sawflies. Tent caterpillars (Lasiocampidae) were 47.60% of all caterpillars identified. Other well-represented families included Geometridae (17%) and Noctuidae (11%) (we applied Noctuidae as in Covell [2005] and Wagner [2005]).

For both Lepidoptera and Hymenoptera:Symphyta,  $\gamma$  diversity of the sample was 76 species. However, many ( $n = 36$ ) of the species identified were represented by





**Figure 2.** Caterpillar density for the 8 host tree species sampled in Allegheny hardwoods forests in 2010 (left panel, lines are stacked so the top line also represents the total caterpillar density summed across all 8 species; 2 panels at right, unstacked trends on each host species separated into 2 panels to reduce clutter). The week of 28 June to 2 July was unseasonably cold, and few caterpillars were collected that week.

a single specimen, which suggests the actual  $\gamma$  diversity of the area was considerably higher than the 76 species identified through this 10-week sampling period.

### Caterpillar Species Richness and Composition on Tree Species

Tree species differed ( $p = 0.0543$ ,  $df = 7,24$ ) in mean species richness of caterpillars. Pin cherry was host to the most caterpillar species, on average. 10.0 species over the entire season per site. Black cherry and sweet birch also had high species richness at 9.0 and 7.5 species per site, respectively (Fig. 3). All tree species had a relatively diverse group of caterpillar species. The lowest diversity was on striped maple, which hosted a mean of 4.25 species per site. The mean  $\alpha$  diversity across all tree species (pooled species richness of all samples for a given tree species) was 19.5 caterpillar species. Rankings of  $\alpha$  diversity among tree species were similar to rankings of mean species richness per site among tree species (Table 1). The fact that total caterpillar richness ( $\alpha$  diversity), when pooled across all samples for a given tree species, was about 3 times higher than mean caterpillar richness across the 4 study sites (compare Fig. 1a to totals in Table 1) further suggests that caterpillar composition was quite variable among study sites and that the actual caterpillar species richness of the study region was higher. Overall  $\beta$  diversity ( $\gamma/\alpha$ ) for the sample was

3.90, a result that indicates a large amount of overlap in caterpillar fauna among the tree hosts.

Despite the high level of variation within an individual tree species, MRBP revealed that caterpillar community composition differed among tree species ( $p = 0.0005$ , chance-corrected within group agreement  $A = 0.055$ ). Although we chose a significance level ( $\alpha$ ) of 0.10 for caterpillar species-level analyses due to low sample size caused by the need to pool across samples, many pairwise comparisons between caterpillar communities on different tree species differed at  $p < 0.05$  (Table 2). Because the somewhat high number (28) of pairwise combinations among tree species may have elevated incidence of type I errors, we focused not on individual significant differences but on patterns that emerge when considering all pairwise comparisons (Table 2) and community data (Table 1) holistically. The 2 cherry species shared a common caterpillar community that was distinct relative to most other tree species (Tables 1 & 2). Red maple and sugar maple differed significantly in community composition from each other ( $p = 0.0470$ ). Striped maple did not differ in caterpillar community composition from any other tree species, most likely because caterpillar density was low on striped maple (Table 2). American beech differed in community composition from every species except striped maple and sweet birch. Yellow birch differed in community composition only from beech and the 2 cherries, whereas sweet birch differed only from the cherries.

**Table 1. Species and number of caterpillars collected on branch tips of different tree hosts 10 May to 16 July 2010 in Allegheny hardwood forests of northwest Pennsylvania.**

Taxon	Common name	Tree species <sup>a</sup>									Total
		AMBE	BLCH	PICH	REMA	STMA	SUMA	SWBI	YEBI		
Hymenoptera											
Argidae											
	<i>Sterictophora</i> sp. TN-2005 <sup>b</sup>			2							2
Cimbicidae											
	<i>Trichiosoma lucorum</i>		2						1		3
Pamphiliidae											
	<i>Pamphilius pallipes (varius)</i> <sup>b</sup>							3	1		4
Tenthredinidae											
	<i>Ametastegia pallipes</i>								1		1
	<i>Anoplonyx apicalis</i>						1				1
	<i>Caliroa annulipes</i>		5	4							9
	<i>Macrophya</i> sp. 3 <sup>c</sup>		1								1
	<i>Pristiphora cincta</i>		1								1
	<i>Tentredo</i> sp. 5 <sup>c</sup>								1		1
	<i>Tentredopsis auriculata</i>								2		2
	Total number of Hymenoptera individuals	0	9	6	0	0	1	3	6		25
	Total number of Hymenoptera species	0	4	2	0	0	1	1	5		10
Microlepidoptera											
Coleophoridae											
	<i>Coleophora pruniella</i>								1		1
Elachistidae											
	<i>Antaeotricha leucillana</i>			1							1
	<i>Antaeotricha schlaegeri</i>	1									1
	<i>Semioscopis packardella</i>			1							1
	<i>Semioscopis aurorella</i>		1	1							2
Gelechiidae											
	<i>Cbionodes bicosmaculella (imber)</i> <sup>b</sup>	1									1
	<i>Cbionodes obscurusella (thoraceobrella)</i> <sup>b</sup>	1				1	10	1			13
	<i>Dicbomeris ligulella</i>		1		1						2
Gracilariidae											
	<i>Caloptilia serotinella</i>		1								1
	<i>Caloptilia abnivorella</i>			3							3
Oecophoridae											
	<i>Macbimia tentorifella</i>		4	4	1		1	2			12
	<i>Psilocorsis reflexella</i>						2				2
Psychidae											
	<i>Psyche casta</i>							1			1
Tortricidae											
	<i>Acleris logiana</i>							1			1
	<i>Acleris maccana</i>							1			1
	<i>Amorbia bumerosana</i>		1	1							2
	<i>Ancylis nubeculana</i>			1							1
	<i>Argyrotaenia mariana</i>	1	1			1	1				4
	<i>Choristoneura factivittana</i>						1				1
	<i>Choristoneura rosaceana</i>								1		1
Yponomeutidae											
	<i>Swammerdamia caesiella</i>			1							1
	Total number of microlepidoptera individuals	4	9	13	2	2	15	6	2		53
	Total number of microlepidoptera species	4	6	8	2	2	5	5	2		21
Macrolepidoptera											
Geometridae											
	<i>Aetbalura intertexta</i>							1			1
	<i>Besma endropiaria</i>				1						1
	<i>Biston betularia</i>					1					1
	<i>Campaea perlata</i>		1	1		1			1		4
	<i>Cladara atrolitratata</i>				1	1					2
	<i>Ennomos subsignaria</i>						2				2
	<i>Eupithecia maestosa (columbiata)</i> <sup>b</sup>	1	1	1	1			3	2		9
	<i>Eutrapela clemataria</i>							1			1
	<i>Hypagyrtis unipunctata</i>						1		1		2
	<i>Lambdina fervidaria</i>	1									1
	<i>Lomographa glomeraria</i>		3	1							4
	<i>Lomographa vestaliata</i>		3	12							15
	<i>Lycia ursaria</i>								1		1
	<i>Macaria pustularia</i>	1	8	12	8	4	1	1	2		37
	<i>Melanolopbia signataria (canadaria)</i> <sup>b</sup>	1				1		1			3
	<i>Pbigalia titea</i>				1						1
	<i>Plagodis alcoolaria</i>				2						2
	<i>Probole alienaria</i>			1							1
	<i>Tetracis cacbexiata</i>							1			1

continued

Table 1. continued

Taxon	Common name	Tree species <sup>a</sup>								
		AMBE	BLCH	PICH	REMA	STMA	SUMA	SWBI	YEBI	Total
Lasiocampidae										
<i>Malacosoma americanum</i>	eastern tent caterpillar	6	31	15	2		2	2	5	63
<i>Malacosoma disstria</i>	forest tent caterpillar	11	18	22	7	11	88	6	2	165
Lymantriidae										
<i>Dasychira tepbra</i>	Tephra tussock moth		1							1
<i>Lymantria dispar</i>	dypsy moth						1	1	1	3
Noctuidae										
<i>Achatia distincta</i>	Distinct quaker		1	1				1		3
<i>Acronicta spinigera</i>	nondescript dagger moth							1		1
<i>Acronicta basta</i>	cherry dagger moth		2							2
<i>Amphipyra pyramidoides</i>	copper underwing			1			1			2
<i>Crocigrapta normani</i>	Norman's quaker								1	1
<i>Eupsilia morrisoni</i>	Morrison's sawfly							1	1	2
<i>Eupsilia</i> sp.					1					1
<i>Lithobane baileyi</i>	Bailey's pinion				1					1
<i>Lithobane patefacta</i>	branded pinion	2	1	1	1	1		1		7
<i>Lithobane petulca</i>	wanton pinion					2				2
<i>Lithobane unimoda</i>	dowdy pinion			4				1		5
<i>Morrisonia confusa</i>	confused woodgrain	1	1	2	1			2	1	8
<i>Morrisonia latex</i>	fluid arches		1	3						4
<i>Orthosia bibisci</i>	speckled green fruitworm	4	1	1	1	2		2	1	12
<i>Orthosia revicta</i>	subdued quaker			1						1
<i>Orthosia rubescens</i>	ruby quaker					2	2	1	1	6
Notodontidae										
<i>Heterocampa guttivitta</i>	saddled prominent						1			1
Nymphalidae										
<i>Limnitis archippus</i>	viceroi							1		1
Pantheidae										
<i>Colocasia</i> sp.	yellowhorn		1			4			2	7
Saturniidae										
<i>Actias luna</i>	luna moth	2								2
Sphingidae										
<i>Amorpha juglandis</i>	walnut sphinx	1								1
<i>Paonias excaecatus</i>	blinded sphinx	1			1					2
Total number of macrolepidoptera individuals		32	73	79	29	31	99	28	22	393
Total number of macrolepidoptera species		12	14	16	14	12	9	18	14	45
Total number of all caterpillar individuals		36	91	98	31	33	115	37	30	471 <sup>d</sup>
Total number of all caterpillar species		16	24	26	16	14	15	24	21	76

<sup>a</sup>Abbreviations: AMBE, American beech; BLCH, black cherry; PICH, pin cherry; REMA, red maple; STMA, striped maple; SUMA, sugar maple; SWBI, sweet birch; YEBI, yellow birch.

<sup>b</sup>Species identity could not be distinguished between 2 equally probable species within the same genus on the basis of comparing DNA sequences with those in the Barcode of Life Database.

<sup>c</sup>Species identified as uniquely matching DNA sequence records in the Barcode of Life Database but for which a definite taxonomy has not been determined.

<sup>d</sup>An additional 76 specimens could not be identified to species, many because they were very small and lost after collection.

## Discussion

Allegheny hardwood forests are host to a diverse group of caterpillar species that differ in density, diversity, and species composition by host tree species. The use of DNA barcoding in combination with field identification and rearing greatly facilitated our ability to assemble a credible species-level inventory of caterpillars because it allowed us to identify many individuals that died while still too indistinct to identify morphologically.

Over the course of the 10-week sampling period, caterpillar density was initially highest on black cherry and sugar maple, but pin cherry became the favored species during the second week (Fig. 2). Shifts in caterpillar density from black cherry and sugar maple to pin cherry coincided with changes in eastern tent caterpillar (on black cherry) and forest tent caterpillar (on sugar maple)

distributions. Specifically, black cherry and sugar maple in these study sites were mostly defoliated by the second week of sampling (late May). Total caterpillar collections generally declined from mid-May to mid-June and started to increase again thereafter (Fig. 2). The overall temporal pattern is similar to that reported by others in forests of eastern North America (e.g., Holmes et al. 1979; Marquis & Whelan 1994; Butler & Strazanac 2000). This dip in density coincides with peak food demands of passerine birds during egg production and feeding of young and suggests that predation by birds drives this pattern (Marshall et al. 2002). Results of some of studies showed a similar pattern even on branches from which birds were excluded, a result that suggests other factors may be responsible or that the effect occurs at the population rather than the branch level (this makes sense given that caterpillars often freely move between branches or even between individual trees).

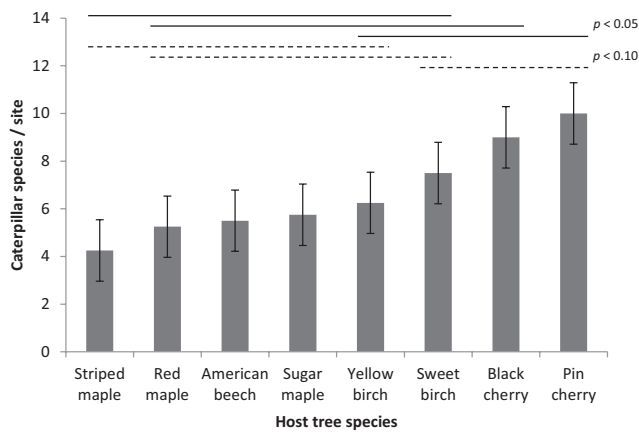


Figure 3. Mean number of caterpillar species found on the dominant tree species in Allegheny hardwood forests of northwestern Pennsylvania during May to July 2010 ( $p = 0.0543$ ,  $df 7, 24$ ). Error bars are 1 SE. Tree species under a common horizontal line do not differ (solid lines,  $p > 0.05$ ; dashed lines,  $p > 0.10$ ).

**Host Distribution Patterns**

Of the 8 tree species we sampled, all but 2 (striped maple and sweet birch) were also sampled in the Canadian Forest Insect Survey (CFIS) conducted in southern Ontario from 1950–1974 (Karban & Ricklefs 1983). Reported rankings in caterpillar density within the 6 shared tree species are similar to the rankings we report here (Fig. 1). Specifically, in the CFIS data pin cherry had the highest number of individual caterpillars per sample, followed by black cherry with about half the density as pin cherry. Other species in the CFIS data had 10–30% the caterpillar density of pin cherry (Karban & Ricklefs 1983). Species richness in the CFIS data is difficult to compare with our species richness data because it was heavily affected by sample intensity on the various hosts (Karban & Ricklefs 1983), whereas in our study sample intensity was uni-

form among hosts (and normalized by foliar biomass). Rankings in caterpillar density on the 8 tree species were also similar to those reported by Nuttle et al. (2011) for a more limited sample in the same study area. In that study, pin cherry had 5 times more caterpillars per kilogram of foliage than black cherry, the host with the next-highest caterpillar density, which is a more dramatic difference than that over the 10 weeks reported here but consistent with late May to June data (Fig. 2), the period of caterpillar sampling common to both studies. Caterpillar species identities were not determined in Nuttle et al. (2011). Of the 4 tree species groups (black cherry, red maple, yellow birch, and mixed oaks) reported by Butler (1992), black cherry had the highest caterpillar species richness and density (Butler did not report results for pin cherry). Tallamy and Shropshire (2009) reported that *Prunus* hosted the highest species richness of caterpillars in the mid-Atlantic region, second only to *Quercus* (they reported only generic-level host use; *Quercus* is uncommon in Allegheny hardwood forests). Hence, there is considerable evidence that pin cherry and black cherry support particularly dense and diverse caterpillar communities.

In addition to having high richness and density, the 2 cherry species also supported similar caterpillar communities that differed significantly from communities on several other tree species (Tables 1 & 2). Judging from use by caterpillars, the 2 cherry species appeared quite similar. However, judging from use by a generalist mammalian herbivore (white-tailed deer) they were on opposite ends of the browse-preference spectrum. Black cherry is often the only species that remains and pin cherry the first species removed by deer when deer density is high (Tilghman 1989; Horsley et al. 2003). Deer are thought to avoid browsing on black cherry because it produces cyanogenic glycosides, which deer find unpalatable (Burns & Honkala 1990). Pin cherry has a dramatically higher growth rate, matures earlier, and has a shorter lifespan than black cherry (Burns & Honkala

Table 2. Results of comparisons of caterpillar community composition across tree hosts in Allegheny hardwood forests during 2010 from blocked multirange permutation procedure (MRBP) performed on the basis of relative abundance on each site by tree species.

Tree species	Tree species <sup>a, b</sup>							
	AMBE	BLCH	PICH	REMA	STMA	SUMA	SWBI	YEBI
AMBE	–	0.0622	0.0722	0.0795	–0.0140	0.1079	0.0147	0.0464
BLCH	0.0663* <sup>c</sup>	–	–0.0021	0.0959	–0.0080	0.1025	0.0480	0.0424
PICH	0.0499**	0.5493	–	0.1337	0.0019	0.1294	0.0645	0.0615
REMA	0.0780*	0.0907*	0.0621*	–	0.0366	0.1159	0.0596	0.0627
STMA	0.7768	0.6326	0.4561	0.1280	–	0.0281	–0.0165	–0.0438
SUMA	0.0491**	0.0908*	0.0617*	0.0470**	0.1009	–	0.0556	0.0955
SWBI	0.3017	0.0751*	0.0369**	0.1393	0.8124	0.2107	–	–0.0142
YEBI	0.0489**	0.0638*	0.0388**	0.1070	0.9110	0.1050	0.7748	–

<sup>a</sup>Abbreviations: AMBE, American beech; BLCH, black cherry; PICH, pin cherry; REMA, red maple; STMA, striped maple; SUMA, sugar maple; SWBI, sweet birch; YEBI, yellow birch. Overall chance-corrected within-group agreement  $\Lambda = 0.055$  ( $p = 0.0005$ ).

<sup>b</sup>Values above the diagonal are chance-corrected within-group agreements ( $\Lambda$  values) for pairwise comparisons; values below the diagonal are the corresponding probabilities ( $p$  values).

<sup>c</sup>Significance levels: \* $p < 0.1$ , \*\* $p < 0.05$ .



1990). Pin cherry lacks chemical deterrents (Burns & Honkala 1990) to deer browsing or has other properties that make it highly preferred by deer. Perhaps chemical differences account for the fact that, despite their similar caterpillar faunas (Table 2), mean caterpillar density was approximately 50% higher on pin cherry compared with black cherry (Fig. 1).

### Caterpillar–Host Relations and Effects of Deer

Allegheny hardwoods stands exposed to high deer density during stand initiation often regenerate to almost pure stands of black cherry (Tilghman 1989; Horsley et al. 2003; Nuttle et al. 2013). Although black cherry had the second-highest caterpillar density (Fig. 1) and species richness per site (Fig. 3), the total caterpillar richness on black cherry was a relatively small proportion of the total caterpillar richness collected across all hosts (34%). Hence, the near elimination of other tree species at high deer density could result in the loss of suitable hosts for 66% of caterpillar species of Allegheny hardwoods.

When present, the other tree species that are most abundant at relatively high deer densities are striped maple and beech. In contrast to pin cherry, which is uncommon at high deer density and dies out rapidly as forests age beyond 30 years, striped maple and beech are shade tolerant and are increasing in relative abundance. They also supported the lowest richness of caterpillars per site (Fig. 3). Excluding singletons, where nonoccurrence on any given host species cannot be distinguished from sampling error, stands composed of black cherry, striped maple, and beech hosted 28 species of caterpillars, or 70.0% of the total caterpillar fauna on the basis of 40 species collected more than once (Table 1).

In contrast, lower deer densities do not create a correspondingly opposite problem for an alternate caterpillar fauna. This is partly because forests that regenerate under lower deer densities are more diverse and black cherry (with its relatively high caterpillar density and diversity) is still a common component of high-diversity stands (Nuttle et al. 2011; Wheatall 2011). Only 5 caterpillar species (6.6%) were collected exclusively on black cherry, and excluding singletons, only one caterpillar species (cherry dagger moth [*Acrionicta basta*]) was observed exclusively on black cherry. Most caterpillar species collected on black cherry were also collected on pin cherry (Tables 1 & 2). Although pin cherry is extremely shade intolerant and will eventually drop out as stands mature, even if pin cherry were completely eliminated from the landscape, stands composed of a mix of the other tree species would still host 97.5% of the overall caterpillar fauna, excluding singletons. Finally, high-diversity stands that regenerate under lower deer density include tree species such as birches, which host distinct caterpillar communities (compared with cherries, Tables 1 & 2) and support high numbers of caterpillar species (Table 1 & Fig. 3). Therefore, our results

support Tilghman's (1989) conjecture that overabundant deer populations could result in reduced caterpillar abundance and diversity. These negative effects of deer on caterpillars may cascade up the food chain and further threaten declining populations of insectivorous forest birds (Nuttle et al. 2011), bats, and specialist parasitoids.

Despite their great diversity and importance to temperate forest communities, taxonomically detailed, quantitative studies of caterpillar communities on multiple tree hosts within a forest community are uncommon (but see, e.g., Karban & Ricklefs 1983; Butler 1992; Butler & Strazanac 2000; Summerville et al. 2003; Singer et al. 2012). Fewer studies relate caterpillar–host relations to conservation issues such as changes in forest tree composition.

Among the tree species in our study area, pin cherry and black cherry supported the richest and most numerous communities of caterpillars. Birches also supported dense and diverse assemblages of caterpillars. Of conservation interest, pin cherry and birches are the species most negatively affected by browsing when deer densities are high (Tilghman 1989; Horsley et al. 2003). In contrast, striped maple, an understory tree that increases in relative abundance under high deer density (Tilghman 1989; Horsley et al. 2003; Nuttle et al. 2013), supported the lowest richness of caterpillars per site and among the lowest caterpillar densities. Beech had the second-lowest richness of caterpillars per site and dominates regeneration in closed-canopy forests exposed to high deer density (Nuttle et al. 2013). Furthermore, forests dominated by black cherry created by clearcutting under high deer density have lower canopy-foilage density than the more diverse stands that establish under lower deer density (Nuttle et al. 2011). Lower foliage density reduces total caterpillar abundance at the stand scale.

In summary, high deer densities reduce canopy-foilage density, diversity of forest tree species, relative abundance of high-quality hosts (e.g., pin cherry and birches) in the canopy, and increase density of low-quality hosts (e.g., striped maple and beech). This multitude of deer effects likely combine to reduced abundance and diversity of caterpillars at the stand scale in areas chronically exposed to high deer density, a condition common throughout large areas of eastern North America. Negative effects of deer on caterpillar abundance and diversity would be important not only to butterfly and moth (and sawfly) conservation but also to the other species that rely on caterpillars and adult Lepidoptera as prey, notably insectivorous birds and bats, and as pollinators.

In many areas, including the Allegheny hardwoods of Pennsylvania, deer densities have been managed since approximately 1990 at more sustainable levels. However, the legacy of pandemically high deer densities during stand initiation—experienced across much of eastern North America during most of the 20th century (McShea et al. 1997)—remains in the forest canopy that survived and recruited through that intense deer filter.

Furthermore, some hunter groups are exerting intense pressure on wildlife agencies to manage deer at higher population densities, despite calls from farmers, highway-safety agencies, and forest managers to manage deer at lower densities. Our results contribute to understanding of the likely consequences of such decisions for an important group of forest animals.

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